

TCOD: an integrated resource for tropical crops

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Abstract

Tropical crops are vital for tropical agriculture, with resource scarcity, functional diversity and extensive market demand, providing considerable economic benefits for the world's tropical agriculture-producing countries. The rapid development of sequencing technology has promoted a milestone in tropical crop research, resulting in the generation of massive amount of data, which urgently needs an effective platform for data integration and sharing. However, the existing databases cannot fully satisfy researchers' requirements due to the relatively limited integration level and untimely update. Here, we present the Tropical Crop Omics Database (TCOD, [https://ngdc.cncb.ac.cn/tcod\)](https://ngdc.cncb.ac.cn/tcod), a comprehensive multiomics data platform for tropical crops. TCOD integrates diverse omics data from 15 species, encompassing 34 chromosome-level de novo assemblies, 1 255 004 genes with functional annotations, 282 436 992 unique variants from 2048 WGS samples, 88 transcriptomic profiles from 1997 RNA-Seq samples and 13 381 germplasm items. Additionally, TCOD not only employs genes as a bridge to interconnect multi-omics data, enabling cross-species comparisons based on homology relationships, but also offers user-friendly online tools for efficient data mining and visualization. In short, TCOD integrates multi-species, multi-omics data and online tools, which will facilitate the research on genomic selective breeding and trait biology of tropical crops.

Graphical abstract

Introduction

Tropical crops, cultivated in tropical regions, encompass a wide range of varieties and can be classified into different categories based on their uses, including rubber crops, tropical food crops, tropical fruit trees, tropical oil crops, tropical spice beverages, tropical medicinal plants and more [\(1\)](#page-7-0). The functional diversity of these crops gives rise to a broad market demand, making a significant positive impact on the economic growth of tropical agricultural producing countries worldwide. Meanwhile, the rapid advancement of next-generation sequencing technologies has facilitated the generation and accumulation of vast amounts of multi-omics data in tropical crops, enabling the comprehensive elucidation of gene func-

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tions and networks under diverse physiological and environmental stress conditions [\(2\)](#page-7-0).

In the field of genomics, the genomes of diverse tropical crops have been successfully deciphered, with the utilization of advanced technologies such as Hi-C, BioNano optical mapping and Telomere-to-Telomere (T2T), leading to enhanced precision and integrity of the genome sequences [\(3–10\)](#page-7-0). Based on population genome studies, variation maps have been generated for several tropical crops, including pineapple, mango, cassava and longan, revealing valuable insights into their domestication history $(11–14)$. In the field of transcriptomics, extensive identification of key genes and signalling pathways has provided crucial clues for increasing yields (e.g. rubber tree latex production, sugarcane sugar content) and enhancing tolerance to biotic and abiotic stresses (e.g. pests, diseases, drought, cold and high salinity) [\(15–17\)](#page-7-0). Additionally, some multiomics analyses have facilitated a comprehensive exploration of complex physiological processes and polygenic traits, leading to a deeper understanding of the interactions and intricate regulatory mechanisms among different molecules (such as mRNAs, proteins and metabolites) underlying phenotypic traits. $(18-21)$. However, the raw sequencing data and genome sequences of these studies are scattered in different databases, which poses great challenges for data reuse and integrated analysis. Therefore, it is necessary to establish a centralized data sharing platform to provide convenient data sharing services for researchers.

Optimal data integration needs to cover a broad range of species and omics levels while ensuring high-quality datasets. At present, several internationally developed tropical crop databases, such as CassavaBase (22) , HeveaDB (23) , PGD (24) , Sapbase (25) , ArecaceaeMDB (26) and TropGeneDB [\(27\)](#page-8-0), have emerged. CassavaBase, HeveaDB and PGD integrate multi-omics data, but they are only designed for a single species. Similarly, Sapbase and ArecaceaeMDB incorporate multi-omics data from multiple species, but they serve the family Sapindaceae and Arecaceae, respectively. TropGeneDB, is an information system to manage genetic, molecular and phenotypic data for 11 tropical crops, but it lacks multi-omics data and is not up to date. A comprehensive compilation of data encompassing diverse species not only facilitates crossspecies research, but also helps to break bottlenecks caused by insufficient data for some species [\(28\)](#page-8-0). While discoveries of new gene functions and transcriptome conservation levels in Arabidopsis, rice and barley through homologous genes [\(29,30\)](#page-8-0), cross-species studies on tropical crops remain limited. Therefore, integrating multi-omics data from multiple tropical crops, refining homologous gene relationships among species and creating an inclusive database for data archiving, analysis, and visualization will significantly advance tropical crop research.

Here, we present TCOD [\(https://ngdc.cncb.ac.cn/tcod\)](https://ngdc.cncb.ac.cn/tcod), a specialized, integrated and open-access resource for tropical crops. Currently, TCOD includes whole-genome sequencing (WGS) data, RNA sequencing (RNA-Seq) data, genomes, gene functional annotations, homolog relationships and germplasm information for 15 tropical crops. Multiple WGS and RNAseq datasets are analyzed using standardized workflows, resulting in the generation of comprehensive variation maps and expression profiles for each species. In addition, TCOD is well-equipped with a diverse set of online analysis tools for data mining, further bolstering its role in providing free public service for scientific research.

Materials and methods

Data collection

High-throughput sequencing data, genome sequences, annotation information and germplasm resource entries for 15 tropical crops were compiled from major databases, with detailed volumes and sources are shown in Table [1.](#page-2-0)

Processing of WGS-Seq data

The collected WGS data were processed using the standard analysis pipelines provided by the Genome Variation Map (GVM) [\(41\)](#page-8-0). After performing quality control on raw sequencing reads using Trimmomatic v0.36 [\(42\)](#page-8-0), clean reads were mapped to the reference genome using BWA-MEM [\(43\)](#page-8-0). Then the mapping results were converted and sorted using Samtools v1.13 [\(44\)](#page-8-0), and duplicates were marked using MarkDuplicates in GATK v4.1.2.0 [\(45\)](#page-8-0). For lack of known variations, the high-quality variants called by GATK HaplotypeCaller and Bcftools v1.13 [\(44\)](#page-8-0) were merged and then input to Basic Quality Score Recalibration (BQSR). Intermediate GVCF files were generated for each sample by Haplotype-Caller, which then were pooled together to generate a VCF file containing all raw variants using CombineGVCFs and GenotypeGVCFs in GATK. These raw variants were further filtered using SelectVariants and VariantFiltration in GATK with recommended parameters. The functional effects of the variants were annotated using VEP v8.4 [\(46\)](#page-8-0). The minor allele frequency (MAF) of the variants were calculated using vcftools v.0.1.13 [\(47\)](#page-8-0).

Processing of RNA-Seq data

The collected RNA-Seq data were processed using the standard analysis pipelines provided by the Gene Expression Nebula (GEN) (48) . After quality control with Fastp v0.20.0 (49) , the reads were aligned to the reference genome using Hisat2 v2.0.5 [\(50\)](#page-8-0) to evaluate data quality. Projects with an average alignment rate above 50% were selected for subsequent analysis. RseQC v2.6.4 (51) was used to determine strand-specific library sequencing. The high-quality reads were aligned to the genome using the STAR v2.7.1a [\(52\)](#page-8-0), generating BAM results, which were subsequently processed by the RSEM v1.3.1 (53) for expression quantification, resulting in the generation of gene expression and transcript expression matrices. Additionally, Limma [\(54\)](#page-8-0) was utilized to perform differential expression analysis under various sample comparison scenarios.

Functional annotation of genomes

To address the issue of lacking information or inconsistent descriptions in genome annotation, we conducted a unified functional annotation on each gene while preserving the original annotation. This involved utilizing the Nr [\(55\)](#page-8-0) and Uniprot (56) databases to identify similar functional proteins, the Pfam [\(57\)](#page-8-0) and Interpro [\(58\)](#page-8-0) databases to identify conserved domains, and the eggnog-mapper webserver [\(59\)](#page-8-0) to obtain the GO [\(60\)](#page-8-0) terms and KEGG [\(61\)](#page-8-0) pathways associated with the genes.

Identification of homologous genes

The protein sequences of each gene are collected and inputted into the OrthoFinder v2.5.4 (62) to identify their homologous genes in other species. The parsing and tabulation of homol-

Table 1. Statistics and sources of data collected

Note: CIAT: The International Center for Tropical Agriculture [\(https://ciat.cgiar.org\)](https://ciat.cgiar.org); IITA: International Institute of Tropical Agriculture [\(https://my.iita.org/accession2/\)](https://my.iita.org/accession2/); HNU: Hainan University; HZAU: Huazhong Agricultural University; ITBB-CATAS: Institute of Tropical Bioscience and Biotechnology, Chinese Academy of Tropical Agricultural Science; RRI-CATAS: Rubber Research Institute, Chinese Academy of Tropical Agricultural Sciences.

ogous gene results are guided by the structural framework of the Homologous Gene Database (HGD) [\(63\)](#page-8-0).

Genome synteny analysis

Collinearity analysis includes comparisons between reference genomes of different species and comparisons between genomes of different subspecies within the same species. Genome-wide synteny analysis was performed using MUMmer v4.0.0.rc1 [\(64\)](#page-9-0). Initially, the 'nucmer' program was utilized to generate comprehensive comparisons of nucleotide sequences, employing the parameters -g 1000 -c 100 for interspecies comparisons and default parameters for intraspecies comparisons. Subsequently, the intraspecies comparison results were filtered using the 'delta-filter' program with the parameters -m -i 90 -l 10000.

Database implementation

TCOD was implemented by SpringBoot (https://spring.io/ [projects/spring-boot;](https://spring.io/projects/spring-boot;) a free and powerful framework for developing standalone java applications) and Mybatis (https: [//mybatis.org/mybatis-3;](https://mybatis.org/mybatis-3;) a first-class persistence framework with support for custom SQL, stored procedures and advanced mappings), referring to the framework of iDog and iSheep database [\(65,66\)](#page-9-0). Data storage and management were realized using MySQL [\(https://dev.mysql.com;](https://dev.mysql.com;) the world's most popular relational database management system). Web user interfaces were developed using JSP (Jakarta Server Pages, a template engine for web applications), HTML (HyperText Markup Language), CSS (Cascading Style Sheets), Bootstrap [\(https://getbootstrap.com;](https://getbootstrap.com;) a powerful, feature-packed frontend toolkit), AJAX (Asynchronous JavaScript and XML; a technique for creating fast and dynamic web pages, allowing partial updates of web pages without reloading the whole page.) and Jquery [\(https://jquery.com;](https://jquery.com;) a fast, small and feature-rich JavaScript library). For dynamic data visualization, Echart [\(https://echarts.apache.org/en/index.html;](https://echarts.apache.org/en/index.html;) a declarative framework for rapid construction of web-based

visualization), Highcharts [\(https://www.highcharts.com;](https://www.highcharts.com;) a JavaScript plug-in to create interactive charts) and DataTables [\(https://datatables.net;](https://datatables.net;) a plug-in for the jQuery JavaScript library to render HTML tables) were incorporated to generate charts and tables. Furthermore, third-party software, including NCBI BLAST+ [\(55\)](#page-8-0),JBrowser2 [\(67\)](#page-9-0), Primer3Web [\(68\)](#page-9-0) and ClusterProfiler [\(69\)](#page-9-0), are invoked for the secondary development of online tools.

Database content and usage

Overview of TCOD

TCOD is dedicated to becoming a comprehensive multi-omics data platform that serves the field of tropical crop research, offering users a one-stop solution for data acquisition and online analysis. By integrating the genome, variome, transcriptome and cultivar data from 15 typical tropical crops, TCOD has achieved the integration of multi-omics data within individual species, utilizing genes as a bridge to connect various dimensions of omics data. Furthermore, leveraging homologous genes as entry points enables the comparison of omics characteristics across different species. As of 1 August 2023, TCOD houses 34 chromosome-level *de novo* assemblies, 1 255 004 genes with functional annotations, 282 436 992 unique variants from 2048 WGS samples, 88 transcriptomic profiles from 1997 RNA-Seq samples and 13 381 germplasm items. Additionally, TCOD incorporates a range of online tools to facilitate data mining within the database and visualization of analysis results (Figure [1\)](#page-3-0).

Genome

The genome in TCOD includes whole genome sequences and genes, and the genome sequences comprise the 'Assembly' module in the system. By integrating assemblies released by multiple public platforms and provided by partners, 34 chromosome-level *de novo* genomes from 15 species have been collected, covering 30 different varieties. Focusing on

Figure 1. The construction pipelines of TCOD, including data collection, data processing and database implementation.

each genome, users can browse basic information such as sequencing technologies, coverage, total length, scaffold number, N50 value, GC content and published literature. In addition, We calculated the number of genes on each chromosome and used the Rideogram package [\(70\)](#page-9-0) to create a heatmap of gene density distribution, visualizing the gene-rich regions in each genome (Figure [2A](#page-4-0)).

The 'Gene' module was committed to facilitate researchers to find functional genes. By collating gene structure and function descriptions extracted from each genome annotation, 1 255 004 gene entries were captured to build this module. It supports dynamic conditional retrieval and target gene set downloads by selecting genome version, chromosome coordinate, gene name and gene function. Gene acts as bridges connecting multiple omics data in TCOD. The detailed gene information includes 'basic information', 'genome and sequence', 'homolog information', 'variant information', 'expression information' and 'visualization', from which users can infer the potential biological function of the gene.

Variation

The 'Variation' module was designed to provide researchers with an overall and reliable genome-wide variation dataset. By collecting WGS data from different samples and using a standard variation analysis pipeline, this module provides genome-wide variation maps for 10 species (Figure [2B](#page-4-0)). To facilitate the search and download of interested variants, a unique identifier was assigned to each variant and a multiconditional retrieval method was supported. For each variant, we provide not only basic information such as variant coordinate, reference and alternative allele, minor allele frequency, etc., but also detailed functional annotation information such as consequence type, variant effect and genotype distribution in the population, which supplies pointcuts for population diversity research.

Expression

The 'Expression' module is dedicated to providing evidence to explore the diverse regulatory mechanisms involved in genes. Through the unified analysis of high-quality RNA-Seq datasets from different projects, this module offers transcriptome profiles of 13 species under various experimental conditions. Moreover, to cater to specific research interests, we have included category tags for each project, such as biotic stress, abiotic stress, disease and infection, allowing users to efficiently access datasets of their interest categories (Figure [2C](#page-4-0)). For each dataset, we support the visualization and download of gene expression profiles, and provide a list of differentially expressed genes under different comparison conditions.

Cultivar

The 'Cultivar' module was intended to provide germplasm data to support research on crop breeding and domestication. By integrating varieties from CIAT, IITA and GRIN, a total of 13 381 non-redundant entries have been collected and the number of varieties in specific geographic regions was plotted on a world map, offering a visual representation of the global distribution of germplasm resources for 15 tropical crops (Figure [2D](#page-4-0)). Taking the cassava accession as an example, researchers can view copious descriptive information for a more comprehensive assessment of the sample. The description consists of three parts, including passport data (such as accession name, synonyms, DOI, origin country), botanical characteristics (such as plant height, stem color, developed leaf color, petiole color) and agronomic characteristics (such as storage root form, root color, dry matter content, hydrocyanic acid content).

Figure 2. Screenshots of TCOD. (A) Gene density distribution in the genome of rubber_tree_reyan8-79. (**B**) Genome-wide variation maps for 10 species. (**C**) Classification of RNA-Seq studies. (**D**) Global distribution map of multiple tropical crops. (**E**) Visualizing collinearity between the genomes lychee_FZX and longan_shixia, the red circle indicates the selected region for a more detailed linear synteny view. (**F**) Heatmap of homologous genes between genome pairs.

Species

The 'Species' module organizes multi-species and multi-omics data collected in the database on a species basis, helping researchers to rapidly access the data resources of concerned species. By aggregating data information from different sections, it not only provides concise scientific overview of each species (including geographical distribution, applications and genome sequencing), but also grants direct access to genomes, genes, variants, expressions, projects, samples and cultivars.

Tools

To facilitate data mining and analysis on TCOD, we have set up several commonly easy-to-use tools in the 'Tools' module, including BLAST, Genome Browser, Primer Design, Literature Search, GO Enrichment, KEGG Enrichment, Synteny Viewer and Homolog Finder. The BLAST tool, built on NCBI BLAST+, is specifically designed for sequence searching against the genome, coding sequence (CDS) and protein

sequences of 15 tropical crops. The Genome Browser provides smooth visualization of genomic sequences, genes and variants in selected region by selecting a reference genome, and supports exporting the visualization results of selected regions to images. The Primer Design is developed based on Primer3web, aimed at assisting users in designing primers for downstream experiments. The Literature Search utilizes the interface offered by the NGDC OpenLB database [\(71\)](#page-9-0) to facilitate rapid retrieval of relevant literature in the field of tropical crops. The GO Enrichment and KEGG Enrichment tools facilitate enrichment analysis of GO and KEGG pathways for target gene sets, providing downloadable results and visualizing enrichment pathway bubble diagrams. The Synteny Viewer allows users to visualize collinear relationships between genomes, offering inter-species and intraspecies collinearity views with dot plots, and the ability to zoom in on specific regions to explore the genes within the collinear regions (Figure 2E). The Homology Finder offers a heat map to illustrate the number of homologous gene be-

Metadata and download

To ensure data traceability and reusability, we included metadata information for all used projects and samples, categorizing them into their corresponding omics categories. Raw sequencing data can be downloaded from the FTP or HTTP addresses provided via the 'runs' link within each module, and variant files (GVCF/VCF) for each WGS sample can also be downloaded. Additionally, the download page provides access to genomes and annotation files, variant results, expression matrices and germplasm resources for local data mining.

An example of using TCOD

Carotenoid production is limited by the expression level of phytoene synthase (PSY). A non-conservative amino acid exchange (A191D) triggered by a single nucleotide polymorphism $(C > A)$ in *PSY2* was reported to lead to a marked increase of carotenoid synthesis in cassava storage roots [\(72\)](#page-9-0). Here, we use *PSY2* as an example to demonstrate how to access data in TCOD.

First, the *PSY2* protein sequence (NCBI accession number: ACY42667) is aligned to the database using the 'BLAST' tool, revealing 100% sequence similarity with Manes.01G124200 (Figure [3A](#page-6-0)). Clicking the ID link in the 'See details' column redirects to view detailed gene information, the 'Basic Information' reveals its function as phytoene synthase and provides its functional domains, as well as GO and KEGG annotations (Figure [3B](#page-6-0)). When searching for the keyword 'A191D' in the 'variant information', we can quickly find the consistent variant as mes5524597 (Figure [3C](#page-6-0)). Clicking on it leads to the 'Variation' module, where we discover that among the 573 cassava samples, 63 have this variation, all of which belong to the Manihot esculenta population (Figure [3D](#page-6-0)). For samples of interest, such as TCODI00359, representing the CM 507-37 variety from Colombia, we can either click on the sampleID to access the 'Sample' module for metadata information (Figure [3E](#page-6-0)) and download the variant GVCF file, or click on the cultivarID mesb4894 to enter the 'Cultivar' module and view corresponding phenotype data, such as the root color being crema (Figure [3F](#page-6-0)). The 'Expression information' displays Manes.01G124200's expression level (TPM value) in each sample of the project. In the project TCODP0025, the TPM value of wild two-month-old cassava seedling samples was lower than that of cassava seedling samples treated with abscisic acid (ABA). The differential expression analysis indicated its significance, suggesting that the gene may be involved in the response to ABA stress (Figure [3G](#page-6-0)).

In addition to supporting published studies with largerscale sample datasets, the 'homologous information' offers inspiration for cross-species functional studies. By utilizing the visualized orthologous gene relationship graph, we can make preliminary predictions regarding which tropical crops may possess similar gene functions (Figure [3H](#page-6-0)). In light of this, our emphasis lies on banana species, as elevating the vitamin A content in banana fruit can effectively combat vitamin A deficiency in developing countries across Africa and Southeast Asia [\(73\)](#page-9-0). The 'Homologous gene list' shows that the gene Manes.01G124200 has two orthologous genes and two paralogous genes in the banana genome (banana_DH- Pahang), suggesting potential similar roles in banana as the gene Manes.01G124200 in cassava and functional analysis can be further conducted based on the GO pathway, KEGG pathway, variation and expression information of the homologous gene. Notably, the expression of Macma4_09_g09940 (with 95% similarity to *MtPsy2a* protein sequence) has been confirmed to lead to an increase in vitamin A content [\(74\)](#page-9-0), implying the *PSY2* gene plays universally applicable function in both cassava and banana. Moreover, TCOD supports gene sequence downloads (Figure [3I](#page-6-0)) and genomic region visualization (Figure [3J](#page-6-0)), facilitating users in conducting subsequent analyses conveniently.

Discussion and future plans

Tropical crops have significant economic value and incomparable biological status, and the rapid development of multiomics research has highlighted an urgent need for the integration and sharing of massive data. Internationally, existing tropical crop databases either lack multi-omics data or have a limited scope, focusing solely on specific species or families. Presently,TCOD stands as the most comprehensive multiomics database, encompassing the largest diversity of tropical crop species.

When compared to other established databases, TCOD exhibits the following key characteristics: (i) multi-species and multi-omics data integration: TCOD aggregates diverse data resources covering 15 tropical crop species, including genome sequences, genome variations, gene functions, gene expressions and germplasm information. By correlating multi datasets in units of genes, TCOD provides a user-friendly platform with efficient data browsing, retrieval and downloading capabilities, making it a one-stop resource for researchers seeking valuable information on tropical crops. (ii) Highquality datasets: Genomes incorporated into TCOD reach a level of chromosomal integrity and are accompanied by uniform and comprehensive gene annotation. Additionally, by collecting raw sequencing data from diverse sources and implementing a standardized analysis pipeline, TCOD generates relatively complete variation maps for each species, along with expression profiles under different physiological conditions, providing a valuable dataset for the artificial intelligence breeding of tropical crops. (iii) Diverse online tools: To enhance effective data mining, TCOD offers a series of online tools for sequence similarity comparison, downstream primer design, literature searches, genes pathway enrichment and pairwise genome consensus linear views. (iv) Cross-species analysis: TCOD furnishes gene homology relationships across various species, allowing cross-species comparisons of gene functions and multi-omics characteristics, which facilitates indepth exploration into the shared biological attributes among different organisms.

In the future, Multi-omics data of tropical crops with extremely rich species diversity will be generated and collected in TCOD. We also plan to add additional types of omics data (e.g. metabolome, proteome) and establish Variant-Gene-Trait associations through manual collection and curation of GWAS related literature, providing a comprehensive prior knowledge module for tropical crop trait research. Moreover, the advancement in machine learning and artificial intelligence technology holds the promise of integrating biological knowledge and omics data to achieve precise breeding [\(75\)](#page-9-0). At present, it has been realized in some staple crops such as

Figure 3. Using TCOD to obtain data for each section associated with the PSY2. (**A**) The gene Manes.01G124200 was identified with 100% sequence similarity to PSY2 in the tropical crop protein database by blastp. (**B**) The function annotation of the gene Manes.01G124200 in TCOD. (**C**) The variant ID mes5524597 was obtained by filtering with the keyword 'A191D' among the 2480 variants in the gene Manes.01G124200. (**D**) Genotype distribution of variant mes5524597 in 573 cassava samples. (**E**) Sample metadata corresponding to the sampleID TCODI00359. (**F**) Cultivar information corresponding to the cultivarID mesb4894. (**G**) The expression level of gene Manes.01G124200 in different samples of project TCODP0025. (**H**) Homologous relationship of gene Manes.01G124200 in other species. (**I**) The corresponding genome and sequence of the gene Manes.01G124200. (**J**) Genome browser for visualizing different tracks in the gene Manes.01G124200.

rice, maize and wheat [\(76–78\)](#page-9-0), but it is still relatively behind in the field of tropical crops. To bridge this gap, TCOD will continue its unwavering commitment to extensively explore multi-omics data using these cutting-edge methods and technologies, providing vital data support for tropical crop breeding to enter the generation of the '5Gs' - (genome, germplasm, gene, genomic breeding and gene editing) [\(79\)](#page-9-0). We also enthusiastically welcome comments and suggestions from researchers worldwide to enhance and improve TCOD.

Data availability

TCOD is freely available online at [https://ngdc.cncb.ac.cn/](https://ngdc.cncb.ac.cn/tcod) tcod and does not require user to register.

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Conflict of interest statement

None declared.

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