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COMMUNITY STANDARDS: A NEW SERIES OF GUIDELINES FOR PLANT SCIENCE

Community standards for *Arabidopsis* genetics

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Introduction

The explosive growth of *Arabidopsis* research over the past 15 years has brought about fundamental changes in the nature of basic plant research. It has also created a number of serious challenges for plant biologists with respect to coordination of research efforts. The *Arabidopsis* community has responded to these challenges by establishing an effective network of national and multinational research programs, advisory committees, and workshops designed to foster coordination and cooperation. The electronic *Arabidopsis* news group, initiated ten years ago to enhance rapid communication among research groups worldwide, and the Multinational *Arabidopsis* Genome Research Project, established in 1990 to stimulate and coordinate research efforts in plant molecular genetics, are two models of community organization that have subsequently been applied to other organisms.

Establishing standards for nomenclature, mapping and genetic analysis in *Arabidopsis* has also required community organization. The importance of such standards has been discussed in the past, and some coordination has been achieved through monographs (Meyerowitz and Somerville, 1994), conferences and the Internet, but without published guidelines it has been difficult to keep the broader scientific audience informed. The purpose of this review is to present accepted standards for *Arabidopsis* genetics to help guide researchers, teachers, editorial offices and granting agencies. We describe here established rules for nomenclature, procedures for selecting a gene symbol, prerequisites for mutant analysis, suggested requirements for publication, strategies for mapping, and community resources through which updated information on gene symbols, genetic maps and sequencing projects can be obtained. Adherence to these standards is needed to maintain consistency in research publications, accuracy in expanding databases, and efficiency in multinational research programs.

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Examples of problems

The need for coordination of *Arabidopsis* nomenclature became apparent in the late 1980s as investigators began isolating large numbers of mutants and assigning them gene symbols without knowledge of related activities in other laboratories. This resulted in the same symbol occasionally being used for mutants with completely different phenotypes. A case in point was the publication, in successive issues of the same journal, of phenotypic descriptions of two unrelated *sin* mutants. One exhibited a short integument in the ovule (Robinson-Beers *et al.*, 1992). The other was defective in sinapic acid biosynthesis (Chapple *et al.*, 1992). This prompted the establishment of a common list of mutant gene symbols that was distributed to community members for consultation before publication of new symbols. This system has expanded to an Internet format in recent years (http://mutant.lse.okstate.edu/) and has reduced but not eliminated the accidental selection of identical symbols.

A second problem has been the assignment of different names and symbols to mutant alleles of the same gene, or in some cases even the same allele. There have been several reasons for this confusion. One has been the failure to recognize that certain phenotypes are related. A good example was the discovery that cytokinin-insensitive (*ckr1*) and ethylene-insensitive (*ein2*) mutants, each characterized from different perspectives in different laboratories (Guzman and Ecker, 1990; Su and Howell, 1992), were in fact defective in the same gene. Another striking example is the allelism between *amp1* (Chin-Atkins *et al.*, 1996), *pt* (Vizir *et al.*, 1995), *cop2* (Hou *et al.*, 1993) and *hpt* (Ploense, 1995). Resolving these conflicts often provides a more complete picture of the mutant phenotype, although it also raises the difficult question of which symbols should be discontinued.

Another common problem occurs when different laboratories identify the same class of mutants simultaneously but select different names. This type of duplication is the most difficult to eliminate without extensive monitoring but it can often be resolved in subsequent publications. For example, three different names (*hy8, fhy2, fre*) were originally given to mutants defective in phytochrome A (Parks and Quail, 1993; Nagatani *et al.*, 1993; Whitelam *et al.*, 1993), but the problem was soon resolved when the

Table 1. Internet resources for *Arabidopsis* information, gene symbols, maps, and stocks

Resource available [a]	Internet address for information	Information provided [b]
Arabidopsis database	http://genome-www.stanford.edu/Arabidopsis/	Primary source of information Links to relevant Internet sites Large-scale sequencing projects
Rules of nomenclature	http://mutant.lse.okstate.edu/	Nomenclature of mutant genes
Information on mutants	http://mutant.lse.okstate.edu/	List of mutant gene symbols Genes identified by mutation Linkage data and map locations
ABRC Stock Center	http://aims.cps.msu.edu/aims	Seed stocks and DNA samples Database for mutants and clones
NASC Stock Centre	http://nasc.nott.ac.uk	Seed stocks; mutant phenotypes Updated recombinant inbred map

[a]The present curator of mutant gene symbols is David Meinke, Department of Botany, Oklahoma State University, Stillwater, OK, 74078, USA (tel. +1 405 744 6549; fax +1 405 744 7673; e-mail meinke@osuunx.ucc.okstate.edu; WWW http://mutant.lse.okstate.edu/).
[b]Emphasis is on information relevant to topics outlined in text.

authors agreed that *phyA* should become the accepted symbol (Quail *et al.*, 1994). A fourth problem has been the failure to perform allelism tests with known mutants that exhibit related phenotypes prior to publication. Often investigators are not familiar with related mutants that should be tested. In other cases, seed stocks for mutants with related phenotypes are difficult to obtain. Special attention must be given in the future to making the phenotypes of novel mutants known to the community, providing seeds to other laboratories for the purpose of complementation tests, and completing appropriate crosses before publication.

Standards for nomenclature

Genes identified by mutation

The following standards of nomenclature have been adopted by the *Arabidopsis* community and should be followed in publications and presentations. Updated rules of nomenclature can be obtained through the Internet as described in Table 1. Mutant gene symbols should have three letters (underlined or italics) written in lower case letters (*abc*). Some gene symbols chosen before these guidelines were established may have two letters. The wild-type allele should be written (underlined or italics) in capital letters (*ABC*). The full descriptive names of the wild-type (*ALPHABETICA*) and mutant (*alphabetica*) alleles should be written in the same manner. Protein products of genes should be written in capital letters without italics (ABC). Phenotypes may be designated by the gene symbol (no italics) with the first letter capitalized. Thus Abc^{+} describes the wild-type; Abc^{-} refers to the mutant. The (+/–) should be a superscript if possible. Different genes with the same symbol are distinguished by different numbers (*abc1* and *abc2*). Different alleles of the same gene are distinguished with a number following a hyphen (*abc4-1* and *abc4-2*). When only a single allele is known, the hyphen is not needed. Thus *abc3* = *abc3-1* if only a single allele is known. The same rules of nomenclature apply to both dominant and recessive mutations. The letter '*D*' may be added to the end of an allele number for the purpose 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. These rules of nomenclature were first adopted at the Third International Meeting on *Arabidopsis* held in 1987 at Michigan State University. They have subsequently become widely accepted by the community.

Much greater variation has been observed in the nomenclature of revertants, suppressors, double mutants, alleles of known mutants isolated in different laboratories, T-DNA and transposon insertions, reporter fusions, and natural variants identified in different ecotypes. Designation of allele numbers has generally been resolved by the groups involved in coordination with the stock centers. Suppressors are typically given a different gene symbol, although in some cases the original symbol may be reversed (e.g. *ted* suppressors of *det* mutants). Intragenic revertants may be designated by adding the letter '*R*' to the allele number. Thus *abc1-3R* refers to the heritable revertant of the *abc1-3* mutant allele. Minor variations in such technical details are considered acceptable until the community decides to adopt more rigid standards. Many journals have their own guidelines for designating multiple mutants. The most direct way to write the double mutant

produced by crossing *abc1* with *def2* is '*abc1 def2* double mutant'. Information on molecular markers associated with insertional mutants should be excluded from the gene symbol. When dealing with genes identified from natural variants in different ecotypes, the Columbia ecotype should be considered wild-type except when it contains the recessive allele. This choice of Columbia as the standard ecotype is consistent with the genome project. In some cases, it may be appropriate to use letters to designate the ecotype in the gene symbol. For example, *FLC-col* has been used to denote the *FLC* allele in ecotype Columbia (Koornneef *et al*., 1994; Lee *et al*., 1994).

Cloned genes not associated with a mutation

There should in theory be no difference between the rules of nomenclature for genes identified by mutation and those not associated with a mutation, particularly in *Arabidopsis* where the nucleotide sequence of every gene will soon be determined. However, for historical reasons, rules of nomenclature for wild-type and mutant genes have arisen from different concerns. For cloned genes where a known function has been established and related proteins have been characterized in other organisms, the main concern has been that *Arabidopsis* gene symbols be consistent with existing standards. Symbols for some genes identified by protein function may therefore require more than three letters and may include 'At' to designate the source organism. Recommendations for a consistent system of nomenclature for cloned genes throughout the angiosperms have been presented by Price (1994). These standards should be consulted for issues of nomenclature in other angiosperms. The primary concern with *Arabidopsis* genes identified by mutation has been that investigators be free to choose their own symbols provided they avoid conflicts with other mutant symbols. It therefore seems inevitable that many genes in *Arabidopsis* will eventually be associated with two different symbols, one based on the known protein product determined from a cloned gene before a corresponding mutation was identified, and the other based on the mutant phenotype analyzed before the disrupted gene was cloned.

When a locus has long been known by the mutant phenotype, this gene symbol should be retained even after the gene is cloned. Otherwise, no classical symbols will remain upon completion of the genome project and valuable links to previous genetic studies will be lost. In cases where the mutant gene symbol is vague, misleading or not widely known, investigators working on the locus and phenotype in question should petition the curator of gene symbols with a proposal to change the symbol. The desire to adopt a gene symbol that reflects protein function can then be weighed against the confusion that may result when nomenclature is changed. With respect to selecting a new symbol, there are at present no centralized lists of symbols for cloned genes of *Arabidopsis* not associated with a mutation to complement existing lists of mutant gene symbols. Efforts are underway to make such a list available through the Internet, but in the interim the best strategy for choosing a symbol for cloned sequences is to consult published recommendations (Price, 1994) and the WWW list of *Arabidopsis* mutant gene symbols.

Selecting a mutant gene symbol

The following procedures should be followed when selecting a gene symbol for natural monogenic variants and all mutants identified following irradiation, chemical mutagenesis and insertional mutagenesis. The first step is to determine whether similar mutants have been previously described. If this is the case, it may be appropriate to retain a standard descriptive name for the phenotype (e.g. *eceriferum*) and simply change the locus number. Alternative names are least acceptable when the phenotype is narrowly defined, as with the *brevipedicellus*, *leafy cotyledon*, *transparent testa*, and *glabrous* classes. Synonyms for such mutants are unnecessary and often confusing to the community. However, alternative names should be considered acceptable and in some cases preferable when the phenotype is more broadly defined, as with dwarfs, male steriles, embryo defectives, and disorganized shoot and root phenotypes, or when the specific cellular defect responsible for the mutant phenotype is determined. Within these limits, investigators should be free to choose descriptive names that reflect their perspective on the mutant phenotypes and proposed gene functions. When a new gene symbol is warranted, the updated list of existing symbols must be consulted before publication to make certain that the desired symbol is available. New symbols must then be reserved with the curator of mutant gene symbols, who maintains a temporary list of reserved symbols pending periodic updates of the master list. Table 1 presents the Internet addresses of the present curator and master lists of gene symbols, along with other community resources for *Arabidopsis* genetics.

Requirements for mutant analysis

Research with *Arabidopsis* has advanced to the point where basic guidelines for mutant analysis are needed to facilitate the long-term goal of saturating the genome with informative mutations. The following procedures have been designed to benefit the multinational research community and should be followed whenever possible, regardless of the mutant phenotype being examined. The basic requirements for genetic analysis should be to: (1) establish monogenic inheritance by segregation analysis; (2) determine dominance relative to wild-type; (3) perform allelism

tests with related mutants; (4) map the location of the gene; and (5) complete a detailed characterization of the phenotype. Mutant screens should utilize standard ecotypes when appropriate to facilitate integration of the results obtained into mapping and sequencing programs. Mutagenesis procedures and sources of parental populations should be documented. Special care should be taken to record stock numbers of parental lines when common pools of insertional mutants are being screened because other investigators may be analyzing the same mutants. Detailed analysis should be performed if possible with mutants backcrossed several times with wild-type to eliminate extraneous mutations. Phenotypic descriptions of mutants identified should extend beyond the specific focus of each laboratory to include the entire life cycle. For example, many laboratories have overlooked subtle root and embryo phenotypes while detailing more obvious defects in leaves and reproductive structures. The discovery of interesting root defects in *ttg* mutants, which had long been known simply for their alterations in trichome formation and seed coat morphology, provides a recent example of this point (Galway *et al.*, 1994). Complementation tests should be performed among mutants within a given collection to determine the numbers of genes involved. Procedures for crossing mutants and interpreting allelism tests have been described (Koornneef and Stam, 1992). Mutant genes must then be mapped and additional complementation tests performed with related mutants that map to the same region of the chromosome. This must become a routine practice in every laboratory in order to limit the proliferation of duplicate names for allelic mutants.

Checklist for publications

Community standards for research publications dealing with *Arabidopsis* mutants are needed to identify potential conflicts in gene nomenclature. The following section is designed to assist editorial offices by defining recommended standards for publications involving mutant analysis. Authors should be encouraged to document their reasons for not meeting any of these requirements upon submission of a manuscript. Reviewers might then be asked to comment on the validity of the explanations presented. Authors are requested to meet the following standards for publication.

1. Choose mutant gene symbols that do not conflict with existing symbols

Editors and reviewers may wish to consult the updated list of mutant gene symbols by accessing the Internet address shown in Table 1. Authors can avoid conflicts by registering new symbols in advance of publication.

2. Use the accepted gene symbol for a locus known by multiple names

This has been a source of considerable frustration and confusion in the past. The *DET/COP/FUS* class of genes illustrates the complications that arise when mutants identified in separate screens are later found to be related (Castle and Meinke, 1994; Mayer *et al.*, 1996; Pepper *et al.*, 1994; Wei and Deng, 1996). In some cases, deciding which gene symbol should be given precedence has been difficult. The community has avoided making strict rules for the resolution of nomenclature conflicts because each case is somewhat different and enforcement cannot be monitored. In the past, the symbol that was first included in a significant research publication or was most widely known to the community was often given precedence. Conflicts were resolved either by having the investigators involved reach a consensus or by having the curator of mutant gene symbols make a decision. The accepted locus name was then listed on the Internet with reference to known synonyms. The WWW address for this table of genetic loci is presented in Table 1. Editors and reviewers are encouraged to consult this table as needed to confirm that the accepted symbol for a locus is used in a manuscript. Some conflicts in mutant gene symbols are nevertheless likely to remain. We propose that when two mutants are discovered to be allelic but a consensus among investigators cannot be reached on the accepted symbol, the curator of mutant gene symbols should make a decision, based on information provided by the groups involved, and post the accepted symbol on the Internet. Appeals to these decisions can be addressed to the Multinational Science Steering Committee. We further propose that when abstracts or publications on related mutants appear at the same time, authors should exchange seeds for complementation tests. If allelism is confirmed, then the procedures outlined above should be followed to establish a common symbol. Authors are requested to complete allelism tests before publishing another abstract or paper on the mutants in question. Editors and reviewers are encouraged to request evidence that appropriate crosses have been performed.

3. Refer to synonyms for a given mutant in the text

When a mutant is known by more than one name, manuscripts should include clear references to synonyms at appropriate places in the text, for example in the abstract, introduction and methods, but elsewhere the accepted name alone may be used. This directs the reader to related work from other laboratories without the distraction of redundant symbols. For example, a paper on *amp1* might describe in the introduction its allelism with *pt*, *cop2*

and *hpt*, but then use *amp1* and not *amp1/pt/cop2/hpt* throughout the remainder of the text.

4. Characterize inheritance patterns and provide thorough descriptions of mutant phenotypes

A superficial description of mutant phenotypes should not be considered appropriate for publication in major journals. The analysis of more than one mutant allele should be encouraged but not required. Phenotypes described should be compared with those of existing mutants.

5. Determine the number of genes represented in a mutant collection

This can be demonstrated through complementation tests, provided the total number of mutants and genes involved is small enough to make this practical.

6. Assign each mutant to a linkage group and preferably to a chromosomal region

This must become a standard requirement for publication. Authors should submit estimated map locations to the curator of mutant gene symbols at the time of publication for posting on the Internet.

7. Perform allelism tests with related mutants that map to the same chromosomal region

Mutants should not be assigned a novel name unless they define a gene not previously identified. The limited resolution of existing maps should be considered when choosing appropriate mutants for allelism tests (Franzmann *et al.*, 1995). Manuscripts that describe common phenotypes without map data or results of allelism tests should be returned to the authors unless an exceptionally strong case can be made for immediate publication. In the case of dominant and gametophytic mutants, where complementation tests are not informative, recombination data should be used in the absence of sequence information to address the likelihood that a single gene is involved.

8. Make seeds of published mutants available to other investigators for allelism tests

Seeds for most established mutants can already be obtained through stock centers. Authors should document their plans to make seeds available to the community upon acceptance of a manuscript and should include accession numbers of appropriate stocks to facilitate ordering from existing resource centers.

9. Submit information to relevant databases

Authors should provide documentation that information presented in a manuscript will be submitted to the *Arabidopsis thaliana* database (AtDB) and other relevant sources upon acceptance for publication.

Approaches to mapping

Mapping of cloned sequences and mutant genes must be a common goal for the *Arabidopsis* community. Mapping procedures in *Arabidopsis* have been reviewed elsewhere (Koornneef, 1994; Franzmann *et al.*, 1995) and will not be repeated here. Our purpose instead is to summarize the types of maps, markers and strategies that are currently available. With respect to cloned genes, one standard approach is to identify a sequence polymorphism that a given clone detects between Columbia and Landsberg ecotypes and then map this clone on recombinant inbred (RI) populations obtained from the stock centers. Results obtained from individual plants within this population are then compared with data available for other mapped markers. The methods involved have been described by Lister and Dean (1993) and the updated map is maintained by the Nottingham Stock Center (http://nasc.nott.ac.uk). Mutants can be added by identifying a linked molecular marker that is already on the map or by cloning the disrupted gene. A second approach for mapping cloned genes is to use hybridization or PCR methods to identify a YAC or BAC that contains the sequence and has also been anchored on the physical map. Information on YACs and BACs can be obtained from the Ohio State Stock Center and from the *Arabidopsis* database (AtDB) noted in Table 1. A third approach is to determine whether the clone in question has been assigned a chromosomal location as part of the multinational genome sequencing project. Internet links to the major sequencing groups can be obtained through AtDB.

Mapping of genes identified by mutation can be accomplished with either molecular markers or visible markers. When molecular markers are used, mutants are localized relative to other markers already placed on the recombinant inbred (RI) map. When visible markers are used, mutants are localized on the classical genetic map. These two maps do not correspond exactly in chromosome length. Integration will become easier in the future as more mutant genes are cloned and incorporated into both maps. In the interim, one rapid method for approximating gene location is to use the ratio: [total length of classical chromosome/total length of RI chromosome] to convert the estimated location of a gene on the RI map to the corresponding location on the classical genetic map. However, this method may further increase the considerable uncertainties in map locations that are characteristic of all genetic maps.

Information on visible markers available for mapping purposes can be obtained from the stock centers. Several recent publications have outlined procedures for mapping mutations with visible markers (Franzmann *et al.*, 1995; Patton *et al.*, 1991). The current classical map can be accessed through the Internet as described in Table 1. Periodic updates are made to this map after sufficient information has been collected from the community. Linkage information on mutant genes not yet placed on the map can be obtained from the linkage table also available through the Internet. Although the original genetic maps of *Arabidopsis* were constructed by computer using combined recombination estimates for all visible markers (Koornneef *et al.*, 1983), mutant genes have more recently been placed on the map by hand using recombination estimates with a more limited set of linked markers (Franzmann *et al.*, 1995). An integrated map that combined data for classical and molecular markers obtained from different mapping populations was published several years ago (Hauge *et al.*, 1993) but proved to be somewhat inaccurate with respect to the order of linked markers in certain regions of the genome.

Several types of molecular markers can be used to map mutants. These include RFLPs (Chang *et al.*, 1988; Nam *et al.*, 1989), RAPDs (Reiter *et al.*, 1992), CAPS (Konieczny and Ausubel, 1993), and SSLPs (Bell and Ecker, 1994). The relative advantages and disadvantages of these different markers have been discussed in many research publications. A collection of RFLP markers designed for efficient mapping of mutants has also been described (Fabri and Schaffner, 1994). In addition, the value of AFLP markers linked to a mutant gene of interest has been discussed in relation to map-based cloning (Cnops *et al.*, 1996; Vos *et al.*, 1995). Our purpose here is not to promote the use of one mapping method over another. Investigators should consider the expertise available within their own laboratories (performing gel-blot hybridizations and PCR amplifications versus scoring the phenotypes of visible markers) and check on materials available at the stock centers before reaching a decision on the most appropriate mapping strategy for their mutants and genes of interest. We hope instead to encourage members of the *Arabidopsis* community to place a greater overall emphasis on mapping both mutant genes and cloned sequences to facilitate the integration of classical and physical maps and to aid in the analysis of gene function. With continued attention to these issues of nomenclature and genetic analysis in the future, it should be possible to maximize the research efforts of plant biologists worldwide and realize the long-term objectives of the *Arabidopsis* genome project.

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