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The Multinational Coordinated Arabidopsis thaliana Genome Research Project

Progress Report : Year Three

The Multinational Science Steering Committee
1993

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PREFACE

In 1990, an ad hoc committee composed of nine scientists from the United States, Europe, Japan and Australia prepared a report entitled "Long-Range Plan for the Multinational Coordinated Arabidopsis thaliana Genome Research Project". This publication (NSF 90-80) outlined a plan for international cooperation in understanding the structure and function of the genome of the higher plant Arabidopsis thaliana. The Committee assumed responsibility in six areas: (1) coordinate programmatic aspects of the Arabidopsis genome project; (2) communicate with the informatics and biological resource centers that were to be /established; (3) monitor and summarize progress of scientific activities of participating laboratories; (4) serve as a liaison to the broader plant biology community; (5) identify needs and opportunities of the Arabidopsis research community and communicate these needs to the funding agencies of participating nations; and (6) periodically update the long-range plan.

This report of the Multinational Science Steering Committee is intended to summarize progress made during the past year and to foster communication among those scientists with a primary research interest in Arabidopsis as well as with other plant scientists and the general scientific community. We also identify areas of present need for the international group of funding agencies concerned with the project, and set forth a series of new goals for the coming year. Previous reports, describing progress made during the first two years of the project are available as publications NSF 91-60 and NSF 92-112.

The information contained in this report was provided by members of the Multinational Steering Committee and by many other colleagues, some of who are acknowledged below 1/. Sources include both the published literature and less formal sources, including abstracts and presentations at symposia, communications of the Arabidopsis electronic newsgroup, and personal communications. Representatives of the Committee outlined this report at Columbus Ohio (USA) in August 1993. It is the nature of any general progress report, representing the work of hundreds of scientists worldwide, that some of the important experiments of the past year may have been overlooked or misrepresented. Therefore, we ask not only that our colleagues overlook such shortcomings but that they feel free to communicate their concerns and plans with their committee representatives, so that future reports will be as accurate as possible.

1/ Among those to whom we are indebted for information used in the initial draft report, and for the subsequent revisions are M. Anderson, F. Ausubel, M. Caboche, S. Catinhour, M. Cherry, K. Davis, J. Dangl, J. Ecker, N. Fedoroff, K. Feldmann, G. Jurgens, D. Kristofferson, J.Martinez-Zapater, D. Meinke, K. Okada, S. Pramanik, R. Scholl, and P. Scolnik.

The Multinational Science Steering Committee

Chair: Liz Dennis
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I. PROGRESS OF THE PREVIOUS YEAR

During the past year Arabidopsis has been ever more widely used as an experimental organism. Many genes have been isolated, map based cloning has proven successful, technical advances in other genome projects have been adapted to Arabidopsis where appropriate, and sequencing of random cDNA clones has commenced in earnest. The most exciting developments have occurred in advancing our understanding of the biology of plants through studies of Arabidopsis. A summary of progress over the past year, new initiatives, and directions for the future are presented below.

1. Genome Analysis

A. Physical Mapping

Last year's report described the international collaboration that had identified and mapped yeast artificial chromosomes (YACs) covering about a third of the Arabidopsis genome. This effort has been continued by a number of groups (Dean group at Norwich, U.K., Ecker group at University of Pennsylvania, and Goodman group at Massachusetts General Hospital) taking advantage of newly available YAC libraries and the increased density of RFLP markers. Total genomic coverage is now estimated to be approximately 60%. Coverage on chromosome 4 and the top of chromosome 5 is even greater.

Efforts to link the cosmid contigs, identified with the fingerprinting method by the Goodman group, with the YAC clones have also been underway. Over 1000 YAC clones and a number of RFLP markers and YAC end-probes have been hybridized to representative cosmids from the 750 contigs. These plus cosmids identified by the Cobbett group (Melbourne University) and the Dean group (Norwich, U.K.) have provided the template for large-scale genomic sequencing of a region of chromosome 4 (see later under ESSA project). In preparation for phase one of this project, restriction mapping of 500kb of genomic DNA has been completed.

B. Genes Characterized and Cloned

The identification of informative mutations continues to be an important and immediate goal of the Arabidopsis genome project. These mutations are needed to assign functions to cloned regions of the genome and determine what roles specific genes play in plant growth and development. Significant advances have been made over the past year in three major areas of mutation research with Arabidopsis: (1) the isolation of a large number of new mutations and assignment of many of these to linkage group or chromosome region; (2) the establishment of a community-based system designed to monitor gene symbols and catalogue the growing list of genetic loci marked by mutations; and (3) the incorporation into existing stock centers of the entire mutant collection of A.R. Kranz (Frankfurt, Germany) and part of the extensive collection of G.P. Redei (Columbia, MO). An overview of these advances is presented in this section of the report. More information on genetic loci marked by mutations is included in Appendix I.

It is impossible to determine the precise number of new mutations that have been identified in Arabidopsis over the past year, in part because large-scale mutant screens are being performed simultaneously in many different laboratories, and putative mutants identified during these screens usually need to be analyzed in some detail before their relationship to existing mutations can be determined. Mutant collections in Arabidopsis have nevertheless reached a level of saturation where it will be increasingly important in the future to perform complementation tests between

mutants that either have similar phenotypes or carry defects in genes that map to similar regions of the genome. This approach is needed to determine which mutations identify new alleles of known genes and which define completely new genes.

One way to document the increased number of known mutations in Arabidopsis is to outline several changes in cataloguing of mutations that have taken place since the last annual report was published. The most detailed genetic map of Arabidopsis available in October 1992 contained roughly 120 genes marked by mutations. An undetermined number of other mutant genes were assigned to linkage groups but were not yet ready to place on the map. New symbols for mutant genes were being chosen by members of the Arabidopsis community at a rapid rate with little attention paid to whether other laboratories had plans to use the same symbol to define an unrelated locus. There was no mechanism to determine what mutations were being characterized in different laboratories, where these loci were located on the genetic map, and what gene symbols were being used by other members of the community before publication.

A small group of Arabidopsis researchers attending the Plant Genome I Conference in San Diego (November 1992) met informally to discuss possible solutions to these problems. David Meinke (Stillwater, OK) volunteered to serve as a temporary curator of mutant gene symbols and coordinator for updating the "classical" map of genes marked by mutations. A new map of 160 visible markers was prepared in December 1992 and distributed to the Arabidopsis community through electronic networks and the Arabidopsis Biological Resource Center at Ohio State. A linkage table that summarized mapping data for those 160 markers and 100 additional genes assigned only to linkage group was distributed at the same time, along with a list of 125 mutant gene symbols being used in Arabidopsis research. These lists represented the first attempt to assemble mapping and nomenclature information on existing mutations of Arabidopsis into a widely-distributed format. Nomenclature rules and a standard procedure for contacting the curator to reserve new gene symbols were included with this material.

An updated list of mutant genes was prepared for the Arabidopsis Conference at Ohio State in August 1993. The most recent version of this list is presented in Appendix I and includes over 800 genetic loci marked by mutation. The extent of characterization of these mutant genes varies widely. Some have been mapped and examined in detail whereas others are in early stages of analysis but still appear to be inherited as single Mendelian factors. Although some entries on the list may later be shown through allelism tests to be defective in the same gene, most are likely to define unique genes. This list includes 100 new gene symbols and several hundred new loci assembled by the curator since last December. An updated map of visible markers that incorporates these additions is planned for release at the end of the year. This information is also being incorporated into existing databases to facilitate access.

The mutant collections of G.P. Redei and A.R. Kranz represent another large resource of informative mutations that has recently been made available to the Arabidopsis community. The entire collection of A.R. Kranz (290 color mutants and 160 form mutants) is now maintained at the Nottingham Stock Center. The Redei collection (140 biochemical mutants, 140 color, 80 form, 15 flower, and 3 photomorphogenic mutants) is currently being prepared for distribution by the Ohio State biological resource center. These mutants are not included in the list of genetic loci (Appendix I)

because many of their names are incompatible with the current system of nomenclature. Nevertheless, they represent a valuable source of new mutations and additional mutant alleles. In order to facilitate incorporation of these mutants into existing research programs, members of the community are encouraged to compare mutants from these collections with similar mutants being examined in their own laboratories.

The ultimate goal of the Arabidopsis genome project is understanding the genome. This includes not only sequence information, but also understanding the contribution that each gene makes to growth, development, and environmental response of the plant. An important first step is to obtain mutations in as many genes as possible, and then to study the effects of loss of single gene function on the physiological and structural properties of Arabidopsis. This work is proceeding at a rapid and accelerating pace, as indicated by the diversity and number of new mutations identified (listed in Appendix I). Among the developmental processes under intense genetic study are embryo development, root development, and flower development. The Year 1 Progress Report described preliminary results on a large screen to saturate the genome for embryo pattern mutants, carried out in the Jurgens laboratory (Munich, Germany). This effort is now fully published, and detailed analyses of individual genes, which mediate key developmental steps that occur as early as the first cell division after fertilization, are in progress. Adding to this work are the longstanding efforts of the Meinke laboratory (Stillwater, OK) on embryo-defective mutations (the "emb" mutations in Appendix I are from this laboratory) and the recent efforts of Goldberg (Los Angeles, CA) and Chua (New York, NY) laboratories on T-DNA insertional mutants defective in embryo development. The study of plant embryogenesis has, therefore, enjoyed a renaissance as a result of Arabidopsis work.

Similar saturation screens for root development and root hair formation mutants are under way, following the detailed studies of root structure and development that revealed an almost uniform cell number and a highly organized meristem structure for the Arabidopsis root. A combined effort of laboratories at the University of Utrecht, the John Innes Institute, the University of Pennsylvania, New York University, and the University of Michigan has revealed that the Arabidopsis root, because of its small size, is amenable to much more detailed developmental analysis than the roots of larger plants. This will enable penetrating new studies of the relation between the activity of individual genes and the structure, development, and function of roots.

Flower development is the most mature of the developmental areas in this genome project: a growing number of laboratories has joined the effort to provide a complete molecular description of the regulatory events and circuits that specify when and where flowers will form, and that direct cells to differentiate to the cell types appropriate to their positions. This international effort includes laboratories at the California Institute of Technology, University of California San Diego, Cold Spring Harbor Laboratory, University of British Columbia, University of Oregon, U.C. Santa Cruz, University of Madrid, Wageningen Agricultural University, John Innes Institute, University of California Berkeley, Yale University, Salk Institute, University of Wisconsin, and many others. The net result has been the identification of multiple alleles at genetic loci necessary for appropriate flowering time, flower position, floral identity (as opposed to the alternate meristem developmental pathway, stem identity), floral organ type, and floral organ number. Many of the important genes have been

cloned (including the homeotic genes AG, AP3, AP2, AP1, CAL, PI, and LFY, see Appendix I) and sequenced, and their actions and interactions studied in great detail. This has led to testable molecular models for floral induction and specification of organ type, and has led researchers to a large degree of control over these processes in the laboratory. That the knowledge gained from Arabidopsis is directly transferable to other plants has been shown in detail in experiments with snapdragon, petunia and maize.

Important progress has also been made in many key areas of plant physiology, including areas in which major efforts had been made in plants other than Arabidopsis, with limited success. To indicate only two of these areas, we mention light reception and hormone response. The past year has seen major progress in sorting out the functions of the different plant light receptors by genetic and molecular means. That the red light receptors, phytochromes, are coded by a diverse family of genes was first shown in Arabidopsis, and the individual functions of the different phytochromes are now being revealed by mutating each in turn. Key recent advances in this have been the analysis of mutations in phytochrome A and phytochrome B (carried on at the USDA Plant Gene Expression Center, the Salk Institute, John Innes Center, and at other locations). A. Cashmore (Philadelphia, PA) has recently announced the first cloning and molecular identification of a plant blue light receptor, coded by the Arabidopsis HY4 gene. Since collections of blue-light nonresponsive mutations are now available (e.g. from the work of K. Poff and collaborators (East Lansing, MI) it is only a matter of time before this signal transduction pathway, with no counterpart in animals but with important implications for agriculture, is understood.

Plant hormones are quite different in structure and in action from animal hormones, but despite decades of effort, the mechanisms of their actions remains unknown. Two reports in the last year promise to change this situation for the gaseous hormone ethylene: a putative ethylene receptor (ETR1) has been cloned and sequenced (California Institute of Technology), revealing that ethylene signal transduction uses components of what was previously known only as the major bacterial environmental response system. These components, recognized in eukaryotes for the first time in Arabidopsis, are parts of the "two-component" signal transduction pathway, which involves a ligand-binding domain that regulates a specific histidine protein kinase, which in turn provides phosphate to an aspartate phosphotransferase, which then activates downstream steps. The other key step in understanding ethylene signaling is the cloning of the CTR1 gene (University of Pennsylvania), which is responsible for steps following the two-component protein. Cloning of CTR1 has shown it to code a homologue of mammalian "raf" protein, a key component in the "ras" signal transduction pathway of animals. How the "bacterial" ETR1 product communicates with the "animal" CTR1 product remains to be seen, but it seems at this point that plants may use a unique form of signal transduction which could reveal a great deal about the evolution and mechanism of signal transduction in plants, animals and bacteria. Since ethylene is a fruit-ripening and wound-damage hormone, it is hard to overstate the potential importance of understanding this pathway for agriculture and horticulture (indeed, patent applications and licensing agreements with major agricultural corporations have resulted from this work). New mutations have also been studied in the gibberellin response pathway (at the University of Minnesota and the John Innes Center) and in the cytokinin response pathway (Boyce Thompson Institute). Mutations with effects on auxin transport have also been found, and are under study at the National Institute of Basic Biology in Japan.

The work described in the previous progress report on plant-pathogen interactions has continued, revealing that Arabidopsis is an excellent model system for studying and cloning the genes that allow crop plants to evade bacterial, viral, fungal and nematode pathogens. The development of Arabidopsis as a model system in plant pathogenesis is of primary importance for the solution of many important agricultural problems.

Abundant progress (too extensive to summarize in a report of this length) has also been made in identification and cloning of genes involved in hormone synthesis, amino acid synthesis, fatty acid synthesis, starch synthesis, nitrate uptake, nitrate metabolism, transport of ions and water through membranes, generation of proton gradients, and many other key areas of plant physiology. This list should expand dramatically in the coming years: at least 40 genes identified by mutation in Arabidopsis are presently the subject of map-based cloned attempts, which are a direct result of the genomic characterizations and libraries made in the Arabidopsis genome project. Further analysis of large collections of insertional mutants is generating sequence information on many additional genes with critical functions.

C. Nomenclature for Genes Identified by Mutations in Arabidopsis thaliana

1. Specific Guidelines:

A. Mutant gene symbols should have 3 letters (underlined or italics) in lower case.

B. Some well-known symbols chosen before these guidelines were established may have only 2 letters.

C. The wild-type allele should have these letters (underlined or italics) in CAPS.

D. Protein products of genes should be in CAPS only.

E. Phenotypes are designated by the gene symbol (no underline) with the first letter capitalised (for example: Abc+ wild type; Abc- mutant). The +/-can be superscript or on the same line.

F. Different genes with the same symbol are distinguished by different numbers (abc1 and abc2).

G. Different alleles of the same gene are distinguished with a number following a hyphen (abc4-1 and abc4-2).

H. When only a single allele is known, the hyphen (-1) is not needed. Thus abc3 = abc3-1 if only a single allele is known.

I. The same rules of nomenclature outlined above apply to both dominant and recessive mutations. The community has discussed this particular feature of nomenclature at length.

Several modifications noted below were recently adopted. Other methods of designating dominant alleles (CAPS, superscripts, etc.) should be avoided and will not be accepted to the Arabidopsis databases.

J. Individuals may choose to add a "D" at the end of an allele

number for purposes of outlining crosses if that allele exhibits simple dominance relative to wild type. Thus abc5-2D indicates that allele #2 is dominant to wild type.

K. A formal list of additional modifiers will be prepared as the need becomes apparent.

L. Incorporation of these letters into the formal allele name maintained in databases is discouraged because such modifiers may be misleading in the absence of information on

reference alleles. Since this designation is optional, it should be noted that some dominant alleles will not have a "D" suffix.

M. A copy of these guidelines for nomenclature in Arabidopsis will be distributed to editorial offices of major journals to help maintain this system in publications.

2. General Guidelines:

A. Mutants should be characterized in some detail before a formal gene symbol is chosen and published. This analysis should include (when possible) mapping the chromosomal location of the mutant locus.

B. Complementation tests should be performed with mutants that map to similar regions and/or exhibit similar phenotypes to ensure that the mutant in question has not already been identified and assigned a different name.

C. Avoid the use of symbols that have another meaning for biologists.

D. Current lists of mutant gene symbols in Arabidopsisare available through stock centers and databases. Consult these lists before selecting a formal gene symbol.

E. Contact the curator of mutant gene symbols before publication to reserve your name and symbol of interest.

F. The present curator is: David Meinke (Department of Botany, Oklahoma State University, Stillwater, OK 74078 USA; Fax 405-744-7673; E-mail: btnydwm@mvs.ucc.okstate.edu).

D. Large-Scale cDNA Sequencing

Because of the rapid proliferation of deduced amino acid sequence information from cloned genes of known function and from purified proteins, it is now frequently possible to infer the general function of a gene or gene product solely on the basis of nucleotide or deduced amino acid sequence homology to genes or gene products of known function. A recent release of the collective non redundant protein (or deduced protein) sequence databases (SwissProt+PIR+GenPept+GPUpdate) contains 87,916 sequences, the vast majority of which are proteins or gene products which have been characterized in non-plant organisms. This database of structural information provides a powerful resource for the identification of plant genes of known structural or catalytic function. Recent experiments involving large-scale partial sequencing of cDNA clones has indicated that, for the community at large, an efficient mechanism for exploiting the proliferation of sequence information is to exploit automated sequencing technology

to obtain the sequence of all the cDNAs in a plant and compare the deduced protein sequence, and the nucleotide sequence, of each cDNA to the database of known genes.

The commercial availability of automated DNA sequenators capable of very high throughput has led to large-scale sequencing of both anonymous cDNA clones and genomic DNA from humans and several model organisms. Because of recent advances in instrumentation for DNA sequencing, current instruments such as the ABI373A have a theoretical throughput of several million basepairs per year. This means that a single instrument operating one run per day, seven days per week, can produce about 450 bp of sequence from 13,140 different templates per year (5,913,000 bp).

Three groups are currently engaged in obtaining partial cDNA sequences from higher plants. A large effort has begun in Japan to sequence rice cDNAs, a consortium of French scientists is sequencing Arabidopsis cDNAs, and a group at the MSU/DOE Plant Research Laboratory at Michigan State University is also sequencing Arabidopsis cDNAs.

The Japanese Rice Genome Research Program (RGP) under the leadership of Yuzo Minobe is managed by the National Institute of Agrobiological Resources and the Society for Techno-innovation of Agriculture, Forestry and Fisheries. This project is funded for seven years by the Ministry of Agriculture and the Japan Racing Association. The cDNA sequencing component of this effort is currently focused on sequencing cDNAs from rice and approximately 5000 cDNAs have been completed with approximately 1023 sequences deposited in the DNA Database of Japan (DDB). Using a cutoff score of 80 with the BLASTX algorithm, about 20% of the first 1000 sequenced cDNAs showed a strong similarity to known gene products or proteins. Progress on the rice genome project is described in the "Rice Genome", the newsletter for the Rice Genome Project.

To subscribe to the free newsletter, send inquires to Ilkka Havukkala, Editorial Office of Rice Genome, National Institute of Agrobiological Resources, 2-1-2, Kannondai, Tsukuba, Ibaraki 305, Japan, Fax 81-298-38-7468, E-mail ilkka@rice.nbh.affrc.go.jp.

The French Arabidopsis cDNA sequencing effort involves a collaboration among a group of laboratories that are sequencing anonymous cDNAs from five different Zap libraries representing various tissues (developing siliques, flower buds, etiolated seedlings, cell suspension, cultured leaf strips). This group has completed the analysis of 1152 ESTs (Hofte et al., Plant J., in press) and the sequences have been deposited in the dbEST database of the National Library of Medicine. Approximately 32% of the sequences had BLASTX scores of greater than 80, a number which is widely used as the lower limit of probable significance. Preliminary agreement has been reached among all parties that the corresponding clones will be made available through the Ohio State Arabidopsis Biological Resource Center. For information about the French project, refer to the Section II and contact H. Hofte at hofte@versailles.inra.fr.

The Michigan State University Arabidopsis Sequencing Project was initiated in 1992. The project is managed by Tom Newman with the advice of a group of twelve MSU faculty. Informatics for the project are being developed by E. Retzel, University of Minnesota. Most of the sequences produced to date have been from a lambda ZipLox library constructed from equal amounts of polyA mRNA from etiolated seedling, roots, leaves, and inflorescences at various stages of development. Approximately 400 bp of sequence was

obtained by automated cycle sequencing from the 5' end of approximately 1500 ESTs. Of these, approximately 30% showed homology to known genes following database homology searches. Approximately 10% of all ESTs have homology to non-plant genes. The sequences of the first 800 of these sequences have been deposited in dbEST and the clones are available through the Ohio State Biological Resource Center. The sequences are also available via the GOPHER maintained by Massachusetts General Hospital. A list of significant homologies was released on the Arabidopsis electronic newsgroup. In order to search for a known gene, the GOPHER can be searched by keyword. Alternately, one may compare a known amino acid sequence against the current translation of all sequences in dbEST by using the TBLASTN search routine (i.e., rather than the more familiar BLASTX routine). Another 800 sequences will be released under similar circumstances by November 1993.

The MSU sequencing project was initiated with support from the U.S. Department of Energy's Energy Biosciences Program and the State of Michigan. In August, 1993, three years of support for the sequencing project was awarded from the National Science Foundation. The goals of this project are to obtain partial sequence information for approximately 85% of all the expressed genes in Arabidopsis within this time period. A major objective is to develop a normalized library which will reduce the frequency of redundant sequences and permit the recovery of cDNAs corresponding to rare mRNA species.

For information about the MSU project contact Tom Newman, MSU/DOE Plant Research Laboratory, Michigan State University, East lansing, MI 48824, Fax 517-353-9168, Phone 517-353-2270, E-mail 22313tcn@ibm.cl.msu.edu.

2. Technology Development

A. Transposon tagging

Considerable progress has been made during the past year in realizing the potential of transposon tagging in Arabidopsis. The first mutations caused by insertion of the maize Activator-Dissociation (Ac-Ds) and Suppressor mutator (Spm) transposable elements have been identified and published. In addition, a family of endogenous elements has been identified that may prove useful in time.

The central challenges for future are to optimize the transposition frequency and minimize the effort involved in identifying desired insertions. These dual goals have been approached in a number of different ways, with a variety of results, each of which will be briefly summarized below. If the transposition frequency is high, transposition tends to occur early in plant development, leading to the generation of many progeny carrying the same transposition event. Moreover, if transposition continues at a high frequency, a mutation that arises by an insertion can persist as a consequence of imprecise excision of the element, giving an untagged mutation. Thus a high transposition frequency both increases the chances of identifying a mutation and of recovering mutations that were created by transposition, but in which the gene is no longer tagged by the transposon. The majority of the work in transposon tagging, however, lies in the identification of lines in which the element has inserted in a gene of interest. In principle, such lines can be identified either by screening for mutations in lines of plants with active transposons, then determining whether the mutant genes are tagged with a transposon, or by deriving lines in which

transposition has occurred, then screening the lines for mutations.

Using both the Ac-Ds and Spm transposable element families, researchers have found that the transposition frequency can be increased by enhancing the supply of the element-encoded proteins required for transposition. This has been done either by increasing element redundancy, replacing the element's weak promoter with a strong promoter, such as the cauliflower mosaic virus 35S promoter, or by expressing the element-encoded proteins from cDNAs driven by strong promoters. As noted above, this has the drawback of creating plants in which transposition occurs very early and one or two different transposition events are represented in all progeny. This seeming drawback has been used to advantage in the design of some of the Ac-Ds-based transposition systems by separating the transposon from the sequence of the element-encoded protein or proteins required for transposition, generically referred to as 'transposase,' to facilitate the maintenance of transposon and transposase in separate plants before initiating transposition, as well as to facilitate their rapid separation following a transposition event. In several laboratories, the transposon was further marked with a positive selectable marker, such as the bacterial aph4 gene which confers resistance to the antibiotic hygromycin, while the transposase source was immobilized and placed immediately adjacent on the Agrobacterium transformation vector's T-DNA to a negative selectable marker, such as the agrobacterial tms2 gene encoding an indoleacetamide hydrolase.

Transposition can then be initiated by a cross between a plant containing the transposon and one containing the transposase. The F1 progeny containing both transposon and transposase are selfed and plants that contain a transposed element, but no transposase can immediately be identified in the F2 generation. This can be facilitated by inserting the transposon itself into a selectable marker, separating it from its promoter in such a way that it can be expressed only after transposition (the selective agent detects plants in which a transposition event has occurred), or by marking both the donor site and the transposase source with negative selectable markers, allowing both to be selected against, whilst the selection is imposed for the presence of the element. The latter approach favors the selection of unlinked over linked elements, simply because the recovery of the desired class of progeny depends on recombination between the negative selectable marker and the newly transposed element. Several laboratories are also exploring the use of inducible promoters, such as the heat-shock promoter, and stage-specific promoters, such as pollen-specific promoters. The former has the obvious advantage that transposition can be activated at will, although the ideal inducible promoter has yet to be found. The latter has the advantage that each transposition event is independent, but the disadvantage that the male and female gametes produced by such a plant are of different genetic constitutions, which either requires an additional outcross to isolate the transposed element or an alteration in vector design to permit recovery of individuals with transposed elements.

Overall, the separation of transposon from transposase source, as well as marking of the various components of the transposition system with selectable markers appears to have substantially enhanced the ability of researchers to directly identify plants with a transposed element and no transposase. At the same time, several laboratories have evaluated the frequency of mutations among progeny of plants with unmarked elements, and then determined the frequency with which the mutant alleles are actually marked by a transposable element.

Several laboratories have adopted an alternative approach to the detection of insertions in and near genes of interest by constructing transposons containing a promotorless or minimal-promoter-driven bacterial beta-glucuronidase (GUS) gene, some with splice acceptor sites included. These permit the detection of the transposon in or near a gene, but do not require that the insertion mutate the gene (they also permit detection of insertions in genes that are redundant in the genome, inactivation of one copy of which may not cause a mutant phenotype). The advantage of such a promoter/ enhancer/gene trapping design is that it permits the rapid identification of the cells in which the affected gene is expressed. These elements are relatively new, and the efficiency with which they will permit cloning of the genes by whose promoters or enhancers the GUS gene is driven is currently being evaluated. In general, it has been found that a fairly large fraction (30-50%) of transposed elements show some pattern of GUS expression, although some patterns are much more general and common than others. Only a small fraction of insertions give a very clearly defined, cell-type or lineage-specific pattern of expression. Such gene-activation transposons may prove very powerful in gene cloning, since a GUS-expressing insertion can be mapped and tested for allelism to existing mutations. Thus, for example, an insertion that results in expression of the GUS gene in root hairs can be tested for allelism to mutations that affect root hair structure.

Several other modifications of transposons are also under development, which may further enhance the utility of transposons in generating mutations. Elements have been constructed, for example, which have a strong, outward-directed promoter at one end.

This type of element would permit the generation of dominant mutations. Others are developing element systems which contain the recognition sites for the cre-lox site-specific recombination system. The principle is that recombination between a recognition site on a transposed element and the T-DNA from which it transposed should permit the derivation of deletions, inversions and translocations. Moreover, such a system can be used to generate mosaics for the expression of mutant genes (as can the elements themselves in the presence of transposase).

A major advance in the past year of analyzing the pattern of Ds transposition is the realization that in Arabidopsis, as in maize, the element tends to undergo short-range transposition. While the precise fraction of short-range transpositions varies depending on the initial location of the transposon-containing T-DNA, it appears that half or more of transpositions are to nearby sites. This property is likely to quite useful in minimizing the effort involved in tagging a gene if a significant number of Ds-containing T-DNAs can be mapped. Considerable effort will probably be put into mapping Ds T-DNAs in the immediate future. If a set of several hundred mapped Ds T-DNA lines is constructed, then an individual investigator should be able to tag a gene for which there is a mutant phenotype readily, simply by selecting a line with a nearby Ds T-DNA and crossing it by a strain that contains the mutant and a transposase gene, seeking progeny which uncover the recessive mutant allele. The goal of mapping T-DNAs containing transposons appears to be fairly widely accepted, although progress toward this goal will undoubtedly be limited by available personnel and funding. Several recent developments in the field of chromosome mapping and sequencing may reduce the amount of effort involved in mapping the initial sites of insertion of the transposon-bearing T-DNA. These include the development of TAIL

PCR, which reduces the effort required to recover a flanking T-DNA sequence, and the anchoring of YACs to the genetic map. Together, these two should make it possible to amplify and map a sequence flanking the T-DNA quite rapidly.

The past year has seen significant progress in the use of transposon tagging in gene analysis. It should be stressed that the major advantages of transposon tagging over conventional mutagenesis are its somatic and germinal reversibility, as well as the physical marking of the gene. This facilitates both gene cloning and the generation of somatic mosaics for gene expression. Its advantages over T-DNA mutagenesis are that it can be initiated by a genetic cross and controlled so that each contains only a single transposed element. Moreover, the insertion is stable in the absence of transposase, but can be destabilized and used for further mutagenesis upon the reintroduction of the transposase. One major advantage of transposon tagging over T-DNA mutagenesis is that it has the potential of becoming a tool that any laboratory Scan use to generate tagged mutations because of the propensity of transposons to jump in close proximity. This may eventually eliminate the necessity to screen very large populations of lines in search of tagged versions of a mutation induced by a non-insertional mutagen. Another advantage is the possibility of generating revertants which can definitively show that the insertion caused the mutation and is not just closely linked.

B. Development of PCR-Based Mapping Markers for Arabidopsis

High density genetic maps consisting of restriction fragment length polymorphic (RFLP) markers have already been constructed for Arabidopsis. RFLP maps are well-suited to mapping newly cloned DNA sequences. However, most genes are first identified by mutation and mapping such a mutation onto a pre-existing RFLP map is a lengthy procedure requiring the isolation of DNA from individual F2 plants or F3 families, and performing DNA blot analysis using each of the RFLP markers as a hybridization probe. Recently, three new categories of genetic markers based on the polymerase chain reaction (PCR) have been developed for Arabidopsis. In contrast to traditional RFLP markers, PCR-generated markers can be scored using a small sample of DNA without the use of radioactivity and without the time-consuming DNA blotting procedure.

The first category of PCR-based markers involves the use of single short PCR primers of arbitrary sequence (called RAPD primers for random amplified polymorphic DNA; Reiter et al., PNAS, 89:1377-1481, 1992) . A major advantage of RAPDs is that they provide large numbers of markers. On the other hand, because the amplification of a specific sequence or sequences using a RAPD primer is frequently sensitive to PCR conditions, including template concentration, it can be difficult to correlate results obtained by different research groups.

A second category of PCR-based markers are called CAPS for cleaved amplified polymorphic sequences. The CAPS method utilizes amplified DNA fragments that are digested with a restriction endonuclease to display an RFLP. Specifically, Konieczny and Ausubel (Plant Journal, 4 :403-410, 1993) synthesized 18 sets of PCR primers, each of which amplifies a single mapped DNA sequence from the Columbia and Landsberg erecta ecotypes. They also identified at least one restriction endonuclease for each of these PCR products that generates ecotype-specific digestion patterns. Using these CAPS markers an Arabidopsis gene can be unambiguously mapped to one of the ten Arabidopsis chromosome arms in a single cross using a limited number of F2 progeny. Given the limited

number of CAPS markers currently available, however, subsequent analysis using traditional RFLP markers is needed to determine a map position accurate enough to initiate a chromosomal walk. Hopefully, many additional CAPS markers will be developed in the near future which would allow the use of CAPS for the generation of high resolution maps.

A third class of PCR markers is based on PCR amplification across tandem repeats of mono- and dinucleotide repeats called "microsatellites". Microsatellites occur frequently and randomly in most eukaryotic DNAs and display polymorphisms due to variations in the number of repeat units. These polymorphisms are called simple sequence length polymorphisms or SSLPs. Bell and Ecker (submitted) estimated the abundance of microsatellites in the Arabidopsis genome and by amplification of DNA from six common ecotypes demonstrated that the microsatellites in Arabidopsis are highly polymorphic. The mean number of alleles for all markers tested was 4.16. Using the set of recombinant inbred lines developed by Lister and Dean (Plant Journal, in press 1993), all thirty markers were assigned unequivocally to a chromosome and linkage for each was established to neighboring markers at greater than LOD 3.0. These results indicate that randomly selected microsatellites are likely to be informative in any given mapping population, and will be especially useful for studying the evolutionary relationships between the many ecotypes of Arabidopsis.

A major advantage of both CAPS and SSLPs is that they are co-dominant genetic markers; that is, different digestion patterns are obtained for plants that are homozygous or heterozygous for the parental alleles. Both CAPS and SSLPs can be used as a dense sequence tagged site (STS) set for the construction of a physical map of the Arabidopsis genome by anchoring (Ewens et al., Genomics 11:799, 1991).

C. Summary of Genome Research Workshop at the 5th International Arabidopsis Conference

One of three auxiliary workshops at the 5th International Arabidopsis Conference in Columbus, Ohio (August 1993) was a genome research workshop organized by A. Schaeffner (University of Munich) and P. Scolnik (Du Pont Company). At this workshop, several researchers presented new tools for genome analysis that could be useful to members of the Arabidopsis research community. Established techniques for mutant isolation, mapping, gene tagging, and chromosome walking were also discussed. Presented here is a brief description of these techniques. For more detailed information, readers are encouraged to contact the participants of the genome workshop, listed with their e-mail addresses in a recent Arabidopsis bulletin board posting by A. Schaeffner.

a. Mutation-based research: Many genes of interest have been tagged with T-DNA constructs using the seed mutagenesis technique of Feldmann (Tucson, AZ) and Marks (Minneapolis, MN). A new method with the potential of vastly exceeding the efficacy of this approach was presented by H. Hofte (Versailles, France). Treatment of soil-grown Arabidopsis plants with Agrobacterium under low-level vacuum results in transformed plants carrying genetic resistance to the herbicide BASTA. The French group has isolated more than 50,000 independent transformants that appear to exhibit Mendelian segregation of the selectable marker. It seems likely that this simple and efficient method could be used to saturate the genome with T-DNA insertions, and could also

be used routinely to generate transgenic Arabidopsis plants.

b. New genetic markers: Three molecular genetic maps of Arabidopsis have already been published, and new creative ways of detecting polymorphisms and mapping mutations were reported at the meeting. Initially, the markers used were restriction fragment length polymorphisms (RFLPs). However,

the trend is towards generating markers based on the polymerase chain reaction (PCR) because of much lower requirements for quantity and purity of the DNA. A practical and economical improvement of classical RFLP analysis was reported by A. Schaeffner (Munich, Germany) by subcloning into plasmids up to 14 DNA fragments corresponding to mapped probes that detect EcoRI polymorphisms. Since each subcloned fragment hybridizes to a single polymorphic band, several markers can be scored in a single hybridization. This Arabidopsis RFLP mappint set (ARMS) can be obtained from the Arabidopsis stock centers. Members of the Ausubel lab (Boston, MA) reported further progress in the generation of CAPS, a version of PCR-based RFLPs (see above). This group is currently using a genome subtraction scheme to generate additional CAPS. P. Scolnik (Wilmington, DE) explained a recently published method for mapping mutations by pooling plants on the basis of their mutant phenotype. The Scolnik's group also reported a 10-fold increase in the number of polymorphisms detected by RAPD primers by resolving the amplification products in denaturing polyacrylamide gels. Members of the R. Davis lab

(Stanford, CA) reported the development of an noligonucleotide synthesis machine for the low-cost production of large number of primers, a crucial factor in large scale mapping and sequencing projects. This group is also developing new PCR-based markers for detecting HindIII polymorphisms between the Landsberg and Columbia ecotypes. R. Whittier (Tsukuba, Japan) reported the construction of a bacteriophage P1 library, and an approach (thermal asymmetric PCR or TAIL-PCR) for chromosome walking. D. Meinke's group (Stillwater, OK) continues to saturate the genetic map with embryo-defective mutations.

c. Positional cloning and sequencing programs: J. Ecker (Philadelphia, PA) and C. Dean (Norwich, U.K.) described the progress of a collaborative effort to physically link the genome. By linking RFLPs to YACs these groups have created more than 100 contigs that correspond to approximately 60% of the genome. The Ecker lab is also developing microsatellite repeats. Based on the combined information of several labs engaged in chromosome walking efforts, 1 cM in Arabidopsis corresponds to 100-500 kilobase pairs. The generation of expressed sequence tags (ESTs) is proceeding at a fast pace in both the U.S.A. and France. The genetic mapping of cDNAs is also being pursued, but the low level of

polymorphism is an impediment. This problem will soon be overcome by the completion of overlapping YAC contigs which will permit a cDNA to be mapped by hybridization to the YAC library.

In summary, it is clear that cloning Arabidopsis genes by a variety

of approaches is becoming increasingly simple, thus allowing us to concentrate our resources and efforts on the much larger task of understanding the genetic control of plant development, growth, environmental response, and metabolism.

3. Potential Applications

An important concept underlying the development of a model plant is the idea that discoveries made by exploiting the advantages of Arabidopsis will be readily applicable to economically important species. Because flowering plants are relatively recently evolved, genes from one plant species are frequently useful probes for the corresponding genes from other species and the cis and trans-acting factors which control gene expression are usually also functionally conserved. Thus, the rapid pace of identification of new Arabidopsis genes is accompanied by a parallel increase in our ability to identify the corresponding genes from economically important plants with a minimum of additional effort and expense.

An example of the application of Arabidopsis genes to improvement of agriculturally important species is the recent cloning, by scientists at Du Pont and elesewhere, of fatty acid desaturase genes from a variety of oilseed species such as soybean and Canola using Arabidopsis genes as probes. The desaturases control the quality of edible oils which comprise about one third of the calories in the American diet. For some plant species, such as soybeans, it has not been possible to obtain plants which produce high oil quality by conventional or mutagenesis breeding methods. Since it has also not been possible to purify the membrane-bound desaturase enzymes, the corresponding genes were isolated by map based cloning of genes which had been defined by mutations in Arabidopsis. The preliminary results obtained by altering expression of these genes in transgenic plants indicate that the genes can be used to increase or decrease significantly the level of the various fatty acids. This is expected to result in production in transgenic field crops of edible oils of optimal composition with respect to reducing the risk of heart disease and other lipid-related disorders, and to reduce the need for chemical modification of edible oils.

Arabidopsis has also been used to explore the possibility of producing useful new polymers in plants. Transgenic plants that accumulate granules of a biodegradable thermoplastic, polyhydroxybutyrate, were produced by introducing several genes from the bacterium Alcaligenes eutrophus. Although many plant species could have been used as hosts for the introduced genes, the availability of a collection of Arabidopsis mutants with altered starch and lipid metabolism provides unique secondary opportunities to examine the effects of alterations in primary carbon metabolism on the production and properties of the polymer.

4. Biological Resource Centers

Since their establishment approximately two years ago, the international network of Arabidopsis Biological Resource Centers, consisting of the Arabidopsis Biological Resource Center (ABRC) at Ohio State University, U.S.A., the Nottingham Arabidopsis Stock Center (NASC) at Nottingham University, U.K., and the European DNA Resource Center at Koln, Germany, have considerably expanded the number of lines available for Arabidopsis biological and genome research and improved the public accessibility of stock and related information.

The NASC and ABRC have released nearly 7,000 individual seed lines

which cover a wide diversity of stocks. These include almost 200 well-defined mutants and multiple marker lines donated primarily by Maarten Koornneef (Waageningen, the Netherlands). A large collection of ecotypes is also available. Stocks shared by both Centers also include pools of 5000 T-DNA lines from Ken Feldmann (Tucson, AZ) as well as individual mutant lines that have been identified in this material. In addition, the recombinant inbred mapping lines of Pablo Scolnik (Du Pont Company, Wilmington, DE) are also available. The visible marker, RFLP and RAPD segregation data for the Scolnik RI lines are currently available from both Stock Centers.

The collaborative efforts of the Centers have facilitated the release of over 1,000 new seed accessions this year. New stocks that have been made available by ABRC include further single and multiple marker lines, 40 ecotypes (both as pure lines and bulk populations) donated by P. Williams (Madison, WI), and approximately 100 lines donated by G. P. Redei (Columbia, MO).

ABRC has been characterizing the Redei collection and has 330 new lines prepared for distribution. This collection includes many types of morphological mutants, biochemical mutants, color mutants, such as variegated lines, related species, and interspecific hybrids. Trisomic lines for all five chromosomes are now nearly ready for distribution. ABRC hopes to have the characterization of the Redei collection completed within the next year.

The Nottingham Center also distributes one hundred recombinant inbred lines derived from a cross between Columbia and Landsberg erecta donated by Caroline Dean and Clare Lister (John Innes Center, Norwich). A mini-database for use with the RI lines and currently containing segregation data for 66 RFLP markers has been incorporated into AAtDB and will be included in AIMS. A central RI database carrying segregation data for all new markers mapped onto the RI lines is held at Norwich, but will also soon be held at NASC. At present, researchers using the RI lines are encouraged to send their mapping data to Norwich for inclusion in the database and thus to increase the number of mapped markers. These lines will also be available through ABRC in November 1993.

NASC has almost completed the characterization of the Arabidopsis Information Service [AIS] Collection donated by Professor Kranz (Frankfurt, Germany). Approximately 160 form mutants, 300 color mutants, and 200 ecotypes are available for distribution. The latest release of lines from NASC also includes 300 T-DNA lines donated by Csaba Koncz (Max-Planck Institute, Koln, Germany) and 200 Ds transformed lines from Ian Bancroft and Caroline Dean (JICPSR, Norwich, U.K.).

All seed stocks are distributed free of charge and as far as possible, upon receipt of order. Stocks can be ordered by mail, telephone, fax, electronic mail or through AIMS. It is expected that stock ordering to ABRC will be conducted through the AIMS on-line and e-mail systems in the future. NASC has now distributed over 10,000 tubes of seed throughout the world. ABRC has distributed in excess of 30,000 lots of seed. The number of stocks distributed is certain to increase with the production of many more T-DNA and Ds transformed lines which are currently being produced throughout the world.

The Stock Centers will offer two new services in the coming year. Information regarding individuals receiving stocks will be provided, upon request, and through AIMS. It is hoped that this policy of openness will foster cooperation among Arabidopsis

researchers. The Stock Centers shall also offer a safe repository for private collections of seed. The seed will be stored and then made available to the community after a period of two years.

The Stock Centers are pleased to report that some individual lines are being deposited by researchers at the time of publication. However, as seen at the recent Arabidopsis Conference at Columbus, Ohio, there are numerous, published lines that have not been deposited. One of the goals of the Stock Centers for the next year is to encourage researchers to deposit lines and clones for distribution, as they are published.

DNA stocks are preserved and distributed by the ABRC and the European DNA Resource Center at Koln. Stocks include the mapped RFLP phage (from E. Meyerowitz) and cosmids (H. Goodman and E. Meyerowitz), YAC Libraries produced by E. Grill and C. Somerville (Zurich, Switzerland and E. Lansing, MI, respectively) and E. Ward (Research Triangle, NC), cDNA and genomic libraries and individual cloned genes. Blotted filters of the YAC libraries ready for hybridization to probes are also distributed by the ABRC. The Koln center has, calendar year 1993 to date (September, 1993) filled over 80 requests for RFLP markers, YAC libraries, and the five various cDNA and Genomic DNA phage libraries. These have gone largely to researchers in the EC, but also the US and Asia. The funding for this service is provided by the EC BRIDGE program, and goes until June 30, 1994. Some form of collaboration will be incorporated into the sequencing effort, site as yet unknown. The ABRC has sent 1400 individual clones (RFLP plus cloned genes), 30 YAC libraries and 7 YAC filter sets.

One of the major developments this year for DNA resources has been the sequencing of ESTs in France and the USA. All of these clones are being deposited at ABRC as they are being produced as discussed above. Nearly 500 samples of the EST-cDNAs have been sent by ABRC already. Data on these stocks will be maintained in AIMS and AAtDB.

In order that the Biological Resources held at NASC are developed with the needs of Arabidopsis genome research in mind, Mary Anderson has become the Strain Curator for AAtDB. Both European Resource Centers maintain the latest version of AAtDB and are happy to access the database and answer queries. All NASC catalogue information is now incorporated frequently into AAtDB and AIMS as well as being available on the AAtDB Research companion as BinHex formatted files that can be retrieved and printed out, or as indexed text which can be queried and browsed. The ABRC is cooperating with Sakti Pramanik and associates (Michigan State University) in developing and maintaining the AIMS database. Stock information, including pictures depicting plant phenotypes and DNA banding patterns, are included. Comprehensive data associated with genome research are also in AIMS, which can be accessed by direct Telnet login, X-Window login or via a simple but powerful electronic mail querying system. A new AIMS gopher contains the latest updates of ABRC stocks and stock information, including an electronic copy of the ABRC Stock List.

For further information please contact:

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5. Informatics

A pair of related phenomena are transforming the ways in which Arabidopsis laboratories interact with each other and become informed of important scientific results. First, researchers are increasingly more comfortable with electronic communication and the skills required to take advantage of electronic resources. Second, as their awareness grows, researchers are insisting that existing resources become more diverse and sophisticated. The result is that as 1993 draws to a close, Arabidopsis information can be obtained from three distinct sources: AAtDB, Gopher/WAIS, and AIMS (reviewed below). In addition, the North American Arabidopsis Steering Committee has recently met and issued a report making specific recommendations to direct the development of future databases (see appendix). It is expected that as the quantity and demand for information grows, the number of choices available to the worldwide Arabidopsis research community will continue to expand.

A. AAtDB

AAtDB (An Arabidopsis thaliana Database) uses the ACEDB software developed by Richard Durbin (MRC-LMB, U.K.) and Jean Thierry-Mieg (CNRS, France). The AAtDB project is funded by the US. Department of Agriculture Plant Genome Research Program through the National Agricultural Library. The AAtDB project is staffed by members of the Department of Molecular Biology at Massachusetts General Hospital and Harvard Medical School, Boston USA. AAtDB is available without charge via Internet FTP transfer and remote X-windows access.

AAtDB features a wide variety of public information that is presented using graphical, text, and tabular formats. The user interface, which was designed to invite browsing, allows users to explore information by pointing and clicking with the work station mouse or by using a versatile query facility. ACEDB allows all parts of the database to be cross-referenced with each other. The large number of interconnections provides a dense navigable network in which information can be located from many different starting points (see sample screen in appendix).

All information contained within AAtDB was obtained directly from the original authors or from publicly available collections and databases. Updates to AAtDB are periodically distributed and the database is now in its fifth data release. A partial list of the information AAtDB 1-5 contains includes:

- The Hague/Goodman cosmid physical map including greater than 14,000 cosmid clones. The contigs of the physical map are associated with the genetic maps.

- Genetic markers, including RFLP, RAPD, and "classical" markers.

- Genetic maps, including the Integrated map from Hauge et al. (1993) The Plant Journal, a visible marker map including many embryo defective loci from David Meinke, and RAPD maps from Scolnik et al. (1992) PNAS.

- Primary F2 and RI population recombination data from the Goodman, Meyerowitz, Scolnik, and Dean laboratories.

- Primary 2-point data from M. Koornneef, D. Meinke, and others.

- Strain list, now maintained and entered for AAtDB by Mary Anderson at the Nottingham Arabidopsis Stock Center. Includes many new entries from the Nottingham and Ohio State stock centers.

- List of Arabidopsis researchers, including postal mail address, telephone and Fax numbers, electronic mail address, publications, research interests, and research associates. Information on over 1200 colleagues is included.

- All Arabidopsis DNA sequences from Gen Bank and EMBL DNA sequence databases with over 2400 entries total.

- NCBI BLASTX (six frame translations searched against the NCBI non-redundant peptide database) defined peptide sequence homologies for all DNA sequences included in AAtDB.

- Phenotype descriptions from the Green Book by Meyerowitz and Pruitt, updated with descriptions from the Nottingham and Ohio State stock centers.

- Scanned images of RFLP auto radiograms from the Goodman lab, photographs of mutant plants from G. Redei and M. Anderson, and ethidum bromide-stained restriction enzyme digests of RFLP probes distributed by the ABRC.

- Bibliographic citations, including references for all articles from the Arabidopsis Information Service, currently numbering 3400.

The ACEDB software provides some analysis features. Of particular interest is the ability to calculate codon usage and splice site consensus tables from all or a subset of sequences contained within the database. The tables calculated from AAtDB 1-5 are included in the appendix.

AAtDB currently requires a Unix workstation running the X-windows display environment. Versions of the ACEDB software are currently available for Sun Microsystems SPARCstation, Digital Equipment DECstation and Alpha, Silicon Graphics Iris series, NeXT, IBM model R6000, Hewlett-Packard, Convex, Alliant, and a public domain version of Unix called Linux for computers based on the Intel 386 and 486 processors. The software and database files for AAtDB are available via anonymous ftp from weeds.mgh.harvard.edu in the AAtDB directory. The ACEDB software and its C source code files are available via

anonymous ftp from ncbi.nlm.nih.gov.

For more information about the AAtDB project please contact John Morris at Fax number 617-726-6893 or via electronic mail at curator@frodo.mgh.harvard.edu. By postal mail contact John Morris, Department of Molecular Biology, Massachusetts General Hospital, Boston, MA 02114, USA. A printed tutorial manual "An Introduction to ACeDB: For AAtDB--An Arabidopsis thaliana database" is available on request from the AAtDB project.

B. The AAtDB Research Companion

Information contained within AAtDB can also be retrieved using a computer connected to the worldwide Internet network. The information is available using the Internet Gopher software or via public access accounts. The Internet Gopher software requires a computer that is directly connected to the Internet (a simple modem connection is not sufficient). A one hundred page manual titled "Internet Gopher User's Guide" edited by Paul Lindner from the Gopher development team at the University of Minnesota is available as a PostScript file. This guide can be retrieved from boombox.micro.umn.edu via either anonymous ftp or Gopher in the directory /pub/gopher/docs. Macintosh, PC and Unix clients are discussed, including sections on installing and configuration.

The AAtDB Research Companion for Arabidopsis Information is provided by the Department of Molecular Biology at Massachusetts General Hospital with the assistance of Digital Equipment Corporation and the United States Department of Agriculture Plant Genome Research Program through the National Agricultural Library. The AAtDB Research Companion Gopher server receives greater than 100 connections per day for users scattered around the world. The AAtDB Research Companion provides the complete information contained within the workstation version of the AAtDB database that was described earlier. In addition, the Companion offers the following:

- AAtDB FTP archive
- Images
- Geographic Distribution of Arabidopsis
- Genetic Maps and Tables
- BioSci Arabidopsis Genome Electronic Conference
- Arabidopsis: Compleat Guide
- Nottingham Arabidopsis Stock Center Catalogue
- Arabidopsis Information Service
- Arabidopsis cDNA Sequences in dbEST

C. AIMS

The Arabidopsis Information Management System (AIMS) is being developed and maintained by S. Pramanik of Michigan State University to support the international initiative on Arabidopsis Genome Research. AIMS, is being supported by a 5-year NSF grant, awarded in September , 1991. A near-term version of AIMS, designed

to meet Arabidopsis stock information and ordering needs has been operational since December, 1992. A version of AIMS with all of the originally proposed features will be available by December, 1993.

AIMS is being developed with active cooperation from Randy Scholl of Arabidopsis Biological Resource Center (ABRC) at Ohio State University and Sue Gibson from the DOE-Plant Research Laboratory, Michigan State University. One of the primary functions of AIMS project is to provide support for data management, including stock ordering and inventory, of ABRC. AIMS will provide support to other stock centers around the world upon request.

A major focus of AIMS has been to develop a mouse driven, self-guided. on-line user interface. This is achieved by a menu driven X-window-based graphics interface. A user can also run AIMS on microcomputers emulations a VT100 type terminal and access the non-graphics features of AIMS. To access AIMS one needs simply to telnet to the following internet address: aims.msu.edu

AIMS manages both data and programs such as Mapmaker. A general mechanism to input private data into these programs and manage output results through AIMS is being developed. Much of the data relevant to the Arabidopsis genome effort is currently available in AIMS and can be searched using diverse criteria and complex query strategies. Both data and features that are currently available or will be added soon are listed below. Data items include:

- Full information on seed stocks. Both ABRC and NASC (Nottingham Arabidopsis Stock Center) stocks are included.
- Information on all cloned genes available at the ABRC. Data on all Arabidopsis clones will be added.
- Information on RFLP and RAPD stocks, including crosses showing the polymorphism and enzymes utilized.
- Information on Yeast Artificial Chromosome libraries available at the ABRC. Cross-homology information between individual YAC clones and RFLP clones will be added.
- Genetic mapping data for markers generated by the recent mapping survey.
- Sequence and homology search results for all EST-cDNA clones of the Arabidopsis genome efforts.
- Color pictures of plant phenotypes for many of the newer stocks. It is planned that all phenotypes that can be seen visually will be recorded and placed in the database as color images.
- Images of gel banding patterns for all RFLP stocks. These are included along with molecular weight standards so that the expected numbers and sizes of bands can be ascertained for the clones.
- Images of comparative hybridization results for many RFLP clones.
- Sequence data and homology results for clones of Arabidopsis will be included soon. Included will be graphic representation of these data.

- References on Arabidopsis, including rapid updates of recent publications. Large numbers of references from early research and all the articles published in the Arabidopsis Information Service are included. The number of references in the database is now approaching 4000.

- Person data from sources including the ABRC mailing list. The number currently included in AIMS is approximately 1000 individuals. When the data from the recent Arabidopsis Conference is added, the total number of persons in the database will exceed 1300.

- Raw recombination data for linkage experiments will be included, and will be linked to the gene information so that recombination data for any locus can be easily accessed.

Features of AIMS include:

- Graphical display of genetic maps showing all mapped genes of Arabidopsis. In the near future, clones will be placed on the genetic map, and different types of maps will be made available for consultation and direct visual comparison. A sample AIMS screen showing map comparisons and pictures of stocks is given in APPENDIX **.

- The physical map of Arabidopsis. Contig information and graphical display of this information will be added soon to the database.

- A mouse-driven search method on phenotypic characters. This will allow efficient searches on phenotype without guessing at terminology used in the database.

- Ability to run linkage analysis programs with private data and compare private maps with other maps stored in AIMS.

AIMS provides support for stock centers to manage and maintain stocks and stock orders. Stocks can be ordered through on-line AIMS or through EMAIL-AIMS. AIMS keeps track of the history of all on-line and email stock orders. A user is able to query stock order history information through AIMS.

AIMS is an on-line transaction oriented database system running on a powerful central machine located at the Michigan State University Campus. This system is able to handle computing intensive functions and relate the results of these computations dynamically with existing information in AIMS. It will process genetic mapping functions as well as store and display a large number of complex images associated with the seed strains and DNA clones.

AIMS is implemented on top of a commercially available, powerful Sybase system. All graphics features of AIMS are implemented in an object-oriented fashion using Xwindows. Thus AIMS provides a careful integration of two important database technologies appropriate for an adaptive and extensible data environment for Arabidopsis genome research.

For more information contact Sakti Pramanik or Randy Scholl via electronic mail at curator@aims.msu.edu

6. Communication

The ARABIDOPSIS newsgroup is distributed worldwide through both USENET news (under the name of bionet.genome.arabidopsis) and

through e-mail. If USENET news access is not available on one's computer, e-mail subscriptions can be requested by contacting one of the following two addresses based upon one's location:

Subscription Address	Location
biosci@daresbury.ac.uk	Europe, Africa, and Central Asia
biosci@net.bio.net	Americas and the Pacific Rim

As of October 1993 there are 723 e-mail subscribers (versus 402 in July 1992, up 80%), 540 (versus 299 in '92) subscribed through the U.S. BIOSCI distribution center at IntelliGenetics and 183 (versus 103 in '92) subscribed through the BIOSCI center at SERC Daresbury Laboratory in the U.K. While it is difficult to estimate precisely the number of people who access the group via USENET news, a survey on another BIOSCI newsgroup in October 1992 indicated that almost 60% of the readership used USENET. This means that the total ARABIDOPSIS newsgroup readership could be approximately 1,300 - 1,400 people worldwide. Readership has increased due to a number of causes, but possibly the most important factor was the publication of several journal articles within the last year about the BIOSCI system, especially the one in the August '93 issue of "Trends in Biochemical Sciences." There were 812 postings to the newsgroup from 7/1/92 through 8/31/93 for a rate of 1.90 messages per day versus an average of 1.65 postings per day reported last year (from January to July of 1992). BIOSCI in the U.S. is supported jointly by the National Science Foundation, the Department of Energy, and two institutes of the National Institutes of Health (the National Center for Human Genome Research, and the National Institutes of General Medical Sciences).

A complete archive of all ARABIDOPSIS postings is maintained for anonymous FTP and Gopher retrieval on the Internet computer net.bio.net in the directory pub/BIOSCI/ARABIDOPSIS.

ARABIDOPSIS postings are also indexed in the general "biosci.src" WAIS source on the computer net.bio.net. WAIS software indexes all text in every BIOSCI newsgroup posting and allows users on the Internet to search for any text string and then retrieve messages bearing the specified text. The WAIS source can also be queried by e-mail. For WAISMAIL instructions, send the word "help" in the body of an e-mail message (leave the Subject: line blank) to waismail@net.bio.net. For other questions about using the archives, please contact biosci@net.bio.net.

7. Workshops and Symposia

The First International Symposium on the Molecular Genetics of Root Development was organized by Philip Benfey (New York University) and John Schiefelbein (University of Michigan) at New York University on November 6 to 8. Nearly 80 participants were present and the 25 talks and several poster presentations were made in four sessions; cellular, genetic and molecular analysis of root development and plant pathogen interactions. More than half of the talks were studies of Arabidopsis, showing the usefulness of Arabidopsis in this field.

An EMBO/EEC Advanced Laboratory Course on Arabidopsis Molecular Genetics was organised by Csaba Koncz (together with Nam Hai Chua and Jeff Schell) at the Max Planck Institute at Cologne from April 5-15, 1992. A group of 16 students from all over the world was selected from a much larger number of applicants and 27 teachers, all specialists in the field of Arabidopsis genetics or plant molecular biology participated in the course. The course involved

lectures, demonstrations and practical exercises covering all aspects of Arabidopsis genetics and molecular biology.

The course manual has been published as "Methods in Arabidopsis Research", which is the first handbook of this type for Arabidopsis. This book appears very useful and is present in almost every Arabidopsis lab.

A meeting of the BRIDGE Arabidopsis "T" project was held in Ghent, Belgium in September 1992. The meeting was attended by approximately 85 people and several topics including transposon tagging, gene replacement, physical mapping, floral induction, seed development and embryogenesis were discussed.

Cold Spring Harbor Summer Course: A new course was established at Cold Spring Harbor Laboratory to provide an intensive overview of current topics and techniques in Arabidopsis biology. The "1993 Arabidopsis Molecular Genetics Course" instructors were: Joanne Chory, Salk Institute, Joseph Ecker (Course Director), University of Pennsylvania, and Athanasios Theologis, Plant Gene Expression Center. The participants included 7 women and 9 men; one-half of the students were Ph.D.'s; one M.S. and seven were B.S./B.A. level.

Enrolment was international; three students currently working in non-US laboratories participated in the Course.

The "Arabidopsis" Course is designed for scientists with experience in molecular techniques who are working or wish to work with Arabidopsis. It consists of a rigorous lecture series, a hands-on laboratory and informal discussions. Speakers provide both an in-depth discussion of their work and an overview of their specialty. Speakers and topic of discussion in the 1993 Course included: Scott Poethig, Plant morphology; Chris Bowler, Phytochrome signal pathways; Ian Sussex, Meristem organization; Philip Benfey, Root morphology; Gary Drews, Applications of in situ hybridization; Elliot Meyerowitz, Flower development; Gerd Jurgens, Pattern formation; Athanasios Theologis, Molecular analysis of hormone action; Mark Estelle, Genetic analysis of hormone action; Hong Ma, G-Proteins; Joanne Chory, Genetic analysis of photomorphogenesis; Peter Quail, Phytochrome; Judy Callis, Ubiquitin pathway; Pamela Green, mRNA stability; Ethan Signer, DNA recombination; Mark Schena, Master regulatory genes; Gerald Fink, Molecular genetics of growth regulation; Mark Johnston, Gene transplacement; Joseph Ecker, Genome analysis; John Browse, Lipid metabolism; Robert Pruitt, Fertilization; Brian Staskawicz, Plant-bacterial interactions; Barbara Baker, Transposon mutagenesis; Steve Kay, Biological clocks. The laboratory session covered: Arabidopsis genetics and development; transient gene expression assays in protoplasts; gene transplacement and complementation of yeast mutants for cloning Arabidopsis genes; transformation by Agrobacterium; in situ hybridization. The Course was supported by a grant from the National Science Foundation and through generous donations of equipment and supplies from numerous companies.

Arabiflora '93: Over 600 scientists from 21 countries gathered at Ohio State University (Columbus, OH; August 19-22, 1993) for the 5th International Conference on Arabidopsis Research. The large number of participants was just one sign of how far the field has progressed since the last meeting was held three years ago in Vienna. The poster session provided perhaps the most graphic display of the breadth and extent of research with Arabidopsis. Roughly 300 posters were presented on topics ranging from metabolism and development to plant- pathogen interactions, photobiology, stress response, and new technologies. The keynote

session gave participants two rather different perspectives on biology in general, and perhaps by analogy, the key role of Arabidopsis in plant research. Craig Venter (Institute for Genomic Research, Gaithersburg, MD) gave an impressive overview of recent advances in human genome research. The obvious conclusion from his presentation was that we currently have the technology available to generate an enormous amount of information on the structure and function of the Arabidopsis genome in a surprisingly short period of time if appropriate resources and strategies are directed towards this objective. The second presentation by Sydney Brenner (Medical Research Council, Cambridge) was equally compelling in calling for an emphasis not just on technology, but on appropriate biological systems and important biological questions. The subsequent sessions at the conference demonstrated in many different ways how effectively Arabidopsis has been used to address issues related to both technology development and basic plant biology.

The major portion of the meeting was divided into ten sessions, each with 6 speakers. The topics of these sessions were growth regulation, photobiology, metabolism, stress and pathogenesis, cell differentiation, embryos and early development, reproductive development, vegetative development, gene regulation, and new technologies. A number of speakers presented new results that provided fascinating updates for well-known stories. Other speakers introduced new topics, systems, and approaches that were less familiar to a majority of participants. Conference organizers were particularly successful in their efforts to have speakers represent the true diversity of the Arabidopsis community. Three workshops featuring collections of short talks were scheduled around the formal conference. This year the topics of these workshops were metabolism, transposon tagging, and genome research.

The frustration expressed by some participants that insufficient time was available to analyze all of the interesting posters displayed at the conference might also be viewed as a positive sign that the research has reached a new level. At least one speaker noted that in contrast to the Vienna meeting, where people were just talking about perhaps looking for a certain type of gene, the concern now was whether someone else had already cloned that gene. If the Vienna meeting demonstrated that Arabidopsis research was beginning to bloom, the highlight of this meeting was the realization that the harvest is starting to come in.

II. STATUS OF NATIONAL AND TRANSNATIONAL RESEARCH PROJECTS

1. Australia

The Australian Government (Department of Industry, Technology and Regional Development) continues to fund an Australian effort in the Multinational Genome Project. Researchers at ANU and CSIRO are studying and mapping a number of genes including those involved in root morphology, male sterility and GA biosynthesis. Researchers at Monash and Melbourne Universities are also funded to characterize genes important in flower morphology and sugar transport. Approximately ten laboratories in Australia use Arabidopsis as their primary experimental material.

2. European Community

An EC-sponsored project (European Scientists Sequencing Arabidopsis - ESSA) to begin the systematic sequencing of the Arabidopsis genome started on 1 August 1993. This pilot-scale effort, which aims to sequence contiguous regions of 1,500 kb on chromosome 4 as

well as nearly 1,000 kb of other regions, will run for three years in the first instance. Random cDNA sequencing carried out by the French national program also forms a significant part of the ESSA project. The project involves 19 labs in Europe and is coordinated by Mike Bevan at the John Innes Center, Norwich, UK. A centralized database using ACeDB/AAtDB software is being set up to integrate and display sequence and physical mapping data. Future goals of the EC network include the entire sequence of chromosome 4. Many aspects of the ESSA are closely coordinated with various national programs which are described below where applicable.

3. France

Apart from specific projects in different CNRS and INRA laboratories, three collective objectives in the field of genome research are being pursued in France.

Sequencing: The EC funded ESSA project coordinated by Mike Bevan includes, as its major component, large or medium scale genome sequencing, to which M. Delseny, Univ Perpignan; B. Lescure Toulouse; R. Mache, Univ Grenoble and M. Kreis, Univ Orsay are contributing. The genome sequencing effort also received funding from the GREG, the French agency for genome analysis. Seven per cent of the money of the ESSA project is devoted to the generation of expressed sequence tags (EST) in eight labs, the four above mentioned, and H. H”fte, INRA, Versailles Cedex; J. Giraudat, ISV CNRS, Gif Sur Yvette; Claude Gigot and Jacqueline Fleck, IBMP CNRS, Strasbourg. This EST sequencing initiative has been supported during the first two years by the CNRS and coordinated by B. Lescure, the team of Jean-Louis Charpenteau (Laboratoire de Biometrie et d'Intelligence Artificielle, INRA Toulouse) taking care of the computer aspects and data bank management. As of September this year approximately 2400 ESTs have been generated from cDNAs clones taken at random in libraries prepared from different sources of plant material: developing siliques; etiolated seedlings; flower buds and cultured cells. A first published report will appear in a coming issue of the Plant Journal. (895 different genes identified, 32% of which showed significant similarity to existing sequences in Arabidopsis and other organisms.) The new sequences are periodically made available to the public databases through automatic submission to the EMBL. The EEC funding will support the production of 3,000 new ESTs. It has been recently agreed to make the clones available through the Ohio Arabidopsis Biological Resources Center.

Mapping: Several laboratories are mapping a number of ESTs on the recombinant inbred lines provided by C. Dean. Since RFLP mapping is tedious for large numbers of cDNAs, it has been decided to map the EST sequences on an ordered YAC library. At the time the EST project was started only 30% of the genome was covered by YACs. It was therefore decided to build a YAC library in collaboration with the group of D. Cohen, CEPH, Paris, and to contribute to the coverage of the genome. A collection of 1,100 clones was obtained this spring, and is being characterized by four labs (M. Dron, Univ Orsay; C. Giot, Strasbourg; G. Picard, Univ Clermont-Ferrand; D. Bouchez, INRA, Versailles). The average size of inserts in the collection is 450kbp, and it carries one to five copies of different genes tested for their presence. It is planned first to order the library through anchoring by PCR, using existing mapped transcripts, and AFLP mapping in collaboration with KEYGENE. cDNAs will then be directly mapped by PCR on ordered contigs. This project has been mainly supported by INRA.

Generation of Insertion Mutants: Five laboratories are

coordinating efforts to generate insertion mutants in the genomes of Arabidopsis. P. Perez (Biocem Company) and G. Picard (Univ Clermont-Ferrand) are generating insertions using As and Ds, and the three other labs (T. Sangwan, Univ Amiens by transformation of immature embryos; M. Delseny, Univ Perpignan by the root transformation technique; and N. Bechtold, and D. Bouchez, INRA Versailles by in plant transformation techniques). Altogether, several thousand transformants have been recently generated and will be characterized for insertions (constructs carrying GUS reporter sequences for promoter trap analysis in Perpignan and Versailles, and gene disruption in all labs). This initiative is supported by INRA and by funds from the French ministry for Education and Research.

4. Germany

The Deutsche Forschungsgemeinschaft (National Research Association of Germany) has established a Special Research Program entitled "Arabidopsis as a model for the genetic analysis of plant development" to be funded for 3 two-year periods from August 1993. The program which is to complement ongoing Arabidopsis research programs in other countries in the EC is coordinated by Gerd J rgens (University of Munich) and Jeff Dangl (MDL, Cologne). For the initial period (August 1993 - July 1995), 15 grant proposals have been approved. The budget allows for some flexibility of membership such that an expected increase in grant proposals can be accommodated in later periods. The program also includes annual meetings, training courses, and infrastructure (support of DNA stock center, access to data bases etc).

The program focuses on 4 aspects of development; (1)pattern formation in embryo and leaf development, (2) growth, differentiation, cell-cell interactions; (3) light as a developmental factor; and (4) control of organelle differentiation.

5. Japan

Arabidopsis research in Japan is becoming increasingly popular. More than 15 laboratories are now working with Arabidopsis. The research topics include mutational analyses of flower organogenesis, responses to physical and chemical stimuli, root morphology, virus infection, hormonal regulation, transcriptional regulation, and shoot regeneration from calli, as well as isolation and characterization of genes involved in heat-shock phosphorylation, and transcription. These studies were funded primarily by the Ministry of Education, Science, and Culture, with some grants from the Science and Technology Agency, the Ministry of Agriculture, Forestry and Fisheries, and some from private foundations.

Several workshops, symposia, and training courses on Arabidopsis research were held in 1992. The 3rd workshop on Arabidopsis studies (organizers: Kiyotaka Okada & Yoshiro Shimura) was held at the National Institute for Basic Biology at Okazaki on December 14-15 with more than 80 participating. Talks presented were on mutant analyses, transformation, transcriptional regulation, and gene cloning. Another workshop on "Recent development of molecular genetic studies on Arabidopsis" was held at Riken Institute at Tsukuba (organizer: Kazuo Shinozaki) on November 9-10 with more than 80 attending. Following the workshop, a training course on the standard experimental techniques on Arabidopsis research was held at the Riken Institute at Tsukuba. The course included lectures, demonstrations, and practice on cultivation and genetic crosses, and transformation and had twelve attendants. Symposia on

Arabidopsis studies were held at the annual meeting of the botanical Society of Japan at Nara on September 18, of the Japanese society of breeding at Nagoya on October 19, and of the Japanese society of molecular biology at Kyoto on December 8.

The interest of young Japanese researchers in the Arabidopsis studies is undoubtedly increasing. Training courses and meetings are planned for this year.

6. Spain

Jose Martinez-Zapater from the Instituto Nacional de Investigacion Tecnologia Agraria Alimentaria in Madrid has assumed responsibility for coordinating a Spanish network on Arabidopsis. The network involves 18 laboratories from Universities and Research Institutes in Spain. The network has been funded by the Spanish agency CICYT (an inter-ministry commission for science and technology) to organize a meeting next November in Valencia. The meeting is expected to facilitate contact and collaboration among the various members of the network and with laboratories outside Spain. The network will also fund visits between laboratories and the compilation and distribution of information on Arabidopsis. The network is open so that as new laboratories develop research interest on Arabidopsis they are free to join.

7. United Kingdom

Following on from the 35 grants funded in the three-year Plant Molecular Biology Arabidopsis program, October 1992 marked the start of the AFRC four-year Plant Molecular Biology II Program. Eighteen of the 44 grants funded are for Arabidopsis research. These grants are coordinated via an electronic network from the John Innes Center (Caroline Dean).

Technology development is still continuing. The Lister and Dean RI lines are now available from NASC and a RI map published with 67 markers. Over 400 other markers have now been mapped. There is now 80% YAC coverage on regions of chromosomes 4 & 5, including a 15cM, 2.2 Mb contig on 4, which will form the basis of the ESSA project (Schmidt, West and Dean; see above under "European Community"). Tagged mutations have now been obtained through the Ac and Ds transposon-tagging systems at the John Innes Center, Norwich, UK and the interposon system developed by Lindsey at Leicester.

UK laboratories are using Arabidopsis to study a range of topics. These include: disease resistance- Crute, Holub and Beynon, (The Horticulture Research International and Wye College), Jones (Sainsbury Laboratory), Maule (John Innes); hormone biology- Harberd (John Innes), Phillips (Long Ashton), Bennett (Warwick), Hall (Aberystwyth); flowering / gametogenesis- Dean (John Innes), Coupland (John Innes) and Mulligan (Nottingham); cell fate- Furner (Cambridge), Roberts (John Innes), Gray (Cambridge); and gene regulation- Jenkins (Glasgow).

8. United States and Canada

The North America Science Steering Committee convened a workshop in Dallas, Texas in June, 1993, to discuss the informatics needs of the Arabidopsis research community from the biological standpoint. The Committee had sought and received through the Arabidopsis newsgroup input from the international Arabidopsis research community. The report of the workshop was published in the newsgroup and is summarized in Appendix II.

The Committee also established a mechanism to rotate its membership as well as an order for its representation on the Multinational Science Steering Committee.

The US. Department of Agriculture, the Department of Energy, the National Institutes of Health and the National Science Foundation (NSF) continued to receive an increasing number of proposals that use Arabidopsis as an experimental system. The four agencies provided approximately $19 million during the period from October 1, 1991 and September 30, 1992 (fiscal year 1992). A majority of the projects supported are individual research projects addressing a broad area of plant biology. Approximately $3.5 million was spent in support of technique development, biological resource centers, resource development, database related activities, research training groups, postdoctoral fellowships, and meetings/workshops. The amount for Fiscal Year 1991 was approximately $15 million and for Fiscal Year 1990 $7.5 million.

III. ANALYSIS AND RECOMMENDATIONS: NEW GOALS FOR THE COMING YEAR

After the third year of the Multinational Coordinated Arabidopsis thaliana Genome Research Project, it is appropriate to review the original short-term and long-term goals, to assess our progress in meeting these goals, and to set new goals for the coming year. The initial goals, stated in the 1990 Long-Range Plan for the Multinational Coordinated Arabidopsis thaliana Genome Research Project, fell into 6 areas. These were genome analysis, technology development, biological resource center, informatics, human resource development, and workshops and symposia.

In genome analysis the one-year goals of instituting mutagenesis projects and establishing YAC libraries have been fully met. The 2-year goal was the linking of ordered collections of YACs. This is progressing well, but is still incomplete, so one important goal for the coming year is to complete the physical linking of the YAC collections. Since programs to do this are in progress, and new technologies for detecting RFLP markers and for correlating the markers to YACs are in place, it is not unreasonable to expect at least 80% of the genome to be linked in the coming year. The 5-year goals for the initial report included completion of chemical and insertional mutagenesis for developmental and physiological phenotypes. The recent advances in transposon tagging and increased T-DNA tagging efficiency make it likely that this goal will be met. For the coming year the goal in this area must be to continue transposon tagging efforts, and to apply the new high-efficiency transformation methods to saturation mutageneses. Another five-year goal was to begin cloning and analysis of genes identified in the mutagenesis projects - in this, the Project is far ahead of the original proposal. As detailed above, many mutagenized genes have been cloned, and have revealed new processes and new directions in plant biology. The final 5-year goal in genome analysis was to initiate sequencing projects; this has been done already in the third year of the program via the ESSA program and the two cDNA sequencing efforts. Our goal in this area must be to begin the genomic sequencing, and to continue the cDNA projects at present rates for the next year. In addition, special emphasis must be paid to using the sequenced cDNA clones as markers for genetic mapping, and at the same time, as probes for YAC clones. By using these expressed sequence tags appropriately, the goals of completing the physical map and of improving genetic mapping methods can both be met.

In the area of technology development there were two 5-year goals. One was to support innovative technologies that directly address characteristics unique to plant genomes, and this has been done, as for example in the development of new plant regeneration and transformation methods, new protoplast transformation and regeneration techniques, and in the production of mapping programs such as Joinmap that allow use of diverse data. We must continue with this in the coming year. The second 5-year goal was to support the importation of genome technologies from animal and microbial systems. This has also been very successful, for example with the application of microsatellite RFLP mapping and chromosome walking to Arabidopsis. This work must also continue.

The third area is Biological Resource Center. In this the Project has rapidly succeeded. The initial recommendation was for establishment of at least two resource centers to handle requests for seed and clone stocks, and recombinant DNA libraries. These are established, extremely well-run, and heavily used. The 5-10 year goals were to maintain long-term support for these centers. Finding mechanisms for the long-term financial support of these valuable resource centers must be a high-priority goal for the coming year.

In the fourth area, informatics, the initial goals have also all been met: these were to convene a data and communications committee, produce a draft of an informatics plan, and to establish at least one Arabidopsis information resource center. These goals have all been met, with the completion this year of the database report (summarized in Appendix II), and the earlier establishment of Internet-based databases for the Arabidopsis community (AAtDB and AIMS). The 5-year goals of developing effective software, creating database tools and developing algorithms for genome interpretation are in sight, and should continue to be pursued. A high priority should be placed on developing mechanisms for making the data available from the Project available in a usable form, that is, on finding governmental funding sources for the recommendations of the database report, and in implementing these recommendations.

In human resource development, the ongoing goals of supporting multinational postdoctoral fellowships and short-term exchanges, and short courses, have only been partially met. The AFRC of the U.K. had a small Arabidopsis postdoctoral program that supported 3 postdoctoral fellows who spent half of their postdoctoral period in U.K. labs, and half in U.S. labs. We are not aware of any other special programs to facilitate multinational Arabidopsis postdoctoral fellowships, though generally-available fellowships such as the NSF Plant Postdoctoral Research Fellowships and the EC Human Capital and Mobility Fellowships have been particularly valuable. Special attention must be paid to designing and implementing specific programs in the future. Short-term exchanges are not supported by any specific programs, and establishing support for such exchanges should also be considered a goal for the coming year. In the area of short courses, though, the Project has succeeded very well, with the institution of the Arabidopsis Molecular Genetics course at Cold Spring Harbor Labs, and of the EMBO Arabidopsis course at the Max-Planck-Institut fur Zuchtungsforschung, as described above. The content of the most recent NATO Advanced Study Institute in Mallorca, Spain was also heavily influenced by recent advances in Arabidopsis research; the participation of scientists working on other plants had an opportunity to learn about the rapid progress of the Arabidopsis genome project.

The final area of the original goals was to support workshops and symposia. As detailed above, this goal is continuing to be met, with for example the most recent International Arabidopsis Congress attracting an unprecedented 600 attendees. In the coming year, support for such symposia should continue.

As a final statement, we emphasize that the remarkable progress of Arabidopsis research in discovering new phenomena specific to plants, and in making rapid advances in many areas (plant hormone signal transduction, plant development, plant light receptors, photomorphogenesis, plant-pathogen interactions, and others) that were previously difficult or intractable, depends on international collaboration and free sharing of results. The Multinational Coordinated Arabidopsis Genome Research Project has provided numerous and crucial mechanisms for this collaboration and sharing, including the resource centers, the electronic mail network, the databases, and the many symposia and meetings that have been supported. We must continue to support the means for collaboration between Arabidopsis researchers, and to find new mechanisms for fostering such collaborations. We must consider new ways to bring the knowledge gained from the analysis of the Arabidopsis genome to researchers in other areas of plant biology and in other areas of biology in general. And
we must continue to commend the goals of the Multinational Coordidnated Arabidopsis thaliana Genome Research Project to researchers and funding agencies around the world, so that the remarkable progress of the past three years may be maintained and expanded.

APPENDIX I:

LIST OF GENES IDENTIFIED BY MUTATION

Genetic Loci of Arabidopsis
Revised September 1993 - David W. Meinke

The attached information lists genetic loci of Arabidopsis thaliana that have been identified by mutation. Molecular markers and cloned genes are excluded. This table includes information from the previous lists of mutant gene symbols and linkage data (distributed by ABRC and email 12/92) as well as new information submitted to stock centers and curators. It should be noted that the same locus may in some cases be given different names by individuals working in different laboratories. These conflicts should be resolved once map locations are determined and complementation tests are performed.

Explanation of Column Headings:

Mutant Locus: Each mutant locus is listed separately. Information on different alleles is not included. Loci marked with (*) are known by more than one name. Conflicts in gene symbols are noted (**).

Name for Gene Symbol: Self explanatory. In some cases, additional information on the mutant phenotype is included. Some investigators have chosen to reserve a symbol before disclosing additional details on the mutant phenotype.

Linkage Group: Self explanatory.

Map: M: This locus was included on the visible marker map distributed on December 15, 1992.
R: This locus should be ready to add to the visible

marker map. In some cases, it has already been placed on the integrated map available through AAtDB.

X: This locus has been assigned to a linkage group but is not yet ready to place on the map.

U: This status of this locus with respect to placement on the map has not been determined for this survey.

-: Mapping data not available when this list was prepared.

Reference Laboratory: Individuals involved with the isolation, detailed characterization, or mapping of this locus. This list does not include all individuals who have worked with a given locus. It is designed to help other researchers obtain further information about a given locus.

[NOTE TO READER: LISTING OF GENETIC LOCI OF ARABIDOPSIS IDENTIFIED BY MUTATIONS DOES NOT APPEAR IN THIS ELECTRONIC DOCUMENT.]

APPENDIX II:

A WORKSHOP SUMMARY

DATABASE NEEDS OF THE ARABIDOPSIS COMMUNITY

To assess the long-term database needs of the Arabidopsis community, an NSF-supported workshop on this topic was convened in Dallas on June 5th and 6th, 1993. The workshop participants, included the following elected members of the North American Arabidopsis Steering Committee (NAASC).

- Elliot Meyerowitz, California Institute of Technology (Chair)
- Fred Ausubel, Massachusetts General Hospital and Harvard Medical School
- Joanne Chory, Salk Institute
- Joseph Ecker, University of Pennsylvania
- David Meinke, Oklahoma State University
- Chris Somerville, Michigan State University

In addition to the NAASC members, the workshop was attended by the following observers.

- Machi Dilworth, National Science Foundation
- Steven Heller, U.S. Department of Agriculture
- A. Vassarotti, Commission of the European Communities

Finally, the following two scientists involved with the human Genome Data Base (GDB) were also present as technical advisers.

- Ken Fasman, Genome Database, Johns Hopkins University
- Robert Robbins, Laboratory for Applied Research in Academic Information, Johns Hopkins University

The general goals of the workshop were to examine the present and future needs for a database and to outline in general terms the main issues which should be addressed in any future proposals concerning the development of new or expanded Arabidopsis databases. The discussions were intentionally focused on biological and community issues and there was no attempt to define or specify issues which are primarily related to specific computer hardware or specific database programs.

The committee concluded that:

- Funding of Arabidopsis Database (ADB) is an appropriate use of federal funds.
- ADB should have both service and research components, with the service component modelled on a scientific journal, including a chief editor, associate editors, and reviewers.
- ADB should be linked to the needs of the community through an oversight committee.
- ADB should be generally accessible both nationally and internationally through electronic networks, with all data available on request.
- The design of ADB should allow portability to new generations of database software and to new generations of computers.
- If properly conceived and constructed, an encyclopedic ADB interrelating everything from nucleotide sequences to ecological data could provide a completely novel research tool that would catalyze new kinds of discoveries in biology.
- Because of the relative ease of data access, ADB might eventually displace scientific journals as a source of certain kinds of primary scientific information.

An abridged version of the database workshop report follows.

SUMMARY

There were six main conclusions from the workshop:

First, although all Arabidopsis information need not be archived in a single database, it is essential that all Arabidopsis databases be able to communicate with each other and with other major databases, such as the nucleic acid databases, in a seamless networked fashion. In this and related respects it was considered essential that ADB be available via international electronic networks.

Second, ADB involves a major service component.

Third, ADB will involve an essential research component. Shorter term research will be required to determine the best way to implement many of the current needs for such a database, and longer term research will be required to ensure that the database can migrate over time to different and improved hardware and software platforms.

Fourth, ADB should provide an intellectual focus for the interpretation, synthesis and integration of biological data. The concept of structuring a database along the lines of a scientific

journal is attractive in this respect (i.e., a database should have editors, reviewers, and production staff).

Fifth, all of the data and knowledge residing in ADB will form an irreplaceable intellectual resource for the scientific community. Therefore, federal support for such a database should be long-term and contingent upon guarantees that all information in the database will be freely available to the international scientific community, now and in the future.

Sixth, the government should support the development of one or more databases, which would collectively contain all Arabidopsis information, using a funding vehicle and management plan that would be designed to provide enough freedom to ensure the success of the research component, while also providing enough oversight and control to ensure the adequacy of the service component.

I. WHAT SHOULD BE IN THE DATABASE?

The information content of the proposed ADB was divided into five sections as outlined below. (A) map-based information; (B) stock-based information; (C) community-based information; (D) sequence-based information; and (E) biology-based information.

A. Map-Based Information

Rapid visualization of updated genetic/molecular maps and ready access to primary mapping data should be given highest priority in database development. Map information should be collected and presented in a manner that allows the user to determine what is known, plus what remains questionable or unresolved, with respect to map locations of genetic and molecular markers in combination with a complete physical map of overlapping cloned sequences. In constructing the database, it should be remembered that recombination data generally provide only rough estimates of map location, and that mapping data may differ widely in quality and reliability.

Some database users may therefore prefer direct access to primary mapping data in order to construct their own maps of specific regions or compare their results with those obtained in other laboratories. A database that provides options for visualizing several different maps constructed with different mapping functions or subsets of markers and primary mapping data would be particularly valuable to the Arabidopsis community.

Any proposal for database development should also discuss in some detail how the integrity of these maps would be verified and maintained through a network of editors and/or curators with appropriate expertise in map-based activities. Although it may eventually be possible to combine all of the physical, genetic, and molecular data generated by the Arabidopsis genome project into a single definitive map of the five chromosomes, at the moment it is likely that three complementary types of maps will need to be included in the database:

(1) a genetic map showing the approximate distances between all well-characterized mutations (visible or biochemical) and molecular markers (RFLP, RAPD, cDNAs, or other cloned sequences);

(2) a map that presents data on recombinant inbred (RI) lines in a visual manner; and

(3) a physical map showing the actual arrangement of cloned

sequences along the length of each chromosome.

Many researchers may want to start with a particular mutation or cloned gene and move directly to the corresponding regions of all three maps. Some mutations and cloned genes are likely to be known by several different names. It will therefore be important to establish a database that will accommodate multiple changes in nomenclature.

Provisions should also be made to add new types of information to genetic and physical maps as they become available (break points of chromosomal aberrations; regions of extensive heterochromatin; regions with a high/low degree of sequence homology to related plants; etc.).

B. Stock-Based Information

The database should contain detailed information on the availability of biological and chemical materials related to Arabidopsis research. One should be able to use the database to determine how a wide range of desired materials can be obtained, propagated, and utilized by the individual investigator. This may be accomplished either by including this information directly in the primary database, or by appropriate linkage with databases at existing stock centers.

Development of this part of the database will require extensive interaction with individuals at the Nottingham Arabidopsis Stock Center (UK) and the Arabidopsis Biological Resource Center at Ohio State University (USA). Major sequencing and molecular mapping centers should also be consulted on the most efficient means of transferring or linking large volumes of molecular data to primary databases. Attention must be given to reducing duplication of effort in order to conserve limited financial resources.

The database should include detailed information on the nature, origin, and availability of seeds, clones, libraries, cDNAs, oligonucleotides, and any other materials that may require distribution to the Arabidopsis community. Emphasis should be placed on careful documentation of biological materials, controlled vocabularies, and maximal utilization of sophisticated graphics to display plant phenotypes, molecular hybridization patterns, and other data where appropriate.

With respect to seed stocks, it should be possible to search the database by general phenotype, not just by gene symbol, in order to obtain a broad listing of ecotypes and mutant lines with similar features.

Information on phenotypes, screening methods, growth conditions, and differences between alleles should be included for all mutants available through the stock centers. It should also be possible to obtain information on additional mutants or alleles that have been isolated in specific laboratories but are not available from the stock centers.

Individuals should be able to search for specialized libraries, vectors, transgenic lines, and molecular reagents (antibodies, purified proteins, unusual compounds, and biochemical standards) required for Arabidopsis research.

C. Community-Based Information

The database should provide easy access to information on a wide range of community issues such as: individual investigators (names, addresses, research interests), messages sent through the Arabidopsis electronic network, general announcements (jobs, meetings, seminars, grants, technical comments, specialized reagents or facilities available), personal communications (protocols, methods, lab data relevant to researchers in the field but not included in publications), and literature (publications on Arabidopsis, meeting abstracts, grant summaries, complete text of Arabidopsis Information Service and other reports with limited distribution).

D. Sequence-Based Information

There is no requirement for all Arabidopsis sequences to be stored in the proposed database. In light of the rapid growth of sequence information and continued budget restrictions, it may be preferable to focus limited resources on maximizing linkages with existing databases. If a separate sequence file is not maintained, the primary emphasis in development of the Arabidopsis database should be on convenience of linkage to GenBank and other large-scale databases with a goal of transparent retrieval of sequences. It should be possible to retrieve from the database sequence information based on map position, type of sequence, or other specific requirements.

E. Biology-Based Information

The focus of research with Arabidopsis is likely to change in the future from the immediate emphasis on mapping, sequencing, and gene identification, to the long-term questions of general biology and gene function during plant growth and development. The Arabidopsis database should therefore include information that may be of critical importance during this second phase.

Examples of topics that might be included in this category include: information on plant pathogens that infect Arabidopsis and details on the molecular interactions that take place between host and pathogen; information on the chemical composition of specific plant parts (sugars, lipids, proteins, polysaccharides, specialized compounds, etc.); physiological data on the normal life cycle and the response of mutant and wild-type plants to various environmental and experimental treatments; protein profiles of different plant parts revealed through 2-D gel electrophoresis; information on the natural distribution and ecology of Arabidopsis and closely related species; detailed comparisons of the different ecotypes with respect to morphology, physiology, and molecular biology; information on the taxonomy of Arabidopsis with particular attention to related plants used in agriculture; light and electron micrographs of different types of cells in wild-type plants; records of expression patterns of specific genes during growth and development; and computer- enhanced reconstructions of serial sections through various plant structures.

II. HOW WILL THE DATABASE BE USED? WHAT LINKS SHOULD BE MADE BETWEEN CATEGORIES OF INFORMATION?

In addition to the specific ability to perform searches as described in the previous sections, the categories of information must be linked with user-friendly interfaces. Attention should be paid to tight coordination between the genetic map and related genes, clones, and sequences, so that selection of any of these will lead transparently to accession of the others. Also, it is highly desirable for the database to have simple links for

comparative sequence and mutant analysis with other plants and beyond that, with all organisms. The interface should allow viewing in a variety of ways.

As examples of the types of links desired, we list below a series of questions that the system should be able to answer. Most of these examples were suggested by current users of AAtDB and AIMS.

(1) If a user enters two cloned markers, the system should return a list of all markers of a specified type that map between them.

(2) If a user points to a location on a genetic map, the genes, clones, and sequences should appear. Likewise, a user should be able to derive map position if a DNA sequence is used as the starting point.

(3) If a user finds a specific clone, the expression pattern of the RNA encoded by the clone should be readily accessed.

(4) If a user finds a mutant that is altered in a particular way, the system should retrieve all mutants altered in a similar manner.

A cross-species accession to similar mutants in other plants might be useful.

(5) If a user desires to see the map positions for all genes in a given biochemical or developmental pathway, she/he should be able to do so.

(6) If a user has new mapping information, the system should have the ability to download archived data in that region for manipulation.

III. WHAT COMMUNITY ISSUES MUST BE CONSIDERED IN THE DESIGN AND OPERATION OF THE DATABASE?

A. Advisory Committee

An Arabidopsis database (ADB) proposal should include a provision for an advisory committee that will represent the community of Arabidopsis researchers and will advise ADB investigators on priorities and data to be included.

One model of how an advisory committee would function is based on an analogy between ADB and a scientific journal. In this model, the ADB investigators who are funded by an ADB grant and are responsible for database assembly, would be analogous to the publisher of the journal. The ADB curator(s) (a permanent professional position) would be analogous to the managing editor of the journal. The ADB advisory committee would be analogous to the editor-in-chief plus the senior editors of the journal. Finally the ADB advisory committee would appoint an editorial board which would evaluate specific submissions to ADB in the same way that the editorial board of a journal reviews submitted manuscripts for scientific content and appropriateness.

B. Curation, Entry, Correction, and Long-Term Storage of Data

Curation: Because ADB will be relatively small compared to the human genome data base and will most likely have limited funds, developers of ADB should make every effort to leverage the database activities undertaken elsewhere and adapt existing software, when appropriate, for use in the Arabidopsis research community. Thus, the major activity of ADB will be the collection, entry, and

correction of data rather than writing software for storing, retrieval, and presentation of data. Therefore, a full-time professional curator(s) will be a key person for the efficient operation of ADB.

C. Relation to Other Databases and Programs

When possible, ADB should use industry-standard hardware and software, so that ADB is both compatible with and can communicate transparently with other data bases. However, as stated elsewhere in this report, the primary goal of ADB should be to collect and store data using currently accepted database models rather than to develop new database software specifically for ADB. The most important principle, therefore, in the design of ADB is that the data be entered in a form that makes it possible to interface easily with other databases and which makes the data in ADB portable to future generation database software. Any software that is written specifically for ADB (display of genetic maps, for example) should be layered and use industry standard interfaces so that the software, as well as the underlying data, is also compatible with and portable to future generation databases. The general principle is that it only makes sense to spend money on the development of generic databases that can be used for a variety of different genomes.

D. Availability of the Database

Data accumulated by a publicly funded database should be community property. There should be no restrictions on the availability of the data in ADB. ADB must be available internationally by INTERNET. However, for the foreseeable future, not all potential users will have access to a high quality INTERNET connection that will support a graphical interface. Therefore, ADB should also be made available in another format such as 9 track tape or CD.

All data should be available for bulk access or bulk downloading. Screen-by-screen retrieval is not sufficient for transferring large amounts of information.

E. One or Several Databases?

There does not have to be only a single Arabidopsis database, but each should have a clear and defined subset of the database task, and appropriate links to the others. If there is more than one Arabidopsis database, it is imperative that they be integrated and that the staff operating the different databases be committed to cooperating with each other. In addition to ADB, simple and fast network access via software like GOPHER will be required to meet all needs of the Arabidopsis community.

F. Education

The ADB investigators should be provided funding for the provision of community education and training. This would include the development of on-line help, training manuals, workshops, and short courses. The ADB developers should maintain complete documentation and source code. This information should be in the public domain. Because educators and students in higher education (including high-school students) may make use of ADB, sufficient documentation for non-sophisticated users should be made available.

IV. WHAT DESIGN-FEATURE ISSUES NEED TO BE CONSIDERED?

As an aid to those who will plan to submit proposals for

Arabidopsis database services, the committee discussed at a general level some of the design features that would allow the ADB to serve the community with maximal efficiency, and recommended that any proposal for database services include a discussion of these design considerations. In addition, the committee recommended that any Arabidopsis database proposal would consist of two parts. One should be for biologists, describing what the database could do, with examples like those in the list of examples given above. The other should be for database and computing experts, to show how the goals will be achieved at a technical level, and how the methods proposed relate to existing technical methods in use in genome databases.

A. Design Considerations that Should be Discussed in the Proposal:

- Any field upon which a user might be expected to initiate a search should contain controlled-vocabulary entries.

- Data must always be in a form that will be portable to new database systems, and new computers and computer types. Current industry trends are towards layered software systems and client-server databases.

- All data should be available for bulk access or bulk downloading, as discussed above.

- The database should have update information on its own contents: date/time coding should be considered for all data and links between data, so that update data can be obtained by users on a regular basis.

- The database should contain cross-references to the following databases (where available): GenBank Nucleotide Sequence Database; Arabidopsis thaliana stock center database; Cell and/or probe repository catalogue number(s); and Genetic map databases for species showing significant synteny with Arabidopsis thaliana.

- To ensure the development of a robust and stable production quality system, the database should be based upon readily available, proven software.

- To facilitate inter-database linking, and referencing of items in the database in an unambiguous manner for publications and other reports, and to ensure the long-term ready availability of the data in the database, primary entities ("unit records") should be identified by public, unchanging unique identifiers (accession numbers).

- The database structure should be described in a data dictionary or repository which would be available to database users.

- To facilitate user and developer access, the database should be maintained on a computer (or network of computers) which uses the Unix operating system and which is connected to the US. Research INTERNET by communications lines which operate at a minimum of 1.54 Mbits/sec.

- The developer should maintain complete documentation and source code for all software developed.

B. Short-Term Research Goals

The developer should consider and propose to carry out some short-term research relevant to improving the quality of the Arabidopsis thaliana database. Some possibilities for short-term research would be:

- Add capability of representing and storing data for other plant species.
- Explore the abstract and generic nature of mapping data and develop generic representation systems in anticipation of adding mapping data generated by as yet undiscovered mapping techniques.
- Develop methods for defining and controlling differential access to the data.
- Develop a means for providing an audit trail, or other historical record, of all changes to the database.
- Investigate methods for facilitating inter-database interactions and connections.
- Develop a stable, documented application program interface (API) to the database.
- Develop a method for representing variations in data quality and for recording uncertainty.
- Develop means for integration of physical mapping data with genetic and cytogenetic maps.
- Develop means for providing ready user access to underlying supporting data (maintained in remote laboratory databases) through the database on-line user interface.
- Develop improvements in data presentation, including graphical representation of maps.

C. Possible Long-Term Research Goals

- Investigate new database systems and new data models.
- Monitor advances in hardware improvement and develop plans for using new hardware to improve the quality of the database.

APPENDIX III

PARTIAL LISTING OF RECENT ARABIDOPSIS PUBLICATIONS

The following represents a partial listing of Arabidopsis research papers published from August 92 to August 16th, 1993 (most recent listed first). This list was downloaded from "Reference Update" (Research Information Systems, Inc., Camino Corporate Center, 2355 Camino Vida Roble, Carlsbad, CA) and updated by Chris Somerville.

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Mechanism of isoxaben tolerance in Agrostis palustris var. Penncross, Heim,D.R., Bjelk,L.A., James,J., Schneegurt, M.A., Larrinua,I.M.: J.Exp.Bot., 44:1185-1189 (1993)

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Photoresponses of transgenic Arabidopsis seedlings expressing introduced phytochrome B-encoding cDNAs: Evidence that phytochrome A and phytochrome B have distinct photoregulatory functions, McCormac,A.C., Wagner,D., Boylan,M.T., Quail, P.H., Smith,H., Whitelam,G.C.: Plant J., 4:19-27 (1993)

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Ammonium inhibition of Arabidopsis root growth can be reversed by potassium and by auxin resistance mutations aux1, axr1, and axr2, Cao,Y., Glass,A.D.M., Crawford,N.M.: Plant Physiol. 102(3):983-989 (1993)

Expression patterns of duplicate tryptophan synthase Beta genes in Arabidopsis thaliana, Pruitt,K.D., Last,R.L.:Plant Physiol., 102(3):1019-1026 (1993)

Arabidopsis thaliana cDNA encoding a novel member of the EF-hand superfamily of calcium-binding proteins, Bartling, D., Buelter,H.,

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