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Arabidopsis Hormone Database: a comprehensive genetic and phenotypic information database for plant hormone research in Arabidopsis

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ABSTRACT

Plant hormones are small organic molecules that influence almost every aspect of plant growth and development. Genetic and molecular studies have revealed a large number of genes that are involved in responses to numerous plant hormones, including auxin, gibberellin, cytokinin, abscisic acid, ethylene, jasmonic acid, salicylic acid, and brassinosteroid. Here, we develop an Arabidopsis hormone database, which aims to provide a systematic and comprehensive view of genes participating in plant hormonal regulation, as well as morphological phenotypes controlled by plant hormones. Based on data from mutant studies, transgenic analysis and gene ontology (GO) annotation, we have identified a total of 1026 genes in the Arabidopsis genome that participate in plant hormone functions. Meanwhile, a phenotype ontology is developed to precisely describe myriad hormone-regulated morphological processes with standardized vocabularies. A web interface (http://ahd.cbi.pku.edu.cn) would allow users to quickly get access to information about these hormone-related genes, including sequences, functional category, mutant information, phenotypic description, microarray data and linked publications. Several applications of this database in studying plant hormonal regulation and hormone cross-talk will be presented and discussed.

INTRODUCTION

Over the past century, extensive physiological and morphological studies have demonstrated that almost every aspect of plant growth and development is regulated by a small set of organic molecules referred to as plant hormones (1,2). In the recent decades, a great effort had been made by using the model plant *Arabidopsis thaliana* to uncover the genetic basis of plant hormonal regulation. Normally, a relatively simple and specific morphological response to a given type of hormone would be used as a screening phenotype to isolate genetic mutations that result in reduced or enhanced sensitivity to such hormone. Dozens of mutants that show altered response to certain type of hormone have been isolated and characterized for

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their involvement in plant hormone actions. As a result, a large number of genes that participate in various plant hormone responses, including hormone biosynthesis, metabolism, transport, perception and signal transduction, have been identified and characterized by means of forward genetic and reverse genetic approaches (3). However, there is so far not a collective database that could provide a systematic and comprehensive description on morphological phenotypes regulated by plant hormones, as well as regulatory genes participating in numerous plant hormone responses.

It has been found that many biological processes are coordinately regulated by multiple hormones. Recent physiological and genetic studies together with the large-scale analyses of microarray data indicated that there exist a wide range of cross-talks among different classes of plant hormones (4). The combination of these signals controls plant growth, development and response to myriad biotic and abiotic stresses in a complex manner (4,5). For example, ethylene and auxin can regulate a number of common processes including primary root elongation, root hair formation, hook formation, leaf epinasty and abscission (6). However, the molecular basis of many cross-talks among different hormones and signals remain poorly understood. It is thus necessary to summarize on how many types of plant hormones and in particularly what genes are involved in each kind of hormone-regulated phenotypes. This collection would certainly be of great help to plant researchers that are interested in deciphering the molecular code underlying those cross-talks among myriad plant hormone actions.

Here, we report a database that collects 1026 Arabidopsis genes related to the actions of eight plant hormones, including auxin (IAA), gibberellin (GA), cytokinin (CK), abscisic acid (ABA), ethylene (ET), jasmonic acid (JA), salicylic acid (SA) and brassinosteroid (BR). The database offers comprehensive information about plant hormone-related genes and plant hormone-regulated morphological processes. Meanwhile, a phenotype ontology is developed to systematically and precisely describe myriad hormone-regulated morphological processes using standardized vocabularies. Users can quickly get access to information about most, if not all, hormone-related genes reported in literatures from the web interface of the Arabidopsis hormone database (AHD) (http://ahd.cbi.pku.edu.cn). This user-friendly website allows searching for hormone-related genes and mutants by names, sequences, free texts, response hormones and mutant phenotypes.

DATABASE CONTENT

Collection of plant hormone-related genes

We have identified Arabidopsis genes related to plant hormone functions (hormone-related genes) by following ways. First, by extensively reviewing literature of more than 330 papers published before August 2008, we collected 302 genes that have been shown to participate in various aspects of hormone functions by genetic evidence (mutant analysis or transgenic over-expression studies). Among them, 282 genes were supported by mutant analysis, 36 genes were derived from transgenic studies (Table 1), and 16 genes were supported by both mutant analysis and transgenic studies. We classified these genes into distinct functional categories, including hormone biosynthesis, hormone transport, hormone metabolism, hormone perception, hormone signal transduction and other aspects of hormone responses (Table 2). Second, we developed a Perl script to extract genes mapped to 72 gene ontology (GO) terms that are related to hormone actions (GO terms are listed in Table S1) from TAIR Arabidopsis gene ontology annotation. We collected totally 923 genes that are implicated in plant hormonal regulation in this manner (Table 1), of which, 199 genes were supported by genetic evidence. Combining the two sources of data together, we identified a total of 1026 Arabidopsis genes related to plant hormone actions (Table 1). This number might change after the database is constantly updated in the future.

Table 1. Hormone-related genes in the AHD

Hormone	No. of genes (supporting evidence)			
	Genetic study		Gene Ontology annotation	All
	Mutant	Transgenic		
Auxin	59	2	323	335
Gibberellin	25	10	146	149
Cytokinin	18	8	72	80
Abscisic acid	78	1	252	289
Ethylene	31	5	156	166
Jasmonic acid	33	7	152	171
Salicylic acid	22	2	116	135
Brassinosteroid	35	2	43	58
ALL hormone	282	36	923	1026

Description of plant hormone-regulated phenotypes

For 302 plant hormone-related genes that have mutant or transgenic plant information, we describe phenotypes of these mutants and transgenic plants by comprehensive literature review.

Integration of expression data of hormone-regulated genes

High-throughput gene expression profiling allows a global analysis of transcriptional regulation in hormone responses. Gene expression arrays have been used to examine the RNA levels of Arabidopsis genes in response to exogenous treatments of a given hormone, or in various hormone-response mutants in Arabidopsis. A large collection of hormone-regulated genes have been identified in a series of published studies and are available to public domain (all references listed in the website). In the AHD, we integrated the expression data of the hormone-regulated genes derived from the supplementary data of numerous published papers. All expression levels of hormone-regulated genes are converted to and presented in log2 ratio to facilitate the comparison. The description of Materials and Methods for the experiments, the calculation of ratio, type of microarray (most of them are AFFYMETRIX chips), URLs of the original data and

Table 2. Functional categories of hormone-related genes

Hormone	Functional categories	No. of all genes[a]
Auxin	Hormone biosynthesis	9
Auxin	Hormone metabolism	3
Auxin	Hormone receptor	4
Auxin	Hormone signal transduction	33
Auxin	Hormone transport	12
Gibberellin	Hormone biosynthesis	15
Gibberellin	Hormone metabolism	2
Gibberellin	Hormone receptor	3
Gibberellin	Hormone signal transduction	9
Cytokinin	Hormone biosynthesis	1
Cytokinin	Hormone metabolism	4
Cytokinin	Hormone receptor	4
Cytokinin	Hormone signal transduction	15
Cytokinin	Hormone transport	2
Abscisic acid	Hormone biosynthesis	9
Abscisic acid	Hormone metabolism	2
Abscisic acid	Hormone receptor	3
Abscisic acid	Hormone signal transduction	65
Abscisic acid	Plant development	2
Ethylene	Hormone biosynthesis	6
Ethylene	Hormone receptor	5
Ethylene	Hormone response	2
Ethylene	Hormone signal transduction	19
Jasmonic acid	Hormone biosynthesis	12
Jasmonic acid	Hormone receptor	1
Jasmonic acid	Hormone signal transduction	24
Salicylic acid	Hormone biosynthesis	1
Salicylic acid	Hormone metabolism	3
Salicylic acid	Hormone signal transduction	18
Salicylic acid	Hormone transport	1
Brassinosteroid	Hormone biosynthesis	12
Brassinosteroid	Hormone metabolism	2
Brassinosteroid	Hormone receptor	3
Brassinosteroid	Hormone signal transduction	18

[a] Genes supported by genetic evidence.

the links to the corresponding papers are enclosed in the general information for each microarray experiment.

WEB INTERFACE

The AHD provides user-friendly interface to display information. The information of hormone-related genes contains four sections (Figure 1). The first section indicates the type of hormone(s) related to the gene. Additional information in this section includes supporting evidence, functional categories, gene description and PubMed ID of the associated references (Figure 1A). The second section describes the basic gene information retrieved from other databases, including locus name, gene description, gene alias, gene model, gene sequences, gene ontology annotation from TAIR version 7 database (7), metabolic pathway annotation from KEGG database (8) and protein–protein interaction (PPI) data (Figure 1B). The third section lists the reported mutants (including transgenic plants) associated with the given gene (Figure 1C). Click on the links to the listed mutants will allow access to their respective phenotypes. The detailed information about the linked mutants is described below. The fourth section displays a graphic view of gene expression data if this gene is differentially regulated by one or multiple types of hormones based on the previously published microarray studies (Figure 1D).

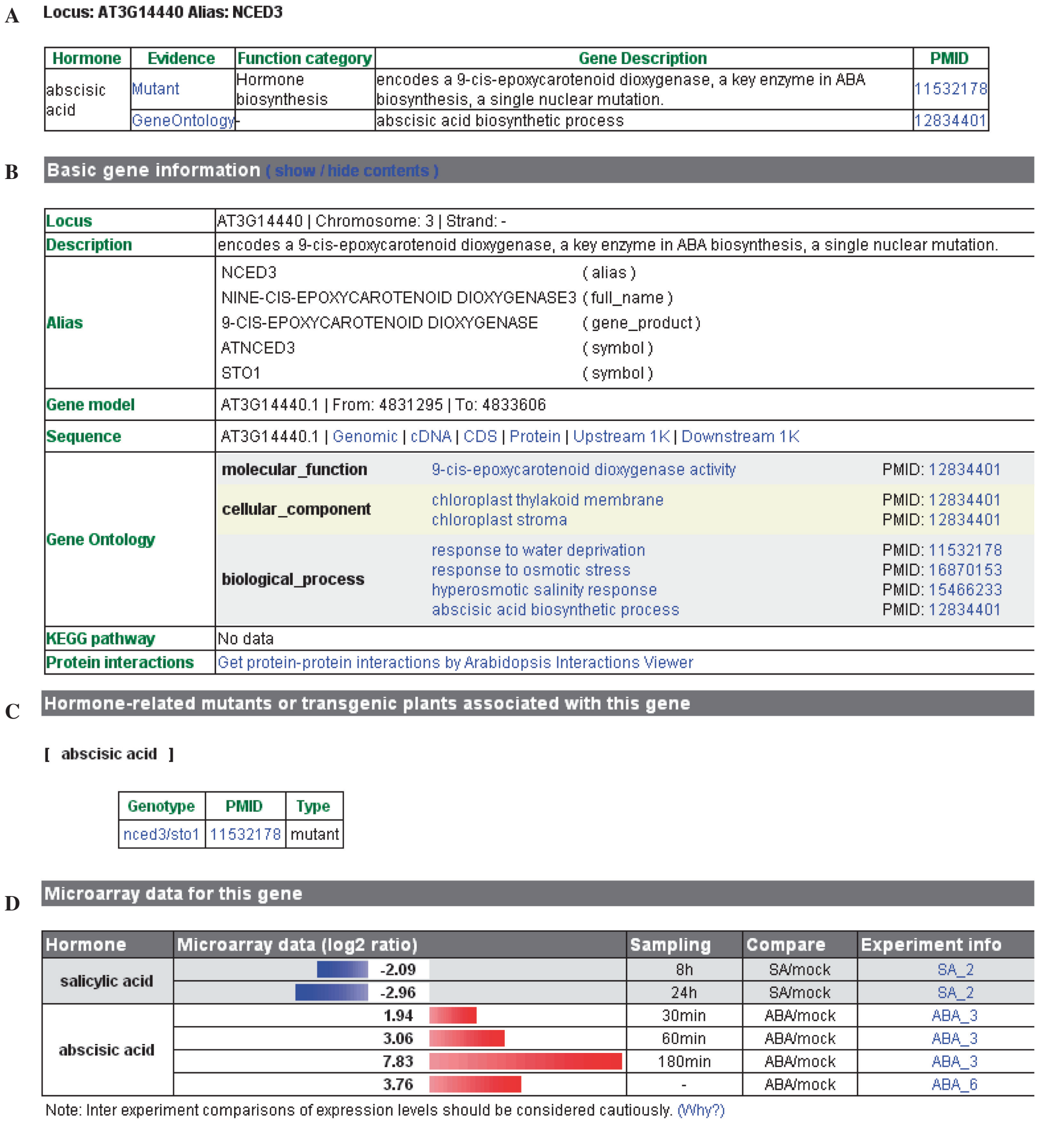
As to the mutant information, each mutant contains three sections: general information, gene(s) associated with the mutant and description of mutant phenotypes (Figure 2). General information includes the mutant's ecotype, mutagenesis type and genetic feature (Figure 2A). The genotype information lists the mutated genes and mutated site for the given mutant (Figure 2B). Click on the links to the genes will allow access to detailed gene information (Figure 1). We have developed a standardized classification system to describe phenotypic traits of mutants identified in plant hormone research (Figure 2C). Phenotypic traits are classified into seven classes: root, cotyledon/leaf, hypocotyl/stem, flower, silique/seed, embryo and stress. These seven classes are further categorized into 63 subclasses (Figure 3). For instance, class 'root' can be further divided into six subclasses: primary root, lateral root, root hairs, agravitropic root, swollen primary roots or lateral roots and other. Most root-related phenotypic traits reported in literatures can be included into the first five subclasses. Occasionally, if the root phenotypic traits are difficult to be classified into any of the above five subclasses, we categorize them into a subclasses designated as 'other' (Figure 3). All phenotypic traits of mutants are described by this standardized classification system.

We have developed powerful search system to help users retrieve information. For gene information, users can search genes by gene name, gene description or responding hormones. We also provide NCBI BLAST to help users to search genes by sequences. For mutant information, users can search mutants by mutant name and hormones. Phenotype search allow users to acquire all mutants that have selected phenotypic traits, as well as genes associated with these mutants. For microarray data, users can search microarray experiments and retrieve expression data by type of hormone treatments and plant organ types. A detailed tutor on how to use the search system is provided on the website (http://ahd.cbi.pku.edu.cn/help).

THE APPLICATION OF AHD

Application of phenotype ontology

Hormone-regulated phenotypes and their associated genes. Although different types of hormones might regulate distinctive aspects of plant growth and developmental processes, a common phenotypic trait could be controlled by multiple hormones (4). To systematically examine the effect of different hormones on any given phenotypic traits, we determine the number of genes and the types of hormones that regulate each subclass of phenotype. Among 60 phenotype subclasses we examined, 51 are regulated by multiple hormones (Table 3). Phenotypic traits that are related to trichome branching, stomata density, nonphototropic hypocotyls, gynoecium protrusion, no embryonic root, embryogenesis stage, cold, drought and osmosis are regulated by a single type of hormone according to literatures (Table 3). Therefore, our analysis support the notion that, although generally considered to



A

Locus: AT3G14440 Alias: NCED3

Hormone	Evidence	Function category	Gene Description	PMID
abscisic acid	Mutant	Hormone biosynthesis	encodes a 9-cis-epoxycarotenoid dioxygenase, a key enzyme in ABA biosynthesis, a single nuclear mutation.	11532178
	GeneOntology	-	abscisic acid biosynthetic process	12834401

B

Basic gene information (show / hide contents)

Locus	AT3G14440 | Chromosome: 3 | Strand: -
Description	encodes a 9-cis-epoxycarotenoid dioxygenase, a key enzyme in ABA biosynthesis, a single nuclear mutation.
Alias	NCED3 (alias) NINE-CIS-EPOXYCAROTENOID DIOXYGENASE3 (full_name) 9-CIS-EPOXYCAROTENOID DIOXYGENASE (gene_product) ATNCED3 (symbol) STO1 (symbol)
Gene model	AT3G14440.1 | From: 4831295 | To: 4833606
Sequence	AT3G14440.1 | Genomic | cDNA | CDS | Protein | Upstream 1K | Downstream 1K
Gene Ontology	**molecular_function**: 9-cis-epoxycarotenoid dioxygenase activity — PMID: 12834401 **cellular_component**: chloroplast thylakoid membrane — PMID: 12834401; chloroplast stroma — PMID: 12834401 **biological_process**: response to water deprivation — PMID: 11532178; response to osmotic stress — PMID: 16870153; hyperosmotic salinity response — PMID: 15466233; abscisic acid biosynthetic process — PMID: 12834401
KEGG pathway	No data
Protein interactions	Get protein-protein interactions by Arabidopsis Interactions Viewer

C

Hormone-related mutants or transgenic plants associated with this gene

[abscisic acid]

Genotype	PMID	Type
nced3/sto1	11532178	mutant

D

Microarray data for this gene

Hormone	Microarray data (log2 ratio)	Sampling	Compare	Experiment info
salicylic acid	-2.09	8h	SA/mock	SA_2
	-2.96	24h	SA/mock	SA_2
abscisic acid	1.94	30min	ABA/mock	ABA_3
	3.06	60min	ABA/mock	ABA_3
	7.83	180min	ABA/mock	ABA_3
	3.76	-	ABA/mock	ABA_6

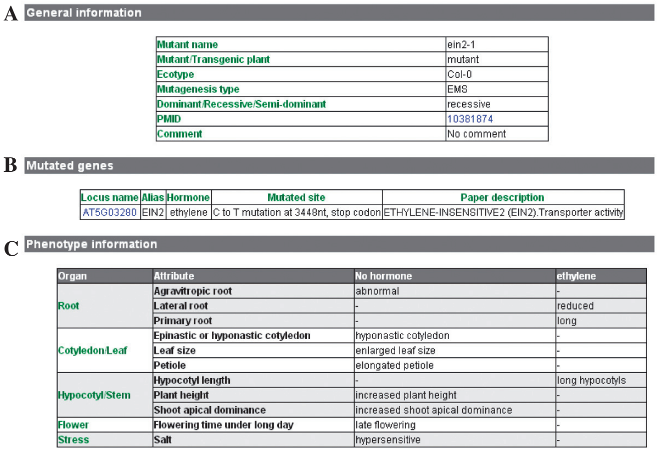
Note: Inter experiment comparisons of expression levels should be considered cautiously. (Why?)

Figure 1. Screenshot of gene information. The information of a hormone-related gene contains four sections, including (**A**) response hormone(s), (**B**) basic gene information retrieved from TAIR and KEGG, (**C**) associated mutants and (**D**) expression data from microarray experiments.

play distinctive roles in regulating various aspects of plant life cycle, different types of hormones also act together to modulate the same biological processes in a complex manner.

In order to determine how different hormones coordinate the regulation of a common phenotypic trait, we further analyzed a phenotypic trait that was reported to be regulated by multiple hormones: primary root elongation. Based on our database search, we have identified 120 mutants that show a longer primary root length than wild type in a normal or hormone-treated condition. These mutants correspond to a total of 63 genes that regulate this phenotype. Among them, 12 genes are related to CK responses, 24 are ET-related genes, 2 are ABA-related, 18 are auxin-related, 11 are JA-related, and 1 is for GA and 1 for BR. To investigate the molecular mechanism of how these genes function coordinately to regulate primary root elongation, we tested whether their encoding products show PPI. Of 63 proteins, 23 can be mapped into protein-protein interaction networks via the web server of the Arabidopsis interactions viewer (http://bar.utoronto.ca/interactions/cgi-bin/arabidopsis_interactions_viewer.cgi). And 17 out of 23 hormone-related proteins are interconnected by direct interactions or through intermediate protein(s) in a single network (Figure 4, Table S2). Interestingly, only three genes are involved in response to multiple hormones, whereas 14 others are related to a single type of hormone. This result implies that different hormones regulate a common process likely by sharing an interconnected regulatory network, but not by the same genes.

Co-regulation of different phenotypes. Based on our database analysis, we found that the majority of phenotypic traits are regulated by a group of genes involved in multiple hormone responses (Table 3). We then surveyed


A General information

Mutant name	ein2-1
Mutant/Transgenic plant	mutant
Ecotype	Col-0
Mutagenesis type	EMS
Dominant/Recessive/Semi-dominant	recessive
PMID	10381874
Comment	No comment

B Mutated genes

Locus name	Alias	Hormone	Mutated site	Paper description
AT5G03280	EIN2	ethylene	C to T mutation at 3448nt, stop codon	ETHYLENE-INSENSITIVE2 (EIN2).Transporter activity

C Phenotype information

Organ	Attribute	No hormone	ethylene
Root	Agravitropic root	abnormal	-
	Lateral root	-	reduced
	Primary root	-	long
Cotyledon/Leaf	Epinastic or hyponastic cotyledon	hyponastic cotyledon	-
	Leaf size	enlarged leaf size	-
	Petiole	elongated petiole	-
Hypocotyl/Stem	Hypocotyl length	-	long hypocotyls
	Plant height	increased plant height	-
	Shoot apical dominance	increased shoot apical dominance	-
Flower	Flowering time under long day	late flowering	-
Stress	Salt	hypersensitive	-

Figure 2. Screenshot of mutant information. The information of a mutant consists of three sections, including (**A**) general information, (**B**) genes corresponding to the mutant and (**C**) mutant phenotype information.

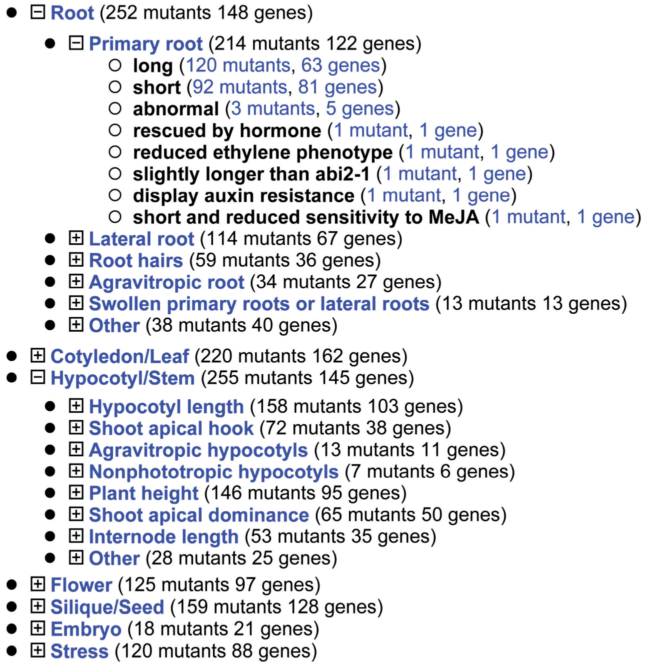

- ⊟ Root (252 mutants 148 genes)
  - ⊟ Primary root (214 mutants 122 genes)
    - ○ **long** (120 mutants, 63 genes)
    - ○ **short** (92 mutants, 81 genes)
    - ○ **abnormal** (3 mutants, 5 genes)
    - ○ **rescued by hormone** (1 mutant, 1 gene)
    - ○ **reduced ethylene phenotype** (1 mutant, 1 gene)
    - ○ **slightly longer than abi2-1** (1 mutant, 1 gene)
    - ○ **display auxin resistance** (1 mutant, 1 gene)
    - ○ **short and reduced sensitivity to MeJA** (1 mutant, 1 gene)
  - ⊞ Lateral root (114 mutants 67 genes)
  - ⊞ Root hairs (59 mutants 36 genes)
  - ⊞ Agravitropic root (34 mutants 27 genes)
  - ⊞ Swollen primary roots or lateral roots (13 mutants 13 genes)
  - ⊞ Other (38 mutants 40 genes)
- ⊞ Cotyledon/Leaf (220 mutants 162 genes)
- ⊟ Hypocotyl/Stem (255 mutants 145 genes)
  - ⊞ Hypocotyl length (158 mutants 103 genes)
  - ⊞ Shoot apical hook (72 mutants 38 genes)
  - ⊞ Agravitropic hypocotyls (13 mutants 11 genes)
  - ⊞ Nonphototropic hypocotyls (7 mutants 6 genes)
  - ⊞ Plant height (146 mutants 95 genes)
  - ⊞ Shoot apical dominance (65 mutants 50 genes)
  - ⊞ Internode length (53 mutants 35 genes)
  - ⊞ Other (28 mutants 25 genes)
- ⊞ Flower (125 mutants 97 genes)
- ⊞ Silique/Seed (159 mutants 128 genes)
- ⊞ Embryo (18 mutants 21 genes)
- ⊞ Stress (120 mutants 88 genes)

Figure 3. Screenshot of phenotype ontology. The phenotype ontology consists of 7 major classes and 63 subclasses. Each phenotype can be classified into a provided subclass. Mutants with a given phenotype and genes associated with those mutants can be accessed through the hyperlinks in phenotype ontology.

whether different phenotypes could be regulated by the same group of genes. We have identified 406 pairs of phenotypic traits, in which over 80% of associated genes in one trait are shared by the other trait (Table S3). For example, 12 genes have been shown to regulate swollen primary roots. Of the 12 genes, we found that all 12 genes regulate small leaves, 11 genes regulate primary root length and shortened petiole, 10 genes regulate either reduced plant height, short hypocotyls, dark green leaf, rounded leaves, more root hairs or reduced lateral root, respectively (Figure 5). This result demonstrates that some phenotypic traits are highly related, suggesting that these correlated phenotypes might be physiologically or ecologically interconnected, or share the same origin in the evolution course.

Hormone-related genes involved in multiple hormone functions

One mechanism of hormone cross-talks is to share key regulatory components in multiple hormone response pathways. We found that almost any two types of hormones share more or less regulatory genes, except for BR and JA, BR and SA, and CK and JA (Table S4). We then explored how many hormone-related genes are involved in multiple hormone responses. Of the total 1026 hormone-related genes supported by either genetic evidence or GO annotation evidence, we found that ~17% of them participate in the function of more than one type of hormones (Figure S1, Table S5). At the extreme situation, we found 21 genes that can respond to six hormones. Interestingly, all 21 genes encode transcription factors, 10 for MYB proteins and 11 for MYB-related proteins, suggesting that transcriptional regulation might be the key integration points in plant hormonal interactions.

DISCUSSION

The AHD integrates a large volume of literature data based on mutant studies, transgenic analysis, gene ontology annotation and microarray studies. A pronounced characteristic of this database is that we have developed a new set of standardized vocabularies to describe the phenotypic traits of a comprehensive collection of mutants identified in plant hormone research. It is easy to search for mutants and genes related to any given phenotype from this phenotype ontology. To date, several databases for Arabidopsis mutants are available (9–12), among which three databases have no mutant phenotype description (9,11,12) and one developed its own phenotypic classification system (10). In comparison with previously developed databases, the AHD phenotype ontology system has several distinctions and virtues: first, this system concentrates on Arabidopsis hormone-related mutants, and such a database had not been developed before. Second, this system integrates phenotypic traits derived from a large number of published studies supported by sound genetic evidence. Third, this system contains a more complete list of phenotype subclasses, and describes phenotypic traits in more details for hormone-related mutants compared with other databases (10).

To our knowledge, this database represents the first effort to systematically collect a wide range of published results, and contains the most comprehensive information on both hormone-related phenotypes and Arabidopsis genes regulating these phenotypes. Users can quickly get access to information about most, if not all, genes reported in literatures that regulate a given hormone function, including gene sequences, functional category, mutant information, phenotypic description, microarray data and linked publications. The phenotype ontology database provides a novel route to study plant hormone actions and interactions. It has been shown that many biological processes are regulated by multiple hormones that interplay in different ways, although the molecular basis of such interactions is not known. By use of this AHD database, we have conducted analyses on the interaction among multiple hormone pathways in regulating primary root elongation. Our analysis suggests that different phytohormones control this common trait probably by

Table 3. The summary of hormone-regulated phenotypes

Phenotypic traits	No. of gene	No. of hormone	List of hormone
Root	148	**7**	IAA, GA, CK, ABA, ET, JA, BR
Primary root	122	7	IAA, GA, CK, ABA, ET, JA, BR
Lateral root	67	6	IAA, CK, ABA, ET, JA, BR
Root hairs	36	6	IAA, CK, ABA, ET, JA, BR
Agravitropic root	27	5	IAA, ABA, ET, JA, BR
Swollen primary roots or lateral roots	13	4	IAA, ET, JA, BR
Cotyledon/Leaf	162	8	IAA, GA, CK, ABA, ET, JA, SA, BR
Cotyledon number	11	5	IAA, GA, ABA, ET, JA
Epinastic or hyponastic cotyledon	28	5	IAA, CK, ABA, ET, BR
Vasculature pattern	26	5	IAA, ABA, ET, JA, BR
Leaf size	83	8	IAA, GA, CK, ABA, ET, JA, SA, BR
Rumpled or serrated leaves	29	5	IAA, ABA, ET, JA, BR
Hyponastic or epinastic leaves	41	6	IAA, GA, ABA, ET, JA, BR
Rounded or narrow leaves	46	5	IAA, ABA, ET, JA, BR
Trichome branching	1	1	GA
Stomata aperture	24	3	ABA, ET, BR
Stomata density	1	1	ABA
Leaf senescence	13	4	CK, ABA, ET, BR
Leaf color	63	7	IAA, GA, CK, ABA, ET, JA, BR
Petiole	52	7	IAA, GA, CK, ABA, ET, JA, BR
Leaf growth in dark	7	4	IAA, ABA, ET, BR
Hypocotyl/stem	145	7	IAA, GA, CK, ABA, ET, JA, BR
Hypocotyl length	103	7	IAA, GA, CK, ABA, ET, JA, BR
Shoot apical hook	38	5	IAA, GA, ABA, ET, BR
Agravitropic hypocotyls	11	2	IAA, ABA
Nonphototropic hypocotyls	6	1	IAA
Plant height	95	7	IAA, GA, CK, ABA, ET, JA, BR
Shoot apical dominance	50	7	IAA, GA, CK, ABA, ET, JA, BR
Internode length	35	7	IAA, GA, CK, ABA, ET, JA, BR
Flower	97	7	IAA, GA, CK, ABA, ET, JA, BR
Flowering time under long day	30	7	IAA, GA, CK, ABA, ET, JA, BR
Flowering time under short day	13	2	GA, ABA
Flower size	16	5	IAA, ABA, ET, JA, BR
Sepal	15	4	IAA, ET, JA, BR
Petal	16	4	IAA, ET, JA, BR
Stamen	26	6	IAA, GA, ABA, ET, JA, BR
Carpel	13	5	IAA, GA, ET, JA, BR
Gynoecium protrusion	2	1	IAA
Anther development	20	5	IAA, ABA, ET, JA, BR
Pollen development	24	6	IAA, GA, ABA, ET, JA, BR
Fertility	71	7	IAA, GA, CK, ABA, ET, JA, BR
Silique/Seed	128	7	IAA, GA, CK, ABA, ET, JA, BR
Silique length	44	6	IAA, GA, ABA, ET, JA,BR
Silique shape	10	4	IAA, ABA, ET, BR
Germination rate	67	5	IAA, GA, ABA, ET, JA
Loss of seed dormancy	21	4	GA, CK, ABA, BR
Seed yield	45	6	IAA, GA, ABA, ET, JA, BR
Seed size	5	4	IAA, CK, JA, BR
Seed shape	3	2	ABA, JA
Embryo	21	6	IAA, GA, ABA, ET, JA, BR
Defective embryo development	15	4	IAA, ABA, JA, BR
No embryonic root	9	1	IAA
Embryo lethality	8	2	IAA, ABA
Embryogenesis stage	2	1	IAA
Stress response	88	6	IAA, GA, ABA, ET, JA
Salt	23	3	GA, ABA, ET
Cold	3	1	ABA
Drought	12	1	ABA
Pathogen	38	3	ET, JA
Osmosis	13	1	ABA

sharing a physically interconnected regulatory network, but not by sharing the same genes. We have discovered that certain groups of phenotypes are highly related due to the large overlap of their regulatory genes. We have also identified a class of multiple-hormone responsive MYB and MYB-like transcription factors that might mediate responses to as many as six hormones. These analyses demonstrate that our database is valuable in unraveling molecular mechanisms of plant hormone cross-talks in regulating various biological processes.

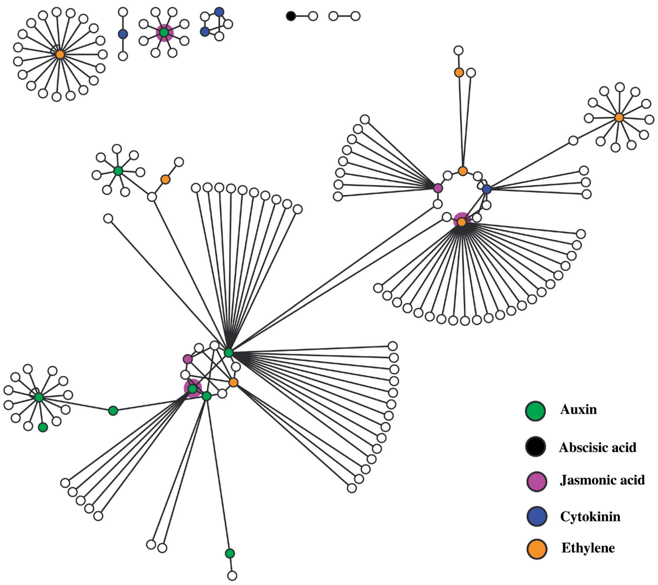


Figure 4. PPI network of genes involved in regulating primary root length. The circles represent proteins and the lines indicate PPIs. The colored circles represent hormone-related proteins when mutated would cause a longer primary root phenotype. Different colors indicate different hormone classes. The uncolored circles represent proteins that show direct interaction with hormone-related proteins.

Our database aims at providing a comprehensive and standardized resource for Arabidopsis hormone research. Each type of hormone has one or two experts to curate the database in a user-compatible manner, and to update the information in a timely manner. It is our belief that the database will benefit plant hormone researchers all over the world. Users can also help to improve the database via our interactive platform (http://ahd.cbi.pku.edu.cn/help.php). All useful information and comments will be properly considered and quickly integrated into the database by corresponding curators for each hormone.

SUPPLEMENTARY DATA

Supplementary Data are available at NAR Online.

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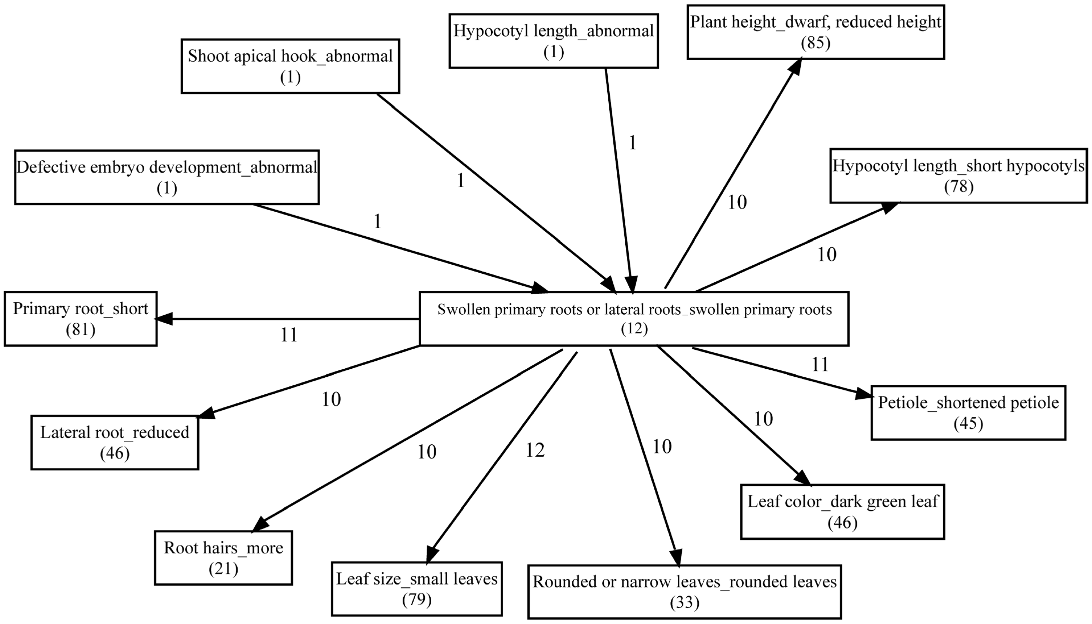

Figure 5. Overlap of regulatory genes among different phenotypes. Each rectangle represents a phenotype. The number of genes regulating that phenotype is shown in parenthesis. The number on the arrow, which arrowhead points to the large geneset and arrowend points to the small geneset, represents the overlap of genes regulating two different phenotypes.

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