

RiceXPro Version 3.0: expanding the informatics resource for rice transcriptome

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ABSTRACT

A wide range of resources on gene expression profiling enhance various strategies in plant molecular biology particularly in characterization of gene function. We have updated our gene expression profile database, RiceXPro (<http://ricexpro.dna.affrc.go.jp/>), to provide more comprehensive information on the transcriptome of rice encompassing the entire growth cycle and various experimental conditions. The gene expression profiles are currently grouped into three categories, namely, 'field/development' with 572 data corresponding to 12 data sets, 'plant hormone' with 143 data corresponding to 13 data sets and 'cell- and tissue-type' comprising of 38 microarray data. In addition to the interface for retrieving expression information of a gene/genes in each data set, we have incorporated an interface for a global approach in searching an overall view of the gene expression profiles from multiple data sets within each category. Furthermore, we have also added a BLAST search function that enables users to explore expression profile of a gene/genes with similarity to a query sequence. Therefore, the updated version of RiceXPro can be used more efficiently to survey the gene expression signature of rice in sufficient depth and may also provide clues on gene function of other cereal crops.

INTRODUCTION

Elucidating the function of all predicted genes in the rice genome is an ultimate goal not only for basic research in plant molecular biology but also for applied aspects of

genomics to accelerate the improvement of rice that serves as staple food for almost half of the world's population. The major achievements in elucidating a high-quality genome sequence (1) have been complemented with worldwide initiatives to develop various infrastructures for characterizing the function of rice genes (2–10). However, despite these extensive efforts, more than half of ~32 000 predicted genes in the rice genome are still classified either as hypothetical or unknown genes because no function has been assigned to their protein products. So far, only ~600 genes had been fully characterized by map-based cloning and other strategies (11,12).

Information on the specificity of gene expression in terms of organ/tissue and developmental stage that can be obtained by comprehensive gene expression profiling may lead to a thorough understanding of gene function. In rice, large-scale gene expression profiling covering different organs, tissues and cell types at various developmental stages have been reported (13–15). The rapid accumulation of rice microarray data in public repositories such as NCBI's Gene Expression Omnibus (GEO) (16,17), EBI Array Express (18) and DDBJ CIBEX (19) also led to the development of informatics resources and analysis tools for integrating and extracting useful information on gene expression (20–23). The Rice Oligonucleotide Array Database (ROAD) contains 1867 microarray data available in the public domain and provides functional analysis tools (20). The OryzaExpress features gene expression information integrated with omics data from public databases (21). The rice component of the PlantArrayNet is basically designed for retrieving gene co-expression information in rice (22).

Our database, RiceXPro, was initially conceptualized with the aim of providing a platform for monitoring gene expression of the rice plant under the natural field

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Table 1. Microarray data in RiceXPro Version 3.0

Category	Data set ID	Microarray analysis	No. of data	Description
Field/development	RXP_0001	One color	143	Spatio-temporal gene expression of various tissues/organs throughout entire growth in the field
	RXP_0002	One color	200	Diurnal and circadian gene expression profile of leaf throughout entire growth
	RXP_0003	One color	51	Leaf gene expression profile throughout entire growth in the field (12:00)
	RXP_0004	One color	34	Leaf gene expression profile throughout entire growth in the field (24:00)
	RXP_0005	One color	28	Leaf gene expression profile during sunrise
	RXP_0006	One color	19	Leaf gene expression profile during sunset
	RXP_0007	One color	14	Root gene expression profile throughout entire growth in the field (12:00)
	RXP_0008	One color	14	Root gene expression profile throughout entire growth in the field (24:00)
	RXP_0009	One color	50	Diurnal and circadian gene expression profile of root
	RXP_0010	One color	54	Gene expression profile during reproductive organ development
	RXP_0011	One color	34	Grain gene expression profile at early developmental stage
	RXP_0012	One color	36	Embryo and endosperm gene expression profile at ripening stage
Plant hormone	RXP_1000	Two color	138	Global gene expression profile in response to plant hormone
	RXP_1001	Two color	18	Root gene expression profile in response to abscisic acid
	RXP_1002	Two color	18	Root gene expression profile in response to gibberellin
	RXP_1003	Two color	18	Root gene expression profile in response to auxin
	RXP_1004	Two color	18	Root gene expression profile in response to brassinosteroid
	RXP_1005	Two color	18	Root gene expression profile in response to cytokinin
	RXP_1006	Two color	10	Shoot gene expression profile in response to abscisic acid
	RXP_1007	Two color	10	Shoot gene expression profile in response to gibberellin
	RXP_1008	Two color	10	Shoot gene expression profile in response to auxin
	RXP_1009	Two color	10	Shoot gene expression profile in response to brassinosteroid
	RXP_1010	Two color	10	Shoot gene expression profile in response to cytokinin
	RXP_1011	Two color	18	Root gene expression profile in response to jasmonic acid
RXP_1012	Two color	10	Shoot gene expression profile in response to jasmonic acid	
Cell and tissue type	RXP_4001	One color	38	Root gene expression profile covering various developmental stages and tissue types

conditions (24). The first release (version 1.5) originally contained two data sets in the field/development category corresponding to spatio-temporal gene expression profiling based on 48 different tissues and organs at various developmental stages (RXP_0001) and continuous profiling of mature leaves from transplanting until harvesting (RXP_0003) (Table 1, Figure 1). As a minor update (version 1.6), we added a data set on root gene expression profile (RXP_4001) obtained via a combined laser microdissection and microarray approaches (25) and created a data category for 'cell- and tissue-type' to distinguish from the two data sets, which were derived from samples grown in the field. The previous versions of RiceXPro included user-friendly interfaces for searching and viewing gene expression profiles, analysis tools and construction of heat maps.

Here, we describe an updated version of RiceXPro (version 3.0) with the expansion of data on field transcriptome, addition of microarray data on plant hormone treatment and categorical grouping of data sets for more efficient browsing of expression data. Major improvements in search options include a global search approach to get an overall view of expression profile in each data category, search for expression profile within a specific region of the chromosome and a Basic Local Alignment Search Tool (BLAST)-based gene expression similarity search that can be useful for other cereal crops.

UPDATED DATABASE CONTENTS

We have added a total of 530 microarray data representing 23 data sets (Figure 1). All data have been deposited in

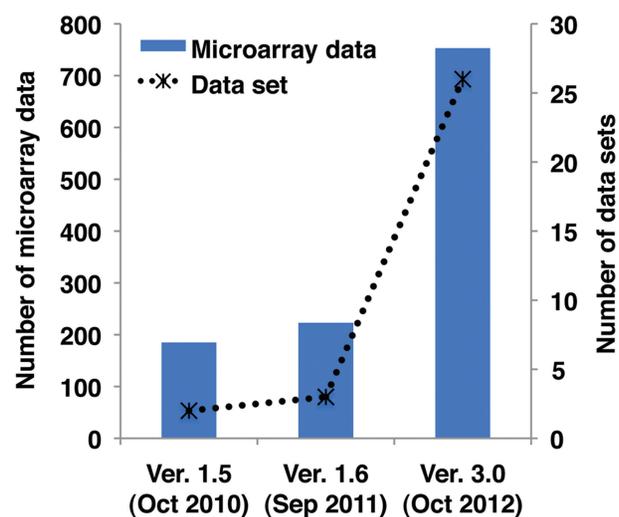


Figure 1. Microarray data and data sets in previous and current versions of RiceXPro.

NCBI's GEO (16,17), and accessible through GEO series accession numbers GSE36040, GSE36042, GSE36043, GSE36044, GSE39423, GSE39424, GSE39425, GSE39426, GSE39427, GSE39429 and GSE39432. The RiceXPro Version 3.0 currently contains a total of 753 microarray data representing 26 data sets grouped into three categories, namely, 'field/development', 'plant hormone' and 'cell- and tissue-type'. Table 1 provides a list of data sets in each category. Other features of each data set such as search options, data type, graph format,

analysis tools and download options are summarized in Supplementary Table S1. All data were generated using a single microarray platform (Rice 4x44K RAP-DB microarray; Agilent Technology).

Field/development category

The first version of RiceXPro consisted of data on spatio-temporal gene expression profiles of tissues/organs (RXP_0001) and leaf expression profiles throughout the entire growth (RXP_0003). With the 10 new data sets, the 'field/development' category currently contains a wide range of gene expression data encompassing the entire growth cycle under natural field conditions and more detailed time course data at various stages of development. All data were obtained during the 2008 cultivation season. Some microarray data are included in two or more data sets to provide sufficient interpretation of expression data. For example, 44 microarray data in RXP_0001 are also included in RXP_0010. Although RXP_0001 basically provides information on organ and tissue specificity in gene expression throughout entire growth, RXP_0010 focuses mainly on reproductive organ development, thereby allowing users to select a data set representing appropriate biological process of interest. RXP_0002 is the largest data set with a total of 200 microarray data corresponding to the uppermost fully expanded leaves in a 48-h period at 2-h intervals from eight different growth stages. Therefore, this data set could be useful for elucidating not only the growth stage specificity but also the diurnal rhythmic pattern of gene expression throughout the entire growth in the field. RXP_0004 represents gene expression profile of the leaf at night-time (12 midnight) based on samples collected at weekly interval from 14 to 126 days after transplanting (DAT). We have also incorporated data sets to characterize the gene expression in response to gradual changes of light intensity in the field. These data sets represent leaf samples collected at 10-min interval during sunrise (RXP_0005) and sunset (RXP_0006). We have three data sets focusing on gene expression of root throughout entire growth at daytime (RXP_0007), night-time (RXP_0008) and diurnal rhythm at 2-h interval (RXP_0009). The two data sets focusing on seed development (RXP_0011 and RXP_0012) could be useful in elucidating the molecular mechanisms during the seed development. Taken together, the gene expression data in the 'field/development' category of RiceXPro provide baseline information underlying various biological processes throughout entire growth of rice under natural field conditions.

Plant hormone category

In addition to the gene expression data of rice under natural field conditions, we performed microarray analysis of rice plants treated with different plant hormones. The newly added data in RiceXPro include 12 data sets (RXP_1001~RXP_1012) representing gene expression profiles of shoot and root in response to six plant hormones, namely, abscisic acid, gibberellin, auxin, brassinosteroid, cytokinin and jasmonic acid (Table 1). These data were collected from 7-day-old seedlings and

included root samples collected at 15 min, 30 min, 1 h, 3 h and 6 h of incubation and shoot samples collected at 1, 3, 6 and 12 h of incubation after hormone treatment. Root and shoot samples from untreated seedlings were used as control (mock treatment). The gene expression data were generated using a two-color microarray system with the treated samples labeled with Cy5 and the untreated control labeled with Cy3. The time course expression profile for each gene is shown as the log-ratio of signal intensity ($\text{Log}_2 \text{Cy5/Cy3}$) (line graph) and Cy3 and Cy5 signal intensity (bar graph). To provide a general view of the expression signature in response to various plant hormones, all microarray data for plant hormone treatment (total of 138 data) were integrated into a single data set (RXP_1000). To our knowledge, although a number of genes related to plant hormone metabolism and signaling control agronomically important traits that determine crop yield (26–30), comprehensive gene expression profiles in response to plant hormones had not been available in rice. Therefore, our gene expression profiles on the response to various plant hormones can provide further insights in understanding gene expression signature in combination with profiles in the field/development category.

GLOBAL VIEW OF GENE EXPRESSION PROFILE

In addition to the gene expression search that can be initiated from the interface for each data set, we incorporated a 'Global Profile' search option to provide an overall view of the gene expression in each data category. The users can now access gene expression data from two entry points in the top page indicated by respective panels for 'Data Sets' and 'Global Profile'. The data set approach facilitates in-depth retrieval of the expression information of a gene/genes within a data set using keyword search, chromosome search, analysis tools and/or heat map option as previously reported (24). However, this approach requires the user to browse each data set for viewing the gene expression under different conditions. On the other hand, the global approach provides the users with a quick overall view of all the gene expression information among all the data sets within a category as summarized in a single web page.

From the 'Global Profile' link, users can currently view the overall gene expression profiles from the 'field/development' and 'plant hormone' categories. The keyword and chromosome search options provide a tabular list of the gene/genes with RAP-DB locus ID (RAP ID), feature number representing the ID number of the probes in the Agilent microarray platform, accession number, probe sequence identifier, gene description and MSU Osal Rice Loci (MSU-ID). The feature number provides the link to the interface with image icons for identification of data sets in each category (Figure 2A). With mouseover on an image icon, a pop-up window opens with an overview of the expression profile for each gene in a data set. The 'sample image' icon and accompanying 'data image' icon also serve as links to the gene expression profile in graph format and the search page of each data

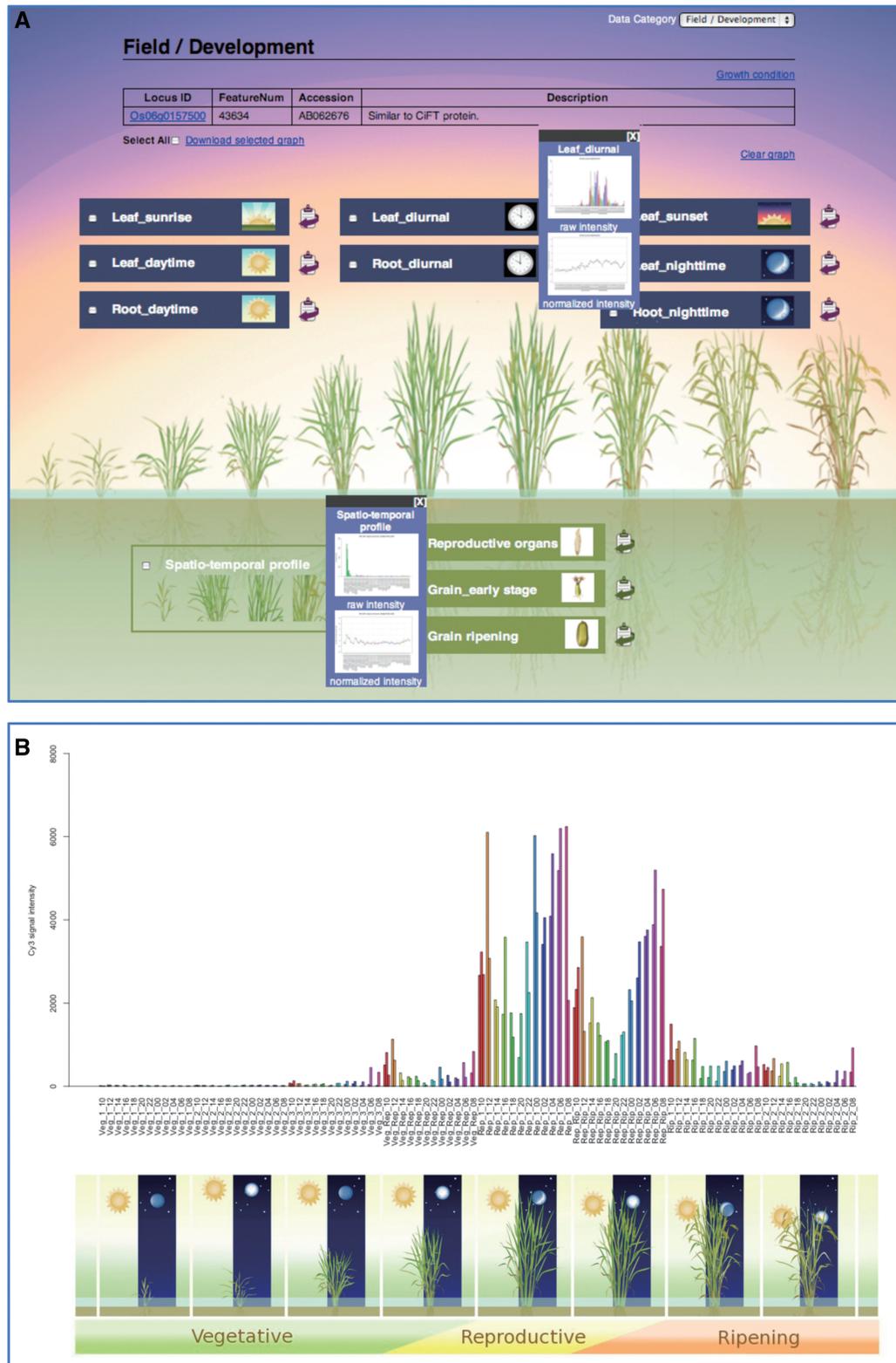


Figure 2. Global profile approach for access to expression data of a gene in multiple data sets. (A) Interface for field/development category in global profile approach. The users can view overall expression profile of a gene within the category from the pop-up windows. The expression profiles of the rice florigen gene, *RFT1* (Os06g0157500), in two data sets (RXP_0001 and RXP_0002) are shown in the pop-up windows. Graphical data of gene expression profile is accessible by clicking the image icon. (B) The bar graph representing raw signal intensity of *RFT1* in a time course sampling at 2-h intervals for 48 h at eight different growth stages (RXP_0002).

set, respectively (Figure 2B). The interface for global profile of the gene provides link to other databases, namely, Rice TOGO Browser (31), RAP-DB (5) and SALAD database (32), via the locus ID, download option for selected graph(s) and switching option to other data category.

As an example, the global expression profile of *RFT1* (Os06g0157500), a rice ortholog of *Arabidopsis* florigen gene *FLOWERING LOCUS T (FT)*, in the field/development category is shown in Figure 2A. The RFT1 protein synthesized in the leaf blade is transported to the shoot apical meristem and functions as a florigen in long-day condition (33). Based on the spatio-temporal profile (RXP_0001), *RFT1* is expressed specifically in the leaf blade at the reproductive stage. The leaf diurnal profile (RXP_0002) provides further insight into the expression signature of this florigen gene (Figure 2B). In particular, this data set shows that *RFT1* was induced just before reproductive transition, then increased during the reproductive stage and eventually decreased during the ripening stage. The peak of expression was recorded at dawn (around 6:00 AM). Therefore, the global profile approach would help researchers to efficiently explore gene expression profile in a wide range of conditions.

IMPROVEMENT OF SEARCH OPTIONS AND VIEWER

We have added several features in the updated version of RiceXPro to further improve the search functions and gene expression viewers. Furthermore, we have incorporated a homology search option that will allow researchers of other cereal crops to explore the gene expression data in our database.

Region search

The information of position and time specificity on gene expression would enhance map-based cloning in forward genetics strategy. Therefore, in addition to chromosome search, we incorporated search option that would allow the user to characterize gene expression of all the genes in a specific region of the genome. This region search function is initiated by entering the two loci flanking a desired region of the chromosome. A list of genes within the region is generated with links to the expression profiles and other information. This function is available in the search options for both global profile and individual data sets.

Gene expression profile viewer

In any interface for expression profile in graph format, the users can view the graphs in either a scroll mode or a tab mode. Although all signal intensity data can be accessed from the GEO link, we have also provided a link for viewing the raw and normalized signal intensity via 'View plot data' link in any page providing gene expression profile in graph format.

BLAST-based expression search

The comprehensive gene expression profile of rice could be useful for researchers of other cereal crops such as wheat, barley and maize. We have incorporated a sequence similarity search, which we named EXP_BLAST, to explore expression profile of a gene/genes with similarity to a query sequence. This search function allows users to extract a gene/genes by BLAST search options (34,35), namely, blastn, tblastn and tblastx against coding sequence of genes with probes in the Rice 4x44K Microarray platform (Figure 3). The search result includes a list of a gene/genes with similarity to the query sequence with the locus ID, description, score, and *e*-value. Details of the search result for each gene, including alignment information, can be viewed from locus ID. The users can access expression profile of selected gene(s) via global profile approach. The example shown in Figure 3 represents the search result generated using the amino acid alignment of wheat *NAM-B1*, a QTL gene involved in accelerating senescence and increasing nutrient remobilization from leaves to developing grains (36), as a query sequence. A more detailed survey of the expression data in RXP_0002 and RXP_0003 confirms that the expression of Os07g0566500, the top hit gene in EXP_BLAST search, is observed specifically in leaves during senescence.

CONCLUSION

The technical protocols for microarray technology have become more standardized and reproducible. This allowed us to perform extensive transcriptome analyses on various aspects of rice growth and development and incorporate the high-quality gene expression information in RiceXPro. Furthermore, as we collected all data in our laboratory using a single microarray system, the gene expression data would be more uniform in all experiments. This provides an opportunity to compare gene expression data across different tissues/organs, different growth stages and different experimental conditions with high reliability.

Growth and development of the rice plant in the field, a much more complex environment than laboratory conditions, is accompanied with various changes in physiological and morphological state of the plant triggered by internal or external stimuli. The transcriptome could be used as an index for monitoring the changes in many biological processes. It is therefore worth understanding the global configuration and complexity of the transcriptome that underlies physiological changes throughout the entire growth in the field to develop strategies for crop improvement. As a major update, we have incorporated a large collection of gene expression profiles of the rice plant from transplanting until harvesting. Therefore, the updated RiceXPro could provide more valuable insights into gene expression networks involved in many biological events throughout growth under natural field conditions that may eventually provide clues for understanding many agronomic traits in rice.

Go to keyword search

Locus	Description	Score(bits)	E value
<input checked="" type="checkbox"/> Os07g0566500	Similar to NAC domain protein.	405	e-113
<input type="checkbox"/> Os01g0816100	Similar to NAC domain protein.	231	7e-61
<input type="checkbox"/> Os03g0815100	Similar to OsNAC6 protein.	225	3e-59
<input type="checkbox"/> Os11g0184900	Similar to NAC-domain protein 5-7.	224	6e-59
<input type="checkbox"/> Os01g0884300	No apical meristem (NAM) protein domain containing protein.	224	7e-59
<input type="checkbox"/> Os03g0327800	No apical meristem (NAM) protein domain containing protein.	221	4e-58
<input type="checkbox"/> Os11g0126900	Similar to NAC domain transcription factor.	218	3e-57
<input type="checkbox"/> Os12g0123700	No apical meristem (NAM) protein domain containing protein.	217	7e-57
<input type="checkbox"/> Os07g0225300	OsNAC3 protein.	215	4e-56
<input type="checkbox"/> Os05g0415400	Similar to OsNAC6 protein.	205	3e-53
<input type="checkbox"/> Os01g0104200	No apical meristem (NAM) protein domain containing protein.	203	1e-52
<input type="checkbox"/> Os08g0436700	Similar to NAC transcription factor.	194	6e-50
<input type="checkbox"/> Os09g0497900	No apical meristem (NAM) protein domain containing protein.	181	7e-46
<input type="checkbox"/> Os03g0624600	No apical meristem (NAM) protein domain containing protein.	180	9e-46
<input type="checkbox"/> Os02g0579000	No apical meristem (NAM) protein domain containing protein.	180	1e-45
<input type="checkbox"/> Os04g0460600	Similar to NAM / CUC2-like protein.	177	6e-45
<input type="checkbox"/> Os06g0344900	Similar to NAM / CUC2-like protein.	177	8e-45

>Os07g0566500
Length = 1278

Score = 405 bits (1041), Expect = e-113, Method: Compositional matrix adjust.
Identities = 232/412 (56%), Positives = 260/412 (63%), Gaps = 36/412 (8%)
Frame = +1

Query: 29 GSAPELPPGFRFHPTDEELVVHYLKKKADKAPLPVNIIEVDLYKFDPWELPEKATIGEQ 88
GSAPELPPGFRFHPTDEELVVHYLKKKA PLPV IIEVDLYKFDPW+LPEKA GEQ
Sbjct: 70 GSAPELPPGFRFHPTDEELVVHYLKKKAASVPLPVTIIIEVDLYKFDPWDLPEKANFGEQ 249

Query: 89 EWYFFSPDRKYPNGARPNRAATSGYWKATGTDKPIILASGTGCGLVREKLGVKKALVFYR 148
EWYFFSPDRKYPNGARPNRAATSGYWKATGTDKPI++SG+ REK+GVKKALVFYR
Sbjct: 250 EWYFFSPDRKYPNGARPNRAATSGYWKATGTDKPISSGS----TREKVGKALVFYR 417

Query: 149 GKPPKGLKTNWIMHEYRLTDASGS--TTATNR--PPPVTGGSRAAASLRLLDDWVLCRIYK 204
GKPPKGLKTNWIMHEYRLTD S S AT R PPP+TGGS+ A SRLRDDWVLCRIYK
Sbjct: 418 GKPPKGLKTNWIMHEYRLTDTSSSAAAVATRRPPPIITGGSGAVSLRLDDWVLCRIYK 597

Query: 205 KINKAAAGDQQRNTECEDSVEDAVTAYPLYXXXXXXXXXXXXXXXXXSYAS-----PS 253
K NKA AG QR+ ECEDSVEDAV AY + + S
Sbjct: 598 KTNKAGAG--QRSMECEDSVEDAVAAAPSSQQHATAAAGMAGSDGAGGVAHAHGGDYSS 771

Query: 254 LLH---HQDSHFLDGLFTADDXXXXXXXXXXXXXXXXXXXXXXXXX---XKKQFLAPSSSTP 306
LLH H+D+ ++GL TA+D KQ LAP S TP
Sbjct: 772 LLHDSHEDFTLVNGLLTAEDAAGLSTGASSLSQLAAAAAATPCDATKQLLAP-SPTP 948

Query: 307 FNWLDASPVGILPQARNFP--GFNR--SRNVGNMSLSSTXXXXXXXXXXXXXXXXXSTY-- 362
FNW +A LP+A+ FP G +R SR++G+MSLSST +
Sbjct: 949 FNWFEA---FLPRAKEFPSSGSRSDIGDMSLSSTVDRSLSEAGAVAITGDAANGAN 1116

Query: 363 -----LPVQDGTYHQHVLGAPLVPEA--AAATSGFQHPVQISGVNWN 404
L VQ TY Q I+GA L E+ AAA FQHP Q+S VNW+
Sbjct: 1117TMPAFINPLGVQATYQQHQAIMGASLPSESAAAAAACNFQHPQLSRVNW 1272

Figure 3. Interface for EXP_BLAST search using amino acid alignment of wheat NAM-B1 as a query sequence. The results page consists of a list of gene/genes with sequence similarity to the query sequence based on score and *e*-values and the pairwise sequence alignment. The expression profile of the gene/genes can be accessed via keyword search from the global profile search option.

We are currently undertaking microarray analysis involving rice plants subjected to biotic and abiotic stresses, as well as cell and tissue types at various stages of development. These data will be added to the database and functionalities will be enhanced further to provide a more extensive platform for exploring the transcriptome of rice and to expand the utility of RiceXPro as a major source of gene expression information for researchers of rice and other cereal crops.

SUPPLEMENTARY DATA

Supplementary Data are available at NAR Online: Supplementary Table 1.

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