Status of Genome Function Annotation in Model Organisms and Crops

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Abstract

Since entry into genome-enabled biology 20 years ago, much progress has been made in determining,
describing, and disseminating functions of genes and their products. Yet, this information is still difficult to
access for many scientists and for most genomes. To provide easy access and graphical summarizations
to the status of genome function annotation for model organisms and bioenergy and food crop species,
we created a web application (https://genomeannotation.rheelab.org) to visualize and download genome
annotation data for 28 species. The summary graphics and data tables will be updated semi-annually and
snapshots will be archived to provide a historical record of the progress of genome function annotation
efforts.

Introduction

Rapid advances in DNA sequencing technologies made genome sequences widely available and
revealed a plethora of genes encoded within the genomes (O'Leary et al., 2016). The timely invention and
wide adoption of the Gene Ontology (GO) system transformed how gene and protein functions are
described, quantified, and compared across many organisms (Acids research & 2021, 2021; Ashburner et
al., 2000). Despite this tremendous progress in genome biology, a snapshot of the status of genome
function annotation across species is still not readily available for scientists.

Status of genome function annotation is not easily accessible for several reasons. First, genome
sequences and their annotations are hosted across multiple databases that use different
gene/protein/sequence identifier systems. Although some databases include cross database references
and provide tools to map IDs, such as UniProt's Retrieve/ID mapping and BioMart's ID conversion
(Guberman et al., 2011), these tools are not available for all sequenced genomes. Second, gene function
information is not generally annotated using the GO annotation and evidence system in the literature and
most databases. Third, genome function annotation databases generally only include annotated genes,
and it is often not straightforward to identify unannotated genes.

To provide scientists and students an easy way to access and visualize the status of genome
function annotations of model species and bioenergy and food crops, we created a web application that
displays these data graphically and tabularly. The website retrieves data from multiple databases, and
generates plots that show the percentages of genes with experimental, computational, or no annotations.
The snapshots are updated semi-annually, and past snapshots will be archived.

Results

To represent the status of genome function annotation, we selected three groups of organisms: model
organisms, bioenergy model and crop species, and most-annotated plant species (Figure 1). Model
organisms are important experimental tools for investigating biological processes and represent key
reference points of biological knowledge for other species (Ankeny & Leonelli, 2020; Fields & Johnston,
2005; A. M. Jones et al., 2008). This panel includes: Arabidopsis thaliana, Caenorhabditis elegans, Danio
rerio, Drosophila melanogaster, Mus musculus, Saccharomyces cerevisiae, and Schizosaccharomyces
pombe (Fig. 1A). We also included Homo sapiens, a species for which many model organisms are
studied. Next, we selected bioenergy models and crops, which are important in expanding the renewable
energy sector needed to combat the climate crisis and steward a more sustainable environment. Biomass
is currently the biggest source of renewable energy (U.S. Energy Facts Explained - Consumption and
Production - U.S. Energy Information Administration (EIA), n.d.) and is projected to become the biggest
source of primary energy by 2050 (Reid et al., 2020). The bioenergy models and crops we selected
include: Brachypodium distachyon, Chlamydomonas reinhardtii, Glycine max, Miscanthus sinensis,
Panicum hallii, Panicum virgatum, Physcomitrium patens, Populus trichocarpa, Sorghum bicolor, and
Setaria italica (Fig. 1B). Finally, we included ten additional plant species that have the highest number of
GO annotations in UniProt (UniProt Consortium, 2019), which include: Oryza sativa Japonica Group
(rice), Gossypium hirsutum (cotton), Spinacia oleracea (spinach), Zea mays (corn), Medicago truncatula,
Solanum tuberosum (potato), Ricinus communis (castor bean), Nicotiana tabacum (tobacco), Papaver
somniferum (opium poppy), and Triticum aestivum (wheat) (Fig. 1C). These include the world's most
important cereal crops, such as corn, rice, wheat, and vegetable crops such as potato ("FIGURE 21:
World Production of Crops, Main Commodities," 2021).

There are several ways of accessing the status of genome function annotation for the 28 species.
From the front page, visitors can get a quick summary of the state of the genome function annotation as
pie charts for the three groups of species (Figure 1). These pie charts show the percentage of genes that
have: 1) annotations with experimental evidence (green); 2) only the annotations that are computationally
generated (blue); or 3) no annotations or annotations as being unknown (gray) (Figure 1). Of the eight
selected model organisms, H. sapiens has the highest percentage of genes with experimental evidence,
followed by S. cerevisiae and M. musculus. A. thaliana has the lowest percentage of "unknown" genes.
Among the model organisms, C. elegans is the least known species, with the greatest number of genes
unannotated or annotated as having unknown function. Most of the plant species have too few GO
annotations based on experimental support to be visible in the pie charts. Visitors can get more detailed
information of any of the species by clicking on the species name below the pie charts. Each species
page shows additional information about annotation status, including displaying the portion of genes
annotated to at least one GO domain (molecular function, cellular component, and biological process
(Acids research & 2021, 2021; Ashburner et al., 2000)), as well as a Venn diagram showing the overlap
of genes annotated to more than one GO domain (Figure 2). This page also has links to source data and
a tabular format of the annotation summary for browsing and downloading.

Discussion

Our website provides a convenient way to obtain and visualize the current state of genome function
annotation for model organisms and crops for bioenergy, food, and medicine. These charts also serve as
a proxy for illustrating how much is known and unknown. These snapshots will be updated on a semi-
annual basis, and comparing the charts across time will reflect how biological knowledge changes over

time. These snapshots can be useful in many contexts, including research projects, grant proposals,
review articles, annual reports, and outreach materials.

In developing our web application, we encountered a few hurdles. First, there was not a single
site where all data were available. To obtain GO annotations from the 28 species, we had to visit several
databases. An encouraging finding was that all sites that had GO annotations were using the GO
Annotation File (GAF) format. Several tools and databases currently provide a single entry point for
multiple species GO annotations. AmiGO by the GO consortium (Carbon et al. 2009) and QuickGO from
the The Gene Ontology Annotation (GOA) project (Binns et al. 2009) provide search functions for taxon
specific GO annotations. However, they require users to set up additional queries to export GAF files of
interested species. BioMart from The Ensembl project (Kinsella et al. 2011) is another tool that users can
query GO annotations for multiple species using evidence codes. But their output fields do not include
publications or references that are linked to the evidence and require users to manually select output
fields to conform to the GAF format. Second, our website includes genes that are unannotated, which are
often missing in gene function annotations and enrichment analyses (Higgins et al., 2022). Currently,
extracting genes that are not annotated requires many steps that differ across species. Including the
unannotated genes in a genome into GAF files would facilitate many downstream applications. Third,
visualizations of the status of genome annotations do not yet exist, which our website provides using pie
charts and tabular summaries.

To our surprise, some plant species with well-maintained, species-specific databases seem to
have a low number of experimentally supported GO annotated genes in UniProt. TAIR (Lamesch et al.
2012) and Sol Genomics Network (Fernandez-Pozo et al. 2015) are the only two taxon-specific plant
databases that provide GAF files with experimental evidence codes. Most plant genome databases stop
at computationally generating GO annotations, and some well-studied species do not appear to have
dedicated databases. PLAZA (Van Bel et al. 2022) is a platform that integrates structural and functional
annotation for many plant species. They do incorporate experimental evidence from GO (Acids research
and 2021) and GOA (Huntley et al. 2015), but additional annotations are computationally generated
using InterProScan or assigned with empirically validated GO annotations from sets of orthologs. More
efforts are needed in experimentally validating functional annotations made from computational
approaches, characterizing genes of unknown function, and curating experimentally supported function
descriptions in the literature into structured annotations such as GO, which will be crucial for accelerating
gene function discovery.

The data summarized on this website can be linked to their sources, which can be used for a
variety of investigations. Successful examples include exploring why certain proteins remain unannotated
(Wood et al., 2019), developing pipelines to infer function without relying on sequence similarity (Bossi et
al., 2017), and assessing annotation coverage across bacterial proteomes (Lobb et al., 2020). As our
society transitions into biology-enabled manufacturing (Committee on Industrialization of Biology: A
Roadmap to Accelerate the Advanced Manufacturing of Chemicals et al., 2015), fundamental knowledge
of how genes and their products function at various scales will be crucial, as our society transitions into
biology-enabled manufacturing and a new bio-economy era.

Methods

Selecting species and data retrieval

For the model organisms, gene function annotations were downloaded as GO Annotation Files (GAF
files) from the GO consortium website (http://current.geneontology.org/products/pages/downloads.html
accessed 13 June 2022) of the 2022-05-16 release. For S. Pombe, data were downloaded from
PomBase (Harris et al., 2022) (http://www.pombase.org/ "pombase-2022-10-01" release) directly. Genes
found in a genome were retrieved from the source indicated on the GO annotation download page as
General Feature Format (GFF) files. If information of the type of genes are provided in the GFF file, we
only included "protein encoding" genes. A detailed description of the files used to generate charts on our
website, including data for the other category of species, can be found in Supplemental Table S1.

Apart from Nicotiana tabacum and Papaver somniferum, all plant species on our website are
included in the most recent version of Phytozome V13, but their GO terms are assigned computationally
(Goodstein et al., 2012). The Sol Genomics Network (SGN) (https://solgenomics.net accessed 13 June
2022) (Fernandez-Pozo et al., 2015) hosts genome annotations of Solanaceae species, including
Nicotiana tabacum and Solanum tuberosum. An annotation file for Nicotiana tabacum is available
(Edwards et al., 2017) but they are assigned with computational support coming from InterProScan (P.
Jones et al., 2014). SpudDB (Hirsch et al., 2014) (http://spuddb.uga.edu/ accessed 13 June 2022)
provides GO annotation for Solanum tuberosum but they are generated with InterProScan and by best hit
to the Arabidopsis proteome (TAIR10) (Lamesch et al., 2012). MaizeGDB (Woodhouse et al., 2021)
(https://www.maizegdb.org/ accessed 13 June 2022) provides GO annotation for Zea mays that are
assigned with GO annotation tools including Argot2.5, FANN-GO, and PANNZER (Wimalanathan et al.,
2018), which are all computational annotations. SpinachBase (http://www.spinachbase.org/ accessed 13
June 2022) provides a centralized access to Spinacia oleracea, and their GO annotations are generated
computationally with Blast2GO (Collins et al., 2019). Oryza sativa Japonica Group GO annotations can
be found on Rice Genome Annotation Project (Ouyang et al., 2007) and they are assigned with BLASTP
searches against Arabidopsis GO-curated proteins (Yuan et al., 2005). Gramene (Tello-Ruiz et al., 2021)
(https://www.gramene.org/ accessed 13 June 2022) hosts genome data for many species but we could
not find GO annotations with evidence codes. We were not able to find species-specific databases that
provide GO annotations for Triticum aestivum, Gossypium hirsutum, Medicago truncatula, Papaver
somniferum or Ricinus communis.

Genome annotation and gene list for bioenergy models and crops were downloaded from
Phytozome version V13 (https://data.jgi.doe.gov/refine-download/phytozome accessed 13 June 2022).
Although some species in this category had GO annotations in the GO consortium database, the
sequence identifiers (IDs) for genes could not easily be mapped to Phytozome IDs. To maintain
consistency within this category, all annotation files were downloaded from Phytozome. All Phytozome
GO annotations are computationally generated (Goodstein et al., 2012). Gene lists were also retrieved
from Phytozome V13.

For the last category of plant species, we selected the most annotated plant species from the
UniProt GO annotation database (Camon et al., 2004) GAF files hosted on the GO consortium website
(http://current.geneontology.org/products/pages/downloads.html 2022-05-16 release, accessed 13 June
2022). We downloaded these species reference proteomes from the UniProt release 2022_02 and
retrieved the number of corresponding genes.

Using the evidence codes provided by GAF files, we generated the numbers of genes annotated
with GO supported by experimental evidence. If a gene has at least one GO term annotated using any of
the following codes: EXP (Inferred from Experiment), IDA (Inferred from Direct Assay), IPI (Inferred from
Physical Interaction), IMP (Inferred from Mutant Phenotype), IGI (Inferred from Genetic Interaction), or
IEP (Inferred from Expression Pattern), we categorized the gene as having "Experimental Evidence" for

function. Genes that have at least one annotated GO term, but no terms have the evidence codes
described above, are categorized as "Predicted". Since Phytozome has only computationally generated
GO annotations, all of their genes are categorized as having their functions "Predicted". By subtracting
the annotated genes from the total number of genes, we retrieved the number of genes without any GO
annotations. GO annotations with the ND (No biological Data available) are also moved to the "Unknown"
category. These numbers were used to generate pie charts to show the proportions of genes in each
category for every species.

All files were processed with scripts written in Python (3.10). All pie charts were generated using
Python Matplotlib version 3.5.2 and Venn diagrams were generated using Python matplotlib-venn version
0.11.7. The repository of codes can be found at GitHub
(https://github.com/bxuecarnegie/AnnotationStats).

Creating the Website

184 To create a website for hosting our charts, we used Node.js (Tilkov & Vinoski, 2010) for our server-side
185 environment, which provides the Application Program Interface (API) for the front end to retrieve the plots
186 generated by Python. The front end of the website uses AngularJS (Jain et al., 2014).

Availability of data and materials

Data used in this study are all publicly available. GO annotation files were downloaded from
(http://current.geneontology.org/annotations/index.html 2022-05-16 release, accessed 13 June 2022) and
Phytozome (https://data.jgi.doe.gov/refine-download/phytozome V13, accessed 13 June 2022). Gene
data were downloaded from sources indicated on the GO
(http://current.geneontology.org/products/pages/downloads.html accessed 13 June 2022), Phytozome,
Pombase (http://www.pombase.org/ "pombase-2022-10-01" release) and UniProt
(https://www.uniprot.org/ accessed 13 June 2022). Supplemental Table S1 provides detailed information
on all species annotation and gene source databases, downloaded versions, and URLs. Scripts used to
process the data and generate the graphs are written in Python 3 and are available at GitHub
(https://github.com/bxuecarnegie/AnnotationStats accessed 13 June 2022).

Author Contributions

201 SYR conceived the project, and BX implemented the project. BX and SYR wrote and edited the
202 manuscript.

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212

213 **Competing Interest Statement**

214 The authors declare no competing interests.
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Figures

Figure 1 Status of genome function annotations

Each pie chart shows the proportion of genes that are annotated to a domain of Gene Ontology (GO):
molecular function, biological process, or cellular component. Green indicates genes that have at least
one experimentally validated GO annotation; blue indicates genes that are annotated with

computationally predicted GO annotations; and gray indicates genes that do not have any GO
annotations or have GO annotations with ND (No biological Data available). The species are ordered by
the average percentage of genes with experimental evidence (or genes with computationally predicted
annotations if experimental evidence is not available) of all three domains. A) selected model organisms;
B) bioenergy models and crops; C) other plant species with the highest percentage of genes with
experimental evidence in UniProt.

Figure 2 An example species-specific annotation web page shown for Arabidopsis thaliana. It consists of
three parts: 1) a table comprising data sources; 2) pie charts showing the proportion of each type of
annotations; and 3) a table showing the numbers of genes in each category, which users can toggle to
either show or hide.

Figure 1 Status of genome function annotations

Each pie chart shows the proportion of genes that are annotated to a domain of Gene Ontology (GO): molecular function, biological process, or cellular component. Green indicates genes that have at least one experimentally validated GO annotation; blue indicates genes that are annotated with computationally predicted GO annotations; and gray indicates genes that do not have any GO annotations or have GO annotations with ND (No biological Data available). The species are ordered by the average percentage of genes with experimental evidence (or genes with computationally predicted annotations if experimental evidence is not available) of all three domains. A) selected model organisms; B) bioenergy models and crops; C) other plant species with the highest percentage of genes with experimental evidence in UniProt.

Arabidopsis thaliana

GAF Source	Gene Ontology
Sequence Source	The Arabidopsis Information Resource (TAIR)
Download Date	06/13/22

[Back to Overview]

Status of gene function elucidation and annotation

Molecular function Biological process Cellular component

A

■ Experimental evidence ■ Predicted ■ Unknown

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B
11668 (42.33%)
1304 (4.73%)
14594 (52.94%)

C
Molecular function   Biological process
1760   2139   1534
3619
687   1144
785
Cellular component

[Copy Link to Image] [Download "Experimental Evidence" Gene List] [Download "Predicted" Gene List] [Download "Unknown" Gene List]

Stats of Arabidopsis thaliana (Taxon: 3702)

[Toggle Table] [Download Table]

Num. of Genes	27566
Num. of Genes w/ Experimental evidence	11668
Num. of Genes w/ Computational evidence	14594
Num. of Genes with no GO annotations	1304
Num. of Molecular function (Experimental evidence)	8205 (29.76%)
Num. of Molecular function (Predicted)	8295 (30.09%)
Num. of Molecular function (Unknown)	11066 (40.14%)
Num. of Biological process (Experimental evidence)	8436 (30.60%)
Num. of Biological process (Predicted)	12468 (45.23%)
Num. of Biological process (Unknown)	6662 (24.17%)
Num. of Cellular component (Experimental evidence)	6235 (22.62%)
Num. of Cellular component (Predicted)	18568 (67.36%)
Num. of Cellular component (Unknown)	2763 (10.02%)

Generation Date: 06/13/22

Archived charts

Link to archives.

Figure 2 An example species-specific annotation web page shown for *Arabidopsis thaliana*. It consists of three parts: 1) a table comprising data sources; 2) pie charts showing the proportion of each type of annotations; and 3) a table showing the numbers of genes in each category, which users can toggle to either show or hide.