

Morphological characterization and transcriptome analysis of petiole inclination angle in sunflower[*Helianthus annuus* L.]

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Abstract

Petiole posture is a crucial agronomic trait in sunflowers, serving as a key indicator for constructing an ideal plant architecture. This study analyzed petiole inclination angles in two inbred lines: G19 (flat-leaf type, large petiole inclination angle) and G20 (compact-leaf type, small petiole inclination angle). Transcriptome sequencing was performed using the Illumina Hi-Seq 2500 high-throughput sequencing platform, followed by functional annotation of differentially expressed genes (DEGs) through GO and KEGG databases. The results revealed 3,851 DEGs between G19 and G20, including 1,841 downregulated and 2,010 upregulated genes. GO enrichment analysis categorized these DEGs into 48 functional groups across biological processes, cellular components, and molecular functions. KEGG pathway annotation indicated that downregulated genes in G19 vs G20 were enriched in 123 secondary pathways. Notably, the "hormone signal transduction" pathway (ko04075) was implicated in regulating sunflower petiole posture, involving auxin, cytokinin, gibberellin, and brassinosteroid signaling pathways. Further analysis highlighted that upregulated expression of nuclear-localized AUX/IAA, GH3, B-type response regulators (B-ARR), gibberellin receptor *GID1*, transcriptional regulator *DELLA*, *BZR1/2* transcription factors, and *TCH4* enzyme was closely associated with compact-leaf posture formation. These findings provide valuable insights into the genetic mechanisms underlying leaf posture regulation in sunflowers.

Introduction

Sunflower (*Helianthus annuus* L.), as an important oil crop worldwide, ranks fourth in global production following oil palm, soybean, and rapeseed (Hladni, 2016). In China, the annual cultivation area of sunflower currently reaches approximately 1.06×10^8 hm², with a total yield of 2.85×10^6 t, positioning the country as the fourth-largest producer globally. Over the next 5–10 years, a consumption gap of approximately 20.0×10^6 t per year is projected. Given limited arable land resources per capita, enhancing yield per unit area to increase total production represents a critical pathway for achieving sustainable development in China's sunflower industry.

Petiole angle, which influences plant architecture through leaf orientation, serves as a key determinant of canopy coverage and a vital indicator of light interception and distribution within plant populations. An optimal petiole angle can maintain high light transmittance within densely planted communities, meeting the light energy requirements for photosynthesis and significantly impacting yield (SUN, 2015). Erect leaves enhance the leaf area index (LAI) for lower-positioned leaves, thereby improving net photosynthesis per unit area and ultimately increasing total biomass and yield (Sinclair and Sheehy, 1999). Under high-density planting conditions, Cao et al. (2022) demonstrated that upright leaves effectively reduce shade avoidance responses (SAR) while enhancing light capture

efficiency in the canopy, leading to improved photosynthetic efficiency and harvest index. Studies on rice revealed that erect leaves with smaller angles facilitate bidirectional light exposure, elevating canopy photosynthetic efficiency and dry matter accumulation (Ning, 2011). In maize, smaller leaf angles under dense planting mitigate mutual shading, sustain higher light interception, and promote grain filling and yield (Stewart, 2003; Lu, 2007). Similarly, soybean research identified petiole angle as a major factor influencing photosynthesis, planting density, and yield (Liu, 2020; Wang, 2020).

Petiole angle is a critical agronomic trait in sunflower. Genetic studies indicate that the erect petiole trait in sunflower is controlled by a recessive monogene (*er1*) (Luczkiewicz, 1975), while the vertical leaf orientation (perpendicular petiole-stem angle) is regulated by another recessive gene (*ul1*). Tolmacheva (2007) further reported that leaf erectness follows recessive inheritance, with genetic patterns including incomplete dominance, dominance, and overdominance, and exhibits no maternal effect. Gene interactions revealed dominant epistasis of *Er* over *er1* and *er2*, and recessive epistasis of *er2* over *er1*, though the underlying regulatory mechanisms remain unclear. Compared to other crops, research on sunflower petiole angle lags significantly.

To address this gap, this study investigates the molecular mechanisms governing petiole angle formation in sunflower. Two inbred lines with contrasting petiole angles—G19 (large angle, flat-leaf type) and G20 (small angle, compact-leaf type)—were subjected to transcriptome sequencing using high-throughput technologies. Differentially expressed genes (DEGs) were screened, followed by functional annotation and metabolic pathway analysis. This work aims to identify key functional genes involved in petiole angle regulation and provide theoretical insights for breeding ideal sunflower plant architectures.

Materials and Methods

Experimental Materials

The experiment was conducted at the Teaching Farm of Inner Mongolia Agricultural University in 2022. Two oilseed sunflower inbred lines, G19 (with large petiole angle and flat-leaf phenotype) and G20 (with small petiole angle and compact-leaf phenotype), exhibiting significant differences in petiole angles, were selected as experimental materials. Sowing was performed on May 15, 2022. Prior to flowering, ten consecutive plants were selected from each line. The petiole angles (the angle between the lower part of the petiole and the stem) of the third to seventh fully expanded leaves from the top were measured using an angle-measuring instrument, followed by t-test analysis. Simultaneously, petiole samples from three biological replicates were collected, rinsed with sterile water, flash-frozen in liquid nitrogen, and stored at -80°C for subsequent

transcriptome sequencing. The plant architecture and petiole angle phenotypes of the sampled materials at the sampling stage are illustrated in Fig. 1.

Total RNA extraction, library construction and transcriptome sequencing

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RNA Quality Assessment

Purity, concentration and integrity of RNA sample were examined by NanoDrop, Qubit 2.0, Agilent 2100, etc. Only RNA with good quality could move on to following procedures.

Library Construction

Qualified RNA were processed for library construction. The procedures are described as follow:

- (1) mRNA was isolated by Oligo(dT)-attached magnetic beads.
- (2) mRNA was then randomly fragmented in fragmentation buffer.
- (3) First-strand cDNA was synthesized with fragmented mRNA as template and random hexamers as primers, followed by second-strand synthesis with addition of PCR buffer, dNTPs, RNase H and DNA polymerase I. Purification of cDNA was processed with AMPure XP beads.
- (4) Double-strand cDNA was subjected to end repair. Adenosine was added to the end and ligated to adapters. AMPure XP beads were applied here to select fragments within size range of 300–400 bp.
- (5) cDNA library was obtained by certain rounds of PCR on cDNA fragments generated from step 4.

Library Quality Control

In order to ensure the quality of library, Qubit 2.0 and Agilent 2100 were used to examine the concentration of cDNA and insert size. Q-PCR was processed to obtain a more accurate library concentration. Library with concentration larger than 2 nM is acceptable.

Sequencing

The qualified library was pooled based on pre-designed target data volume and then sequenced on Illumina sequencing platform.

Comparison with reference genomes

The clean reads were aligned to the reference genome (*Helianthus_annuus*.GCA_002127325.2.genome.fa) using HISAT2 (Kim et al., 2015) to obtain their genomic mapping positions. Subsequently, the aligned reads were assembled through StringTie (Pertea et al., 2015) for transcriptome reconstruction, which served as the foundation for downstream analyses. analysis was performed using BMKCloud (www.biocloud.net).

Results and Analysis

Analysis of Petiole Inclination Angle Differences

Before sunflower flowering, the petiole inclination angles were measured as shown in Fig. 2. The results demonstrated that from the 3rd to 7th leaves from the apex (counted basipetally), both cultivars G19 and G20 exhibited decreasing trends in petiole inclination angles, with G19 consistently displaying larger angles than G20. Statistical analysis revealed that the average petiole inclination angles of G19 and G20 were 42.8° and 16.7°, respectively, for these leaves, indicating a significant difference of 26.1° between the two cultivars. The t-test results confirmed that this difference reached statistical significance ($P = 0.05$), suggesting that these cultivars are suitable candidates for subsequent transcriptome sequencing analysis.

Transcriptome Sequencing Analysis

Assembly and Statistics of Sequencing Data

Raw sequencing reads were preprocessed to remove adapter sequences and low-quality sequences. The filtered data were then assembled and aligned, with the results presented in Table 1. As shown in Table 1, the average numbers of valid reads for flat leaves (G19) and compact leaves (G20) were 23,305,741 and 22,810,977, respectively. The average valid base pairs reached 6,968,406,193 and 6,818,078,903, while the mean GC contents were 94.19% and 93.89% for G19 and G20, respectively. These results indicate the high reliability of the sequencing data, confirming their suitability for subsequent analyses.

Table 1
Summary of sequencing data assembly and mapping to the sunflower genome

Sample name	Replication	Clean reads	Clean bases	GC Content(%)	%≥Q30
G19	G19-1	22,158,561	6,628,922,636	45.91	94.46
	G19-2	23,484,982	7,018,986,172	44.70	94.15
	G19-3	24,273,681	7,257,309,770	44.51	93.95
	Total	69,917,224	20,905,218,578	135.12	282.56
	Average	23,305,741	6,968,406,193	45.04	94.19
G20	G20-1	23,473,995	7,018,817,606	44.92	93.43
	G20-2	22,658,946	6,774,207,430	44.70	94.11
	G20-3	22,299,990	6,661,211,674	44.95	94.13
	Total	68,432,931	20,454,236,710	134.57	281.67
	Average	22,810,977	6,818,078,903	44.86	93.89

Expression Analysis of Differentially Expressed Genes (DEGs)

Following sequencing data acquisition, datasets with excessive inter-replicate variation, data drift, or non-significant differences ($p = 0.01$) were excluded. A total of 3,851 DEGs were identified, of which 1,841 genes (47.8%) were down-regulated in flat-leaf genotype G19 compared to compact-leaf genotype G20, while 2,010 genes (52.2%) were up-regulated (Fig. 3).

GO Annotation of Differentially Expressed Genes

The 3,851 DEGs were functionally annotated using the GO database, yielding annotations for 3,419 genes (Fig. 3). These genes were classified into 48 functional groups across three major categories: "Biological Process" (19 subcategories), "Cellular Component" (16 subcategories), and "Molecular Function" (13 subcategories). In "Biological Process", the most enriched terms were metabolic processes, cellular processes, and single-organism processes. For "Cellular Component", the predominant annotations included cell, cell part, organelle, and membrane. In "Molecular Function", catalytic activity and binding were the most frequently annotated terms (Fig. 4).

KEGG Annotation of Down-Regulated Differentially Expressed Genes

KEGG enrichment analysis of the 3,851 DEGs revealed that down-regulated genes in G19 vs G20) were annotated to 123 secondary pathways (Fig. 4). The metabolic pathways included: "Cellular Processes": 47DEGs, "Environmental Information Processing":128DEGs, "Genetic Information Processing":171 DEGs, "Metabolism":467DEGs, "Organismal Systems":73DEGs.

The "Metabolism" category encompassed 33 secondary pathways, with notable enrichment in starch and sucrose metabolism (31 genes), carbon metabolism (30 genes), glycolysis/gluconeogenesis (29 genes), and amino acid biosynthesis (21 genes). "Environmental Information Processing" included hormone signal transduction (63 genes), MAPK signaling pathway (47 genes), ABC transporters (9 genes), and phosphatidylinositol signaling (9 genes). "Genetic Information Processing" involved RNA transport (29 genes), spliceosome (26 genes), and ubiquitin-mediated proteolysis (24 genes). All 73 DEGs in "Organismal Systems" were annotated to the "plant-pathogen interaction" pathway. "Cellular Processes" included peroxisome (16 genes) and endocytosis (31 genes).

Notably, the "hormone signal transduction" pathway (ko04075) under "Environmental Information Processing" was identified as potentially associated with sunflower leaf architecture regulation (Figs. 5).

Signal Transduction Analysis of Differentially Expressed Genes

Based on the preceding analytical results, this study identified four metabolic pathways within the "hormone signal transduction" pathway that may be associated with petiole inclination angle formation (Figs. 6-9: in Figs. 6-9, Panel A represents the upregulated pathways in G20 compared to G19, while Panel B represents the downregulated pathways).

"Figure 6" illustrates ubiquitination modification of the auxin receptor protein (TIR1) in the nucleus. In the upregulated pathway (Fig. 6A), the expression levels of (AUX/IAA) and ARF proteins were elevated, promoting the upregulation of (AUX/IAA), GH3, and SAUR. This indirectly facilitated plant cell expansion and organ growth, leading to a compact leaf posture where petioles adhere closely to stems. Conversely, in the downregulated pathway (Fig. 6B), reduced ARF protein expression suppressed SAUR synthesis, ultimately increasing the petiole-stem angle and resulting in a prostrate leaf morphology. Collectively, these findings suggest that the upregulated expression of (AUX/IAA) and GH3 contributes to the compact leaf posture observed in G20.

"Figure 7A" demonstrates that CRE1 participates in transmembrane signaling to promote cytokinin-mediated processes. In the cytoplasm, phosphorylation enhances the synthesis of the cytokinin receptor AHP. Subsequently, AHP activates the upregulation of B-type

response regulators (B-ARR) through phosphorylation, indirectly promoting cell division and shoot initiation, thereby reinforcing the compact leaf posture. In contrast, "Figure 7B" shows that downregulation of B-ARR protein expression leads to a prostrate leaf morphology. This analysis infers that the upregulated expression of B-ARR represents another mechanism underlying the compact leaf posture of G20.

"Figure 8" highlights the role of gibberellin signaling. In the nucleus, the expression abundance of the gibberellin receptor protein GID1 modulates the expression of the transcriptional regulator DELLA, indirectly regulating growth processes to influence leaf posture. "Figure 8A" indicates that the upregulation of DELLA protein expression may serve as a third potential factor contributing to the compact leaf morphology of G20.

"Figure 9" reveals differential phosphorylation levels of the heterodimer formed by BRI1 (a serine/threonine-dependent receptor kinase) and its co-receptor BRK1 on the cell membrane. In Fig. 9A, sequential phosphorylation of BAK1 and BRI1 amplifies and transmits signaling to the nucleus, upregulating the downstream transcription factors BZR1/2 and initiating the expression of TCH4 enzymes. In contrast, Fig. 9B shows downregulation of this pathway. These observations suggest that differential TCH4 enzyme expression levels may underlie the distinct leaf postures between G20 and G19.

Conclusions and Discussion

Under the constraints of limited arable land resources, increasing plant density to enhance sunflower seed yield per unit area has become a critical issue in Chinese sunflower production. This necessitates consideration of plant morphological adaptability to high-density planting conditions.

In this study, transcriptome sequencing of two sunflower inbred lines with distinct leaf morphologies (flat-leaf G19 and compact-leaf G20) revealed 3,851 differentially expressed genes (DEGs). Comparative analysis showed 1,841 downregulated and 2,010 upregulated genes in G19 relative to G20, suggesting these DEGs may directly or indirectly regulate petiole angle formation. Gene Ontology (GO) annotation classified these DEGs into 19 biological process subcategories, 16 cellular component subcategories, and 13 molecular function subcategories, indicating complex genetic regulation in sunflower petiole angle development.

KEGG enrichment analysis demonstrated that 886 downregulated genes in G19 compared to G20 were annotated to 123 secondary pathways. These included:

1) Metabolic pathways: starch/sucrose metabolism, carbon metabolism, glycolysis/gluconeogenesis, amino acid biosynthesis

- 2) Environmental information processing: hormone signal transduction, MAPK signaling, ABC transporters, phosphatidylinositol signaling
- 3) Genetic information processing: RNA transport, spliceosome, ubiquitin-mediated proteolysis
- 4) Organismal systems: plant-pathogen interaction
- 5) Cellular processes: peroxisome and endocytosis.

Phytohormones including brassinosteroids (BRs), gibberellins (GAs), auxin (IAA), abscisic acid (ABA), and ethylene play crucial roles in leaf angle regulation (Li, 2020; Zhou, 2017; Luo, 2016; Sakamoto, 2013; Tang, 2018). Auxin signaling components (Aux/IAA, ARF, SCF complex) regulate cell elongation and leaf angle in rice (Song, 2009). Type-B ARR transcription factors mediate cytokinin signaling by regulating target genes (Zubo, 2020). DELLA proteins, GA signaling repressors, form GA-GID1-DELLA trimers that undergo SCF-mediated 26S proteasomal degradation to release growth inhibition (Blanco, 2020). BRs critically regulate leaf erectness through biosynthesis and signaling pathways (Yamamuro, 2000; Hong, 2005; Zhang, 2014).

This study identified four nuclear signaling pathways (ko04075: plant hormone signal transduction) potentially associated with sunflower leaf morphology:

- 1) Tryptophan metabolism: Upregulation of GH3 and Aux/IAA in G20 may contribute to compact architecture
- 2) Zeatin biosynthesis: Elevated Type-B ARR expression represents a secondary mechanism
- 3) Diterpenoid biosynthesis: DELLA protein upregulation suggests a tertiary regulatory pathway
- 4) Brassinosteroid biosynthesis: Enhanced BZR1/2 transcription factor activity amplifies signaling, initiating TCH4 enzyme upregulation that differentiates G20 and G19 leaf phenotypes.

These findings provide molecular insights into leaf angle regulation and propose potential genetic targets for optimizing sunflower plant architecture under high-density cultivation systems.

Declarations

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Author Contribution

Authors' Contribution Statements: BAO Haizhu, CAO Kai and ZHOU Yanan contributed equally to this work, conducted field testing and collected phenotype data, analyzed data, and wrote the first draft of the manuscript. GAO Julin and ZHANG Xiaohong conceived the project and produced the final version of the manuscript. LU Jiafeng, QU Juanyong, LU Chunguang, LU Mingyue, HANG Yang, FU Xinyao, WANG Shiyao's main contribution was writing-editing. All authors provided suggestions during revision of the manuscript.

Data Availability

Sequence data that support the findings of this study have been deposited in the GEO repository with the primary accession code GSE295140

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Figures



Figure 1

flat-leaf type G19 and compact-leaf type (G20)

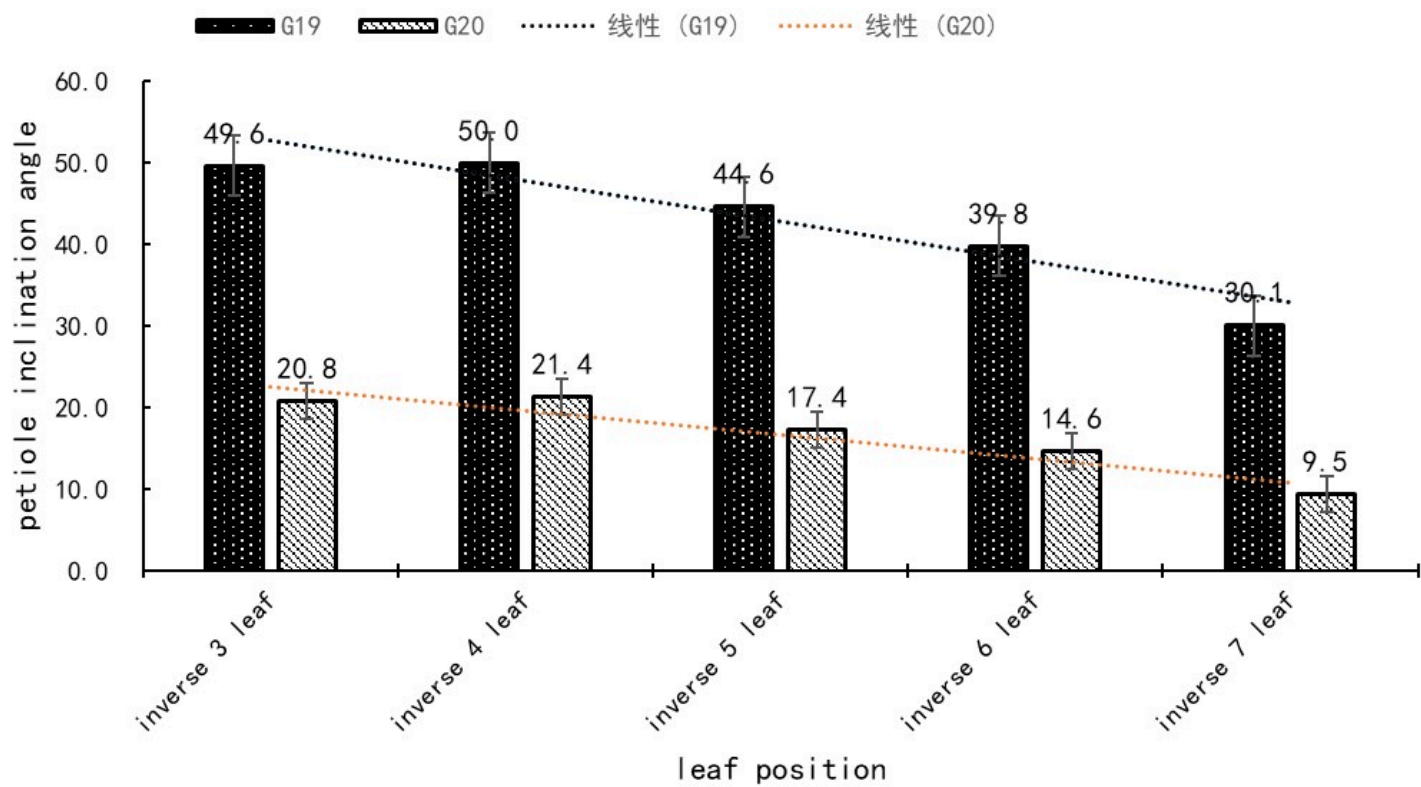


Figure 2

Comparison of petiole angle between G19 and G20

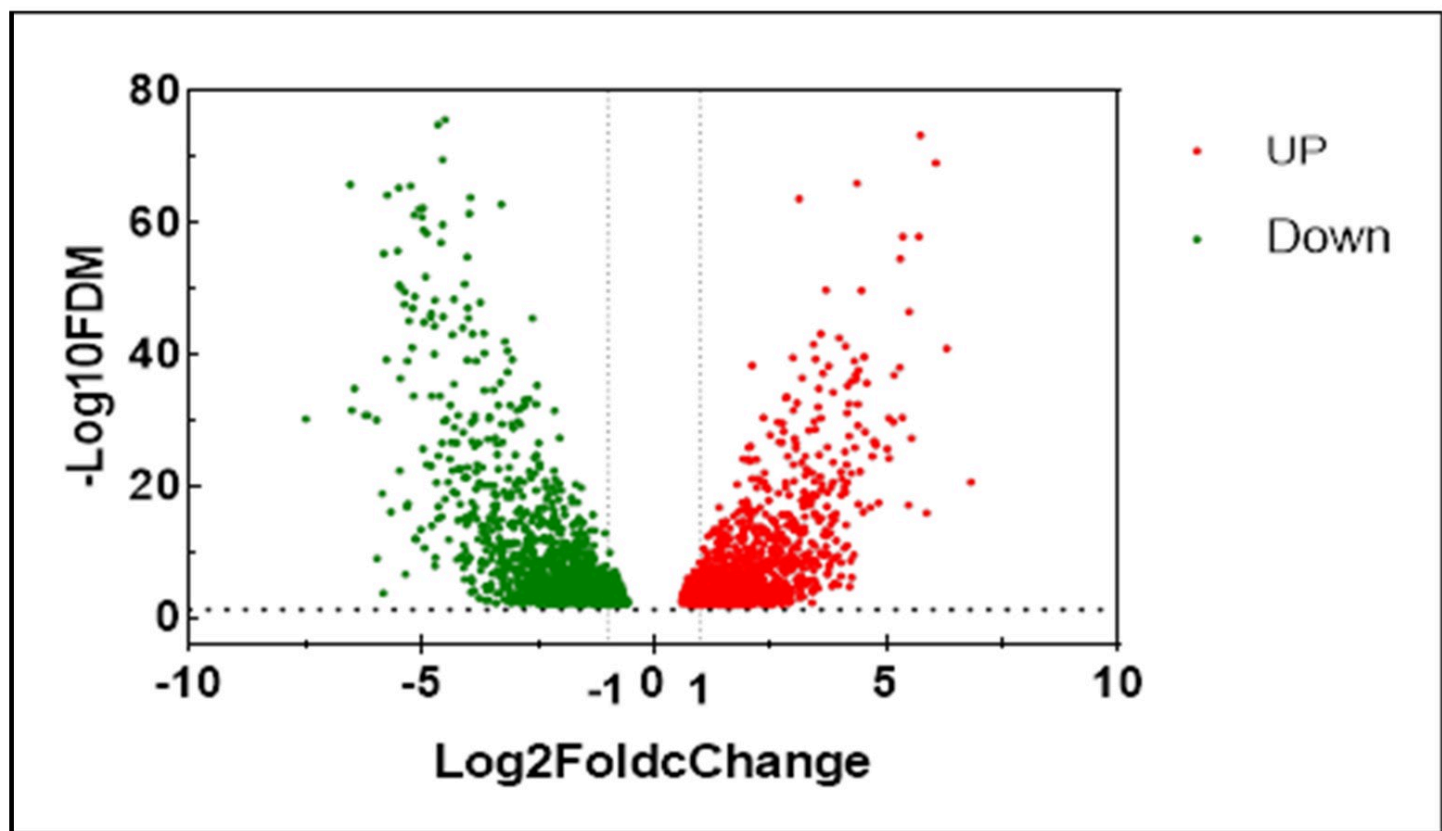


Figure 3

G19 vs G20 differentially expressed gene volcanomap

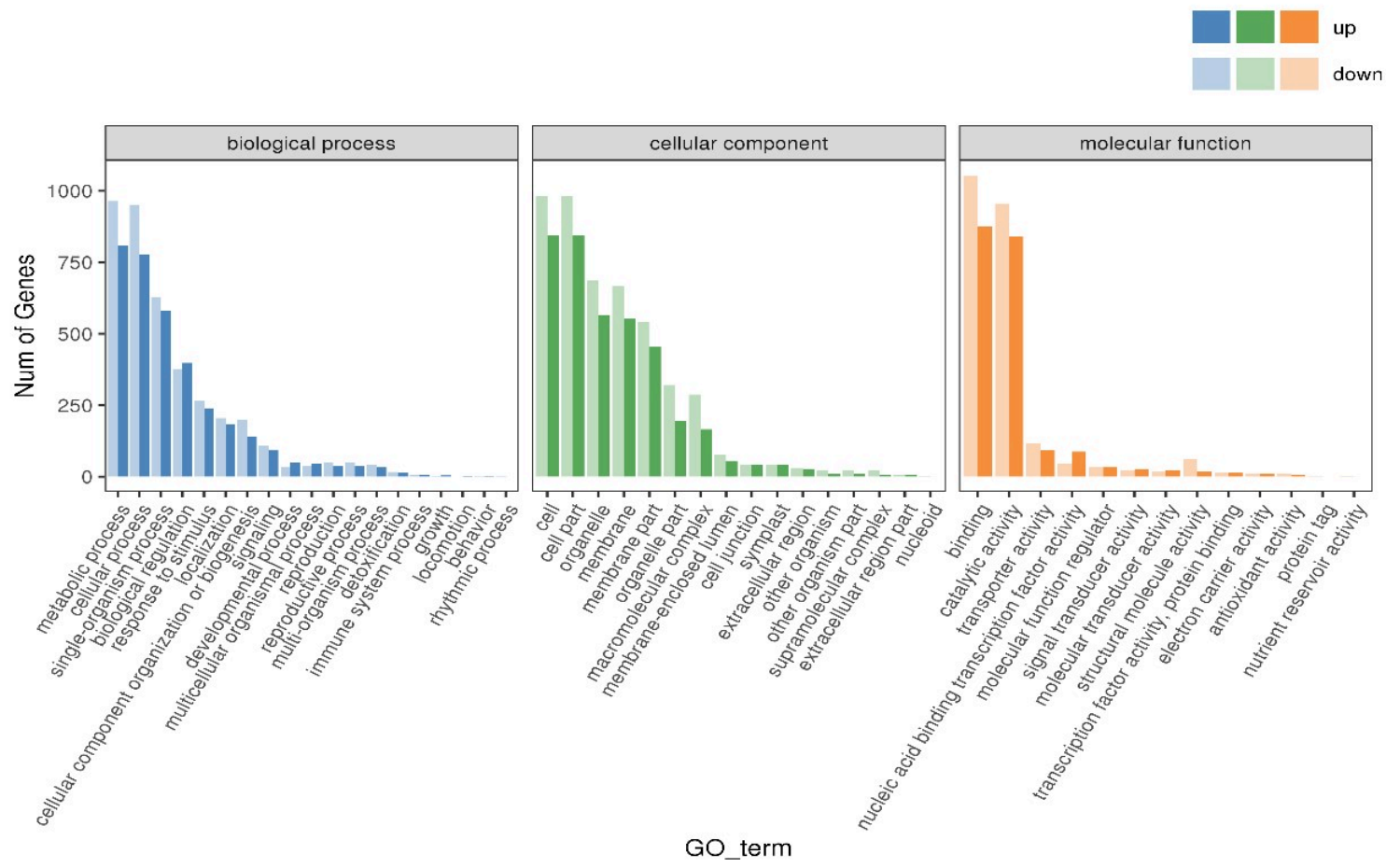


Figure 4

GO classification of differentially expressed genes in G19 vs G20

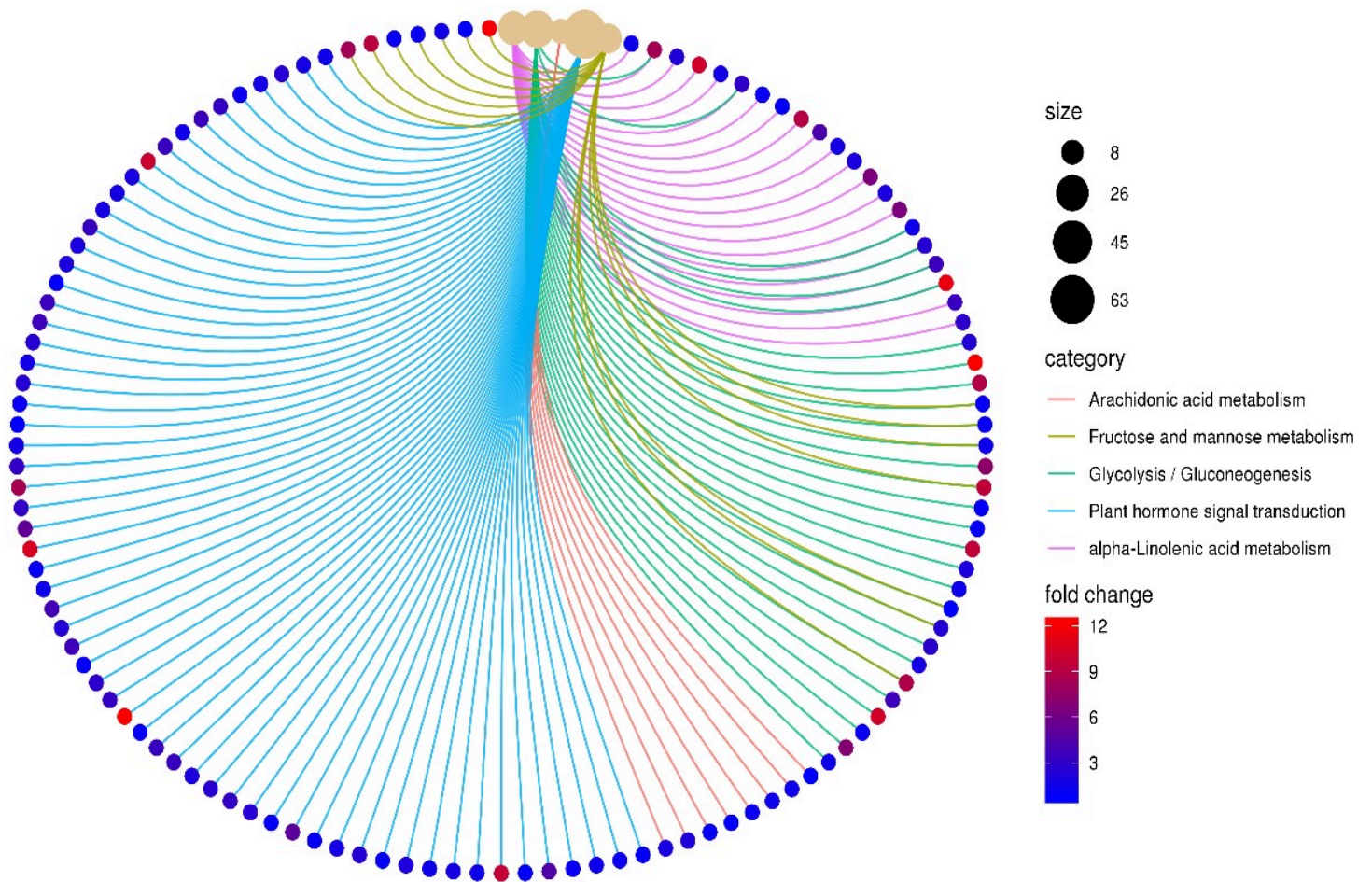


Figure 5

KEGG classification of DEGs in G19 vs G20

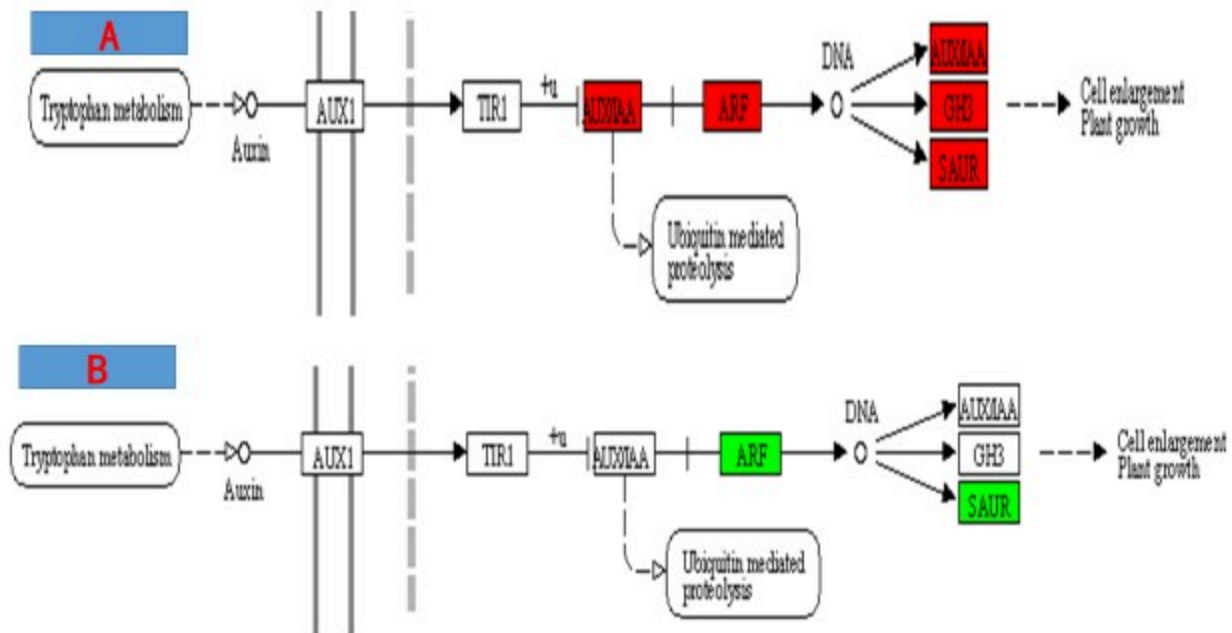


Figure 6

Tryptophan metabolism pathway

Data source: https://www.kegg.jp/kegg-bin/search_pathway_text?map=map&keyword=04075&mode=1&viewImage=true

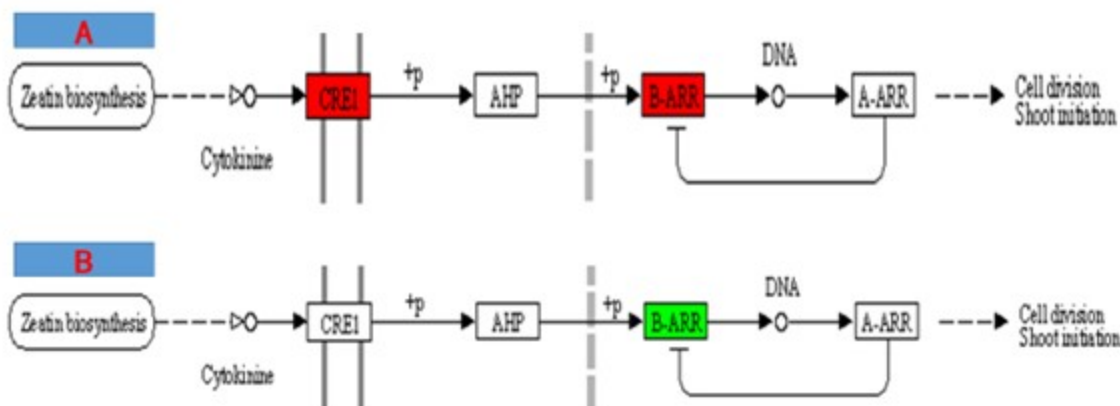


Figure 7

Zeatin biosynthesis pathway

Data source: https://www.kegg.jp/kegg-bin/search_pathway_text?map=map&keyword=04075&mode=1&viewImage=true

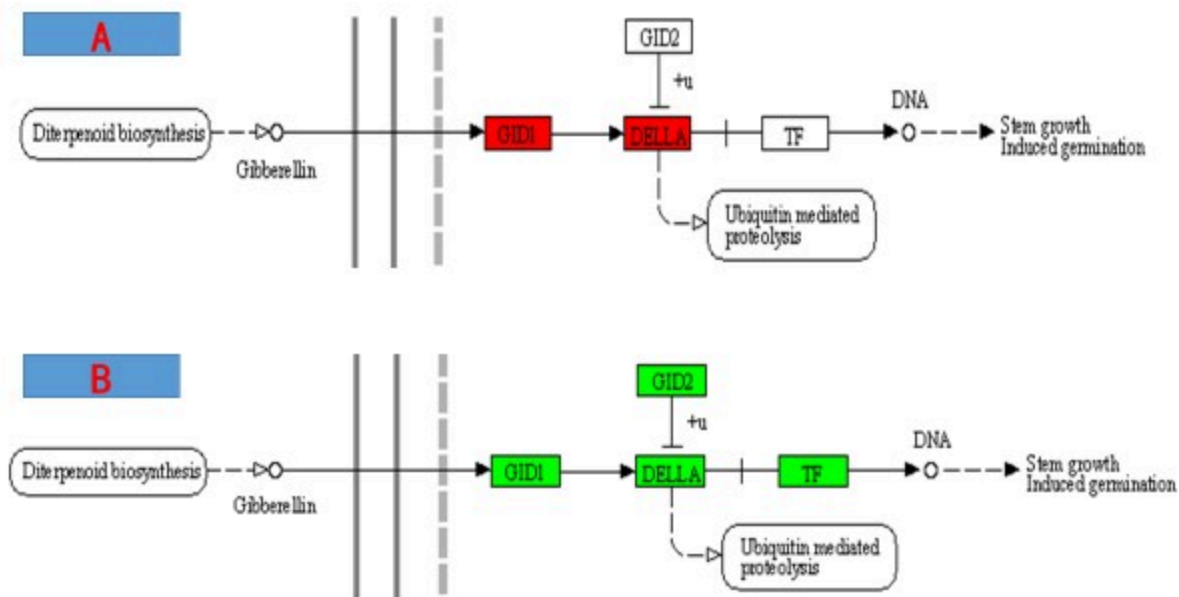


Figure 8

Diterpenoid biosynthesis pathway

Data source: https://www.kegg.jp/kegg-bin/search_pathway_text?map=map&keyword=04075&mode=1&viewImage=true

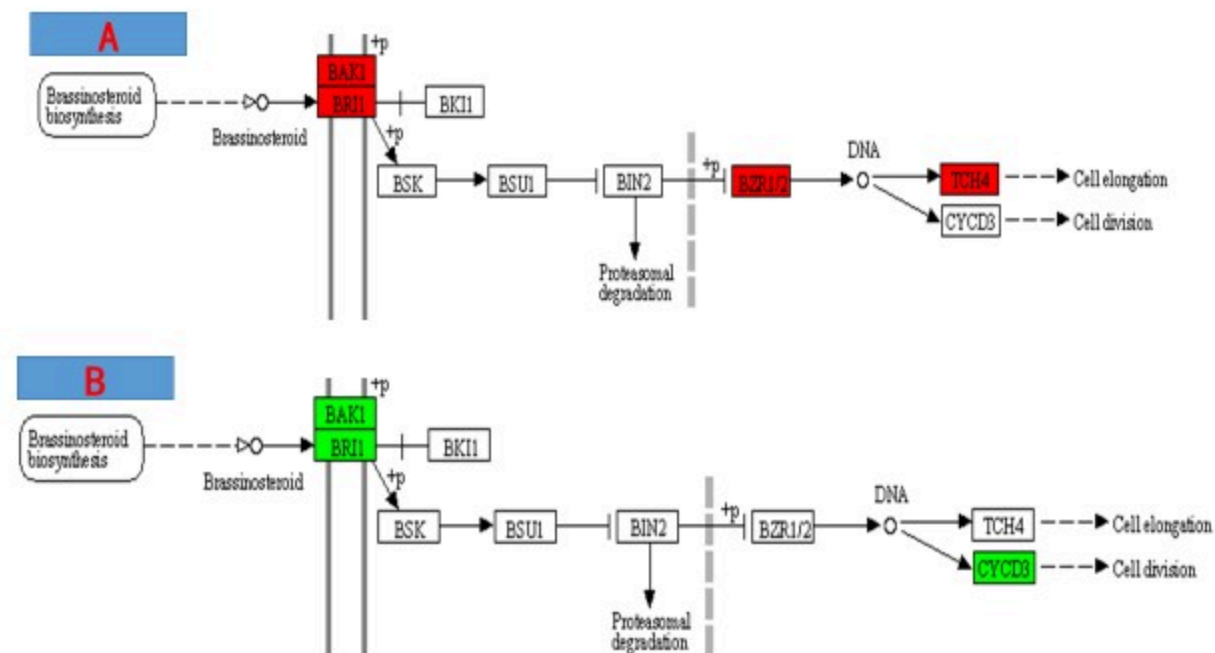


Figure 9

Brassinosteroid Biosynthesis pathway

Data source: https://www.kegg.jp/kegg-bin/search_pathway_text?map=map&keyword=04075&mode=1&viewImage=true