

60Co- γ irradiation disrupts leaf polarity by modulating PeAS1 and PeKAN2 expression in *Phalaenopsis equestris*

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Research Article

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Abstract

Background

The establishment of adaxial-abaxial polarity in leaves is fundamental to their planar growth, regulated by intricate genetic networks. While ^{60}Co - γ -irradiation is a widely used physical mutagen for generating novel plant germplasm, the molecular links between radiation-induced morphological variations and endogenous developmental programs remain unclear.

Results

Using *Phalaenopsis equestris* as a model, we observed that 40Gy ^{60}Co - γ -irradiation significantly induces heteromorphic leaf phenotypes. Morphological and cytological analyses revealed increased leaf length-to-width ratios and decreased surface area post-irradiation, characterized by disordered palisade and spongy tissue arrangement and a significant reduction in cell roundness. Transcriptomic analysis identified numerous differentially expressed genes enriched in cell wall metabolism and adaxial-abaxial polarity establishment pathways. Both the abaxial determinant *PeKAN2* and the adaxial determinant *PeAS1* were significantly downregulated post-irradiation. The synergistic downregulation of *PeAS1* and *PeKAN2* disrupted the dynamic balance between adaxial and abaxial determinants, driving abnormal anisotropic cell expansion and ultimately altering leaf polar growth. Virus-induced gene silencing of *PeKAN2* or *PeAS1* individually resulted in significant changes in *Phalaenopsis* leaf morphology and caused cascading dysregulation of the entire polarity gene network, including *PeHD-ZIP*, *PeYABBY*, and *PeARF*.

Conclusions

This study provides new insights into leaf polarity regulation in non-model plants and establishes a theoretical foundation and molecular targets for radiation mutagenesis breeding in orchids.

1.Introduction

Phalaenopsis orchids, often lauded as the “Queen of Orchids”, are among the most significant economically important ornamental cut flowers globally, owing to their graceful morphology, vibrant colors, and extended blooming period [1]. With the rapid expansion of the floriculture industry, continuous innovation in inflorescence structure, flower shape, and leaf morphology has become a primary objective in *Phalaenopsis* breeding. Among various breeding strategies, physical mutagenesis, exemplified by ^{60}Co γ -ray induced mutation, offers distinct advantages due to its high mutation frequency, broad mutagenic spectrum, strong penetration, and absence of exogenous gene insertion [2]. Radiation can induce direct or indirect DNA damage and reactive oxygen species bursts, thereby globally remodeling plant physiological metabolism and developmental patterns [3]. Previous studies have

indicated that in Orchidaceae, ^{60}Co γ -irradiation induces mutant phenotypes including floral color variation, foliar malformations, and modifications of plant architecture. Exposure of different *Phalaenopsis* cultivars to graded doses of ^{60}Co γ -rays revealed cultivar-specific responses, reflecting differential radiosensitivity. Using primary bulbs of *Phalaenopsis* as the irradiation material, doses of 20–40 Gy elicited leaf mutations. Other studies report that 10 Gy induces vegetative mutations, 25 Gy produces floral mutations, and doses ≥ 40 Gy suppress flowering [4]. Appropriate doses of γ -ray irradiation can promote *Phalaenopsis* leaf growth, enhance antioxidant enzyme activity, and increase soluble sugar content, demonstrating significant potential in regulating plant growth and development [5].

Beyond promoting growth, irradiation often induces pronounced morphological alterations, including leaf curling, distortion, and malformation [6]. Similar changes have been reported in *Oryza sativa* L, *Solanum lycopersicum* L, *Triticum aestivum* L, and *Chrysanthemum morifolium* Ramat [7–9]. However, the precise molecular mechanisms by which gamma-ray irradiation disrupts endogenous developmental networks to induce aberrant leaf polarity in *Phalaenopsis* orchids remain largely unknown.

As the primary organs for photosynthesis and gas exchange, leaf morphology dictates a plant's efficiency in light capture and reflects species evolution and environmental adaptation [10]. The formation of flattened, functional leaves fundamentally relies on the correct establishment and maintenance of adaxial-abaxial polarity within early leaf primordia, a process regulated by a network of antagonistic and synergistic transcription factors [11]. In model plants like *Arabidopsis thaliana*, Class III Homeodomain-Leucine Zipper (*HD-ZIP*) genes are the principal determinants of adaxial cell fate, while the *KANADI* and *YABBY* gene families specify abaxial identity [12]. The *ASYMMETRIC LEAVES1/2* (*AS1-AS2*) complex functions in the adaxial domain, suppressing ectopic expression of the abaxial gene *KANADI* through mechanisms such as epigenetic silencing, thereby maintaining a stable polarity boundary [13]. Any perturbation to this delicate balance typically results in severe leaf curling, loss of polarity, or even developmental arrest [14].

In *Oryza sativa* L, the *KANADI* family member *SHALLOT LIKE1* (*SLL1*) regulates leaf rolling by controlling adaxial-abaxial polarity development [15]. In *Brassica campestris*, overexpression of the *YABBY* family gene *BcYAB3* induced downward leaf curling, while *BcAS2* overexpression induced upward leaf curling, suggesting conserved roles for *YABBY* and *AS2* genes in establishing leaf adaxial-abaxial polarity [16, 17]. Although the regulatory framework for leaf polarity is largely understood in model plants, its conservation and response to radiation stress in non-model horticultural species, particularly orchids, remain to be systematically elucidated. Our prior transcriptomic analysis revealed that irradiation significantly impacts genes associated with cell expansion and proliferation in *Phalaenopsis* [5]. Concurrently, we observed a specific dumbbell-shaped leaf phenotype following 40Gy ^{60}Co - γ irradiation, suggesting that irradiation may interfere with the polarity network governing planar leaf growth.

This study employed a 40Gy dose of ^{60}Co - γ irradiation on *Phalaenopsis equestris* to investigate the phenotypic characteristics, cytological basis, and molecular regulatory pathways of irradiation-induced

abnormal leaf polarity growth. By integrating morphological, cytological, and transcriptomic analyses, we demonstrated that synergistic suppression of *PeAS1* and *PeKAN2* expression by 40Gy ^{60}Co - γ irradiation disrupted adaxial-abaxial polarity, resulting in dumbbell-shaped leaves. This research elucidates a novel regulatory mechanism of leaf polarity in *Phalaenopsis* and provides crucial genetic resources and theoretical support for targeted improvement of leaf traits in orchid breeding.

2. Materials and Methods

2.1. Plant Growth Conditions and Irradiation Treatment

The plant material used in this experiment was *Phalaenopsis equestris* of uniform and vigorous growth. The plants were cultivated in an artificial climate chamber under the following environmental conditions: temperature of 23–27°C, relative humidity of 60%-80%, and a photoperiod of 12h light/12h dark. Twenty plants in the irradiation treatment were exposed to a ^{60}Co γ -ray source at a dose rate of $150\text{ Gy}\cdot\text{h}^{-1}$, receiving a cumulative absorbed dose of 40 Gy. The control (WT) comprised five non-irradiated plants. Following treatment, all plants were returned to the aforementioned growth environment for continued cultivation.

2.2. Transcriptome Analysis

Leaf samples were collected from control and 40 Gy FZ irradiated groups, with three biological replicates per treatment. Total RNA was extracted using the TRIzol reagent and subjected to paired-end sequencing on the Illumina Novaseq 6000 platform. Raw sequencing data (clean data) were mapped to the *Phalaenopsis* reference genome. Differentially expressed genes (DEGs) were identified using DESeq2 software with criteria of $|\log_2(\text{Fold Change})| \geq 1$ and adj. P-value < 0.05 . Subsequently, gene functional annotation and pathway enrichment analyses were performed using GOseq and KOBAS software.

2.3. Functional Validation of Virus-Induced Gene Silencing (VIGS)

To functionally validate the candidate genes *PeAS1* and *PeKAN2*, a VIGS expression vector based on the Cymbidium mosaic virus (CymMV) was constructed. Specific fragments of approximately 300 bp of the target genes were amplified and cloned into the pCymMV vector using the BP reaction. Recombinant plasmids were transformed into *Agrobacterium tumefaciens* strain EHA105 and inoculated into tender leaves of *Phalaenopsis* by injection. Plants inoculated with the pCymMV empty vector served as the negative control. Leaf morphology variations were observed 30 days post-inoculation, and samples were collected to assess silencing efficiency.

2.4. Leaf Growth Observation

Following irradiation and VIGS treatments, plant phenotype photographs were taken periodically. The ImageJ software was employed to measure leaf length, width, and total surface area, from which the

leaf aspect ratio was calculated. By comparing the growth rates and morphological characteristics of leaves before and after treatment, the impact of irradiation on polarity development was assessed.

2.5.Measurement of Leaf Transverse Curvature Index

The leaf's degree of curling was quantitatively assessed using the Curvature Index (CI)[18]. The CI is calculated as: $CI = (Lw - Ldist) / Lw \times 100\%$, where Lw is the actual width of the flattened leaf blade, and Ldist is the straight-line distance between the leaf margins in its naturally curled state. A higher CI value indicates a more pronounced adaxialization, or upward curling, of the leaf blade.

2.6.SEM and paraffin sections

Scanning Electron Microscopy (SEM): Fresh leaf segments (5x5mm) were fixed in 2.5% glutaraldehyde, dehydrated through an ethanol series, and critical-point dried. Samples were then sputter-coated with gold and observed under SEM to characterize epidermal cell morphology. Paraffin Sectioning: Specimens were fixed in FAA for over 24 hours, dehydrated using a gradient ethanol series, cleared with xylene, and embedded in paraffin. Transverse sections (8–10 μ m thickness) were cut using a microtome, stained with safranin-fast green, and imaged with a light microscope. Circularity of mesophyll cells was quantified using ImageJ software.

2.7.Real-time PCR Analysis

Total RNA was extracted from each sample group using a plant total RNA extraction kit and then reverse transcribed into cDNA. Using *PeActin* as the internal reference gene, amplification was performed on a real-time fluorescence quantitative PCR instrument with a SYBR Green fluorescent quantitative kit. Three technical replicates were set up for the experiment. Relative expression was calculated by the $2^{-\Delta\Delta Ct}$ method, normalized to Actin, and statistically analyzed by one-way ANOVA with Tukey's test ($P < 0.05$). Statistical analysis of the data was conducted using GraphPad Prism software.

3.Results

3.1.⁶⁰Co- γ Irradiation Induces heteromorphic Leaf Formation in *Phalaenopsis*

Comparative observations between the 40 Gy irradiation group (40GyFZ) and the wild-type (WT) control revealed that irradiation significantly altered the growth habit of *Phalaenopsis*. The results indicated that compared to the flat, broad leaves of WT plants, newly developed leaves in the irradiated group (40 Gy FZ) exhibited a distinct dumbbell-shaped aberrant phenotype characterized by marginal leaf curling (Fig. 1A, B). Morphological quantitative analysis demonstrated that the length-to-width ratio of leaves in the 40 Gy FZ group was significantly increased compared to WT, signifying a more elongated leaf morphology. Concurrently, the leaf surface area was significantly reduced (Fig. 1C, D). These data suggest that ⁶⁰Co- γ ray irradiation influenced leaf expansion and polar growth.

3.2. Cytological Abnormalities and Altered Polar Gene Expression Under Irradiation Response

SEM images revealed that the epidermal cells of WT leaves exhibited regular arrangement and morphology. In contrast, post-irradiation leaf epidermal cells displayed significant shrinkage and irregular morphology (Figs. 2A, B). Histological analysis via paraffin-embedded sections showed that WT leaves possessed distinct tissue differentiation, with the adaxial surface composed of compactly arranged columnar palisade mesophyll and the abaxial surface consisting of loosely organized, irregular spongy mesophyll. However, in the 40 Gy FZ group, the clearly demarcated tissue boundaries became blurred, and the arrangement of both cell types trended towards disarray (Figs. 2C, D). To quantify cellular morphological changes, we analyzed cell circularity, which indicated significantly higher values in irradiated leaf cells compared to WT, confirming a transition from columnar to more isodiametric shapes (Fig. 2E). Furthermore, qRT-PCR analysis of key genes associated with adaxial-abaxial polarity establishment demonstrated significant alterations in the relative expression levels of adaxial-specific genes *PeAS1* and *PeAS2*, as well as the abaxial-specific gene *PeKAN*, in the irradiated group compared to WT (Fig. 2F). This suggests that the core polarity regulatory system was suppressed.

3.3. Transcriptome Analysis Reveals Alterations in Global Expression Profiles

To systematically elucidate the molecular mechanisms underlying radiation-induced polar growth at the whole-genome level, transcriptomic sequencing was performed on leaf tissues from wild-type (WT) and 40 Gy FZ-treated groups. Principal component analysis demonstrated excellent intra-group reproducibility and clear inter-group separation, indicating high data quality and reliability (Fig. 3A). Venn diagram analysis revealed 15,521 co-expressed genes between the two groups, with an additional 817 radiation-specific genes in the irradiated group (Fig. 3B). Correlation and clustering analyses showed distinct clustering of WT and irradiated samples (Fig. 3C), confirming the suitability of the transcriptomic data for subsequent analyses. Volcano plot analysis indicated greater expression level changes in upregulated genes compared to downregulated genes in the WT versus irradiated groups, identifying a total of 978 upregulated DEGs and 730 downregulated DEGs (Fig. 3D). Gene Ontology (GO) functional enrichment analysis highlighted significant enrichment of differentially expressed genes in pathways such as "photosynthesis," "photosystem," and "oxidoreductase activity" (Fig. 3E). Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment predominantly focused on pathways including "ABC transporter," "starch and sucrose metabolism," and "phenylpropanoid biosynthesis" (Fig. 3F). These findings suggest that the aberrant polar growth induced by irradiation is a complex biological process involving the synergistic participation of multiple pathways, including cell wall remodeling and secondary metabolism.

3.4. The Adaxial-Abaxial Polarity Regulatory Network Exhibits Synergistic Suppression Based on transcriptomic data, we reconstructed the leaf polarity regulatory network and analyzed differential

expression of key genes (Fig. 4A). Heatmap analysis revealed significant differential expression of multiple critical polarity genes, including *PeHD-ZIP III*, *PeKAN2*, *PeAS1*, *PeYABBY*, *PeARF*, and *PeAUXIN*, post-irradiation (Fig. 4B). qRT-PCR validation of several core genes demonstrated high concordance with RNA-seq data (Fig. 4C). These findings indicate that irradiation synergistically suppresses the adaxial-abaxial polarity regulatory module.

3.5. Gene Silencing of *PeKAN2* Mimics Radiation-Induced Leaf Wrinkling and Triggers a Polarity Network Cascade Disruption

To validate the pivotal role of *PeKAN2* in radiation-induced polar growth phenotypes, we conducted virus-induced gene silencing (VIGS) experiments. Compared to the empty vector control group (Fig. 5A, B;Supplementary Figure.1A), plants with silenced *PeKAN2* exhibited severe leaf curling and distortion (Fig. 5C, D;Supplementary Figure.1B). Histological analysis revealed a complete disorganization of mesophyll cells and a near-complete loss of adaxial-abaxial polarity (Fig. 5E, F), with a significant reduction in cellular roundness (Fig. 5G). Expression of the viral coat protein (CP) gene confirmed successful infection (Fig. 5H), while substantial downregulation of *PeKAN2* verified silencing efficiency (Fig. 5I). Furthermore, silencing of *PeKAN2* led to widespread alterations in the expression of genes such as *PeHD-ZIP*, *PeARF*, *PeAUXIN*, *PeAS*, and *PeYABBY* (Fig. 5J–N), indicating that *PeKAN2* acts as a central hub in the polar gene regulatory network, and its disruption results in a cascading disorder of the entire polarity regulatory network.

3.6 Gene silencing of *PeAS1* results in severe upward leaf curling

Silencing of *PeAS1* led to a marked upward curling of leaves (Fig. 6A-D). Histological analysis of mature leaves from wild-type (WT) plants revealed that adaxial epidermal cells were larger than abaxial epidermal cells. In *PeAS1*-silenced plants, the adaxial epidermal cells were smaller than WT, while the spongy mesophyll cells were larger, and the intercellular spaces within the spongy mesophyll region were reduced. This suggests adaxialization of the leaf surface, leading to upward curling and confirming disrupted cellular arrangement and weakened adaxial-abaxial polarity (Fig. 6E, F). The lateral curvature index (CI), where positive values indicate downward bending and negative values indicate upward bending, was significantly reduced in the silenced group, confirming severe upward curling (Fig. 6G). High expression of the CP gene indicated effective infection (Fig. 6H), and the significant downregulation of *PeAS1* confirmed high silencing efficiency (Fig. 6I). Similar to *PeKAN2* silencing, *PeAS1* silencing also resulted in widespread dysregulation of polarity-related genes, including *PeHD-ZIP*, *PeARF*, *PeAUXIN*, *PeKAN2*, and *PeYABBY* (Fig. 6J-N). These findings indicate that both *PeAS1* and *PeKAN2* are indispensable for maintaining normal leaf polarity and planar growth. Impairment of either gene disrupts network homeostasis, ultimately causing similar polar growth defects, namely upward leaf curling or altered leaf morphology.

4. Discussion

This study integrates morphological, cytological, transcriptomic, and functional gene validation analyses, revealing that the fundamental cause of the significant alteration in leaf phenotype of *Phalaenopsis equestris* following 40 Gy $^{60}\text{Co-}\gamma$ irradiation (Fig. 1A, B) lies in the disruption of the antagonistic balance between the adaxial and abaxial determinant genes (AS-KAN module). The 40 Gy $^{60}\text{Co-}\gamma$ radiation induces abnormal polarity growth by synergistically suppressing the adaxial determinant gene *PeAS1* and the abaxial determinant gene *PeKAN2*, thereby disrupting the adaxial-abaxial balance and resulting in the dumbbell-shaped and curled leaves observed in *Phalaenopsis equestris*.

The establishment and maintenance of leaf flatness depend on the precise antagonistic interaction between adaxial and abaxial identity genes [19, 20]. In *Arabidopsis thaliana*, the AS1-AS2 complex promotes adaxial development, while *KANADI* genes determine abaxial identity [13, 21]. Loss-of-function mutations in *KAN* genes result in adaxialization and upward curling, whereas *AS1* silencing leads to polarity disorganization [22, 23]. In rice, the *KANADI* gene *SLL1* regulates leaf curling by controlling abaxial cell development [15]. Our findings indicate that under irradiation, both *PeAS1* and *PeKAN2* are simultaneously downregulated (Fig. 4B), diverging from the unilateral changes typically observed in model plants. This co-suppression pattern blurs the polarity boundary, leading to the distinct dumbbell-shaped leaf phenotype in *Phalaenopsis*.

Alterations in leaf macroscopic morphology originate from modifications in microscopic cellular morphology [24]. Cytological observations (Fig. 2C, D) revealed that radiation exposure impaired the normal anisotropic expansion capacity of leaf cells. Consequently, cells failed to differentiate into the typically elongated palisade tissue or the structurally distinct spongy mesophyll, exhibiting reduced circularity and restricted lateral expansion. These cellular aberrations directly resulted in narrower, smaller, and curled leaves. Similar cytological disorganization has been documented in radiation-induced mutants of rice, tomato, and wheat leaves [7–9]. Our findings establish a link between cellular morphological changes and the molecular regulation of polarity genes, thereby providing a cytological basis for radiation-induced leaf shape variations.

Environmental stresses often target developmental networks through specific signal transduction pathways in a biased manner. Transcriptomic analysis revealed differential gene expression in pathways associated with cell wall metabolism, hormone signaling, and stress responses (Figs. 3, 4B). Auxin-related genes, including *PeARF* and *PeAUXIN*, were significantly affected, suggesting that radiation may disrupt auxin distribution and subsequently modulate polarity networks. The HD-ZIP III, YABBY, and ARF gene families form a complex regulatory circuit [12]. Our findings indicate that silencing of *PeAS1* or *PeKAN2* induces a cascading disruption across the entire polarity network (Figs. 5, 6), highlighting their crucial roles as central hubs in maintaining polarity homeostasis.

From an evolutionary perspective, the functions of *AS1* and *KAN2* in leaf polarity exhibit partial conservation between *Phalaenopsis* and model plants [25–27]; however, their co-suppression patterns under radiation represent a unique characteristic of orchids. This study presents the first comprehensive

evidence linking ^{60}Co -irradiation, polar gene regulation, and leaf shape formation. In terms of horticultural breeding, 40Gy is an effective and practical dose for inducing novel leaf shapes in *Phalaenopsis*. The identified *PeAS1* and *PeKAN2* genes serve as crucial molecular targets for directed leaf structure modification via gene editing or marker-assisted selection. Our research enhances the understanding of leaf polarity regulatory mechanisms in non-model plants and establishes a robust foundation for radiation breeding and molecular design breeding in orchids.

5. Conclusion

In Conclusion, this study systematically elucidates the molecular mechanisms underlying polarity growth in *Phalaenopsis* leaves induced by ^{60}Co - γ irradiation (Fig. 7). Doses of 40 Gy ^{60}Co -irradiation induced dumbbell-shaped and curled leaves in *Phalaenopsis equestris*, potentially mediated by the synergistic downregulation of the adaxial determinant *PeAS1* and the abaxial determinant *PeKAN2*. This disruption perturbs the dynamic equilibrium of the intricate polarity regulatory network, comprising *HD-ZIP III*, *KAN*, *YABBY*, and auxin signaling factors, leading to significant abnormalities in cellular morphology and internal tissue organization. Phenotypically, this manifests macroscopically as characteristic polarity growth, resulting in dumbbell-shaped and curled leaves. Virus-induced gene silencing (VIGS) experiments confirmed the critical roles of both *PeAS1* and *PeKAN2* in maintaining normal leaf growth and polarity. This research offers novel insights into leaf polarity regulation in *Orchidaceae* and provides valuable genetic resources and theoretical support for irradiation-induced germplasm innovation and molecular breeding in *Phalaenopsis*.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Author Contribution

Yingxin Chang: Writing – original draft, Investigation, Methodology, Formal analysis. Wenjuan Yang: Validation, Methodology, Data curation. Jinjie Wu: Resources, Methodology, Investigation. Su Ni: Visualization, Validation, Formal analysis. Yuxia Lou: Resources, Data curation, Methodology. Chunyan Dong: Resources, Methodology, Investigation. Yiqiang Li: Conceptualization, Supervision, Writing – review & editing, Funding acquisition. Feng Ming: Conceptualization, Supervision, Writing – review & editing, Project administration, Funding acquisition.

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Data Availability

The datasets generated and/or analysed during the current study are available in the [NCBI] repository, with the accession number [PRJNA1502433]

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Figures

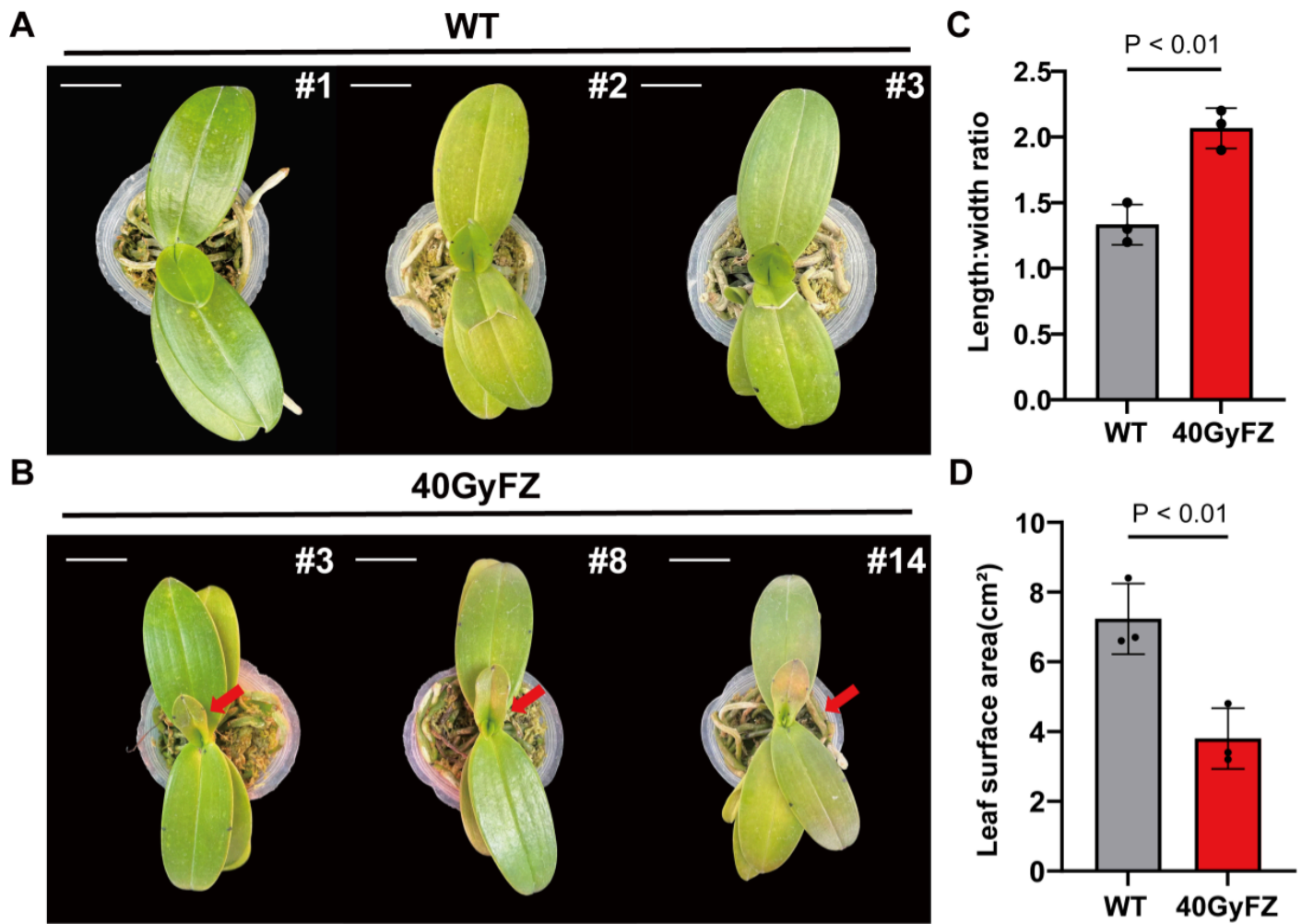


Figure 1

Phenotypic and morphological changes of *Phalaenopsis equestris* leaves induced by 40 Gy ⁶⁰Co-γ irradiation. (A) Wild-type plant. Scale bar = 5 cm. (B) 40 Gy-treated plant. (C) Leaf length-to-width ratio. (D) Leaf surface area. Data are mean ± SD.

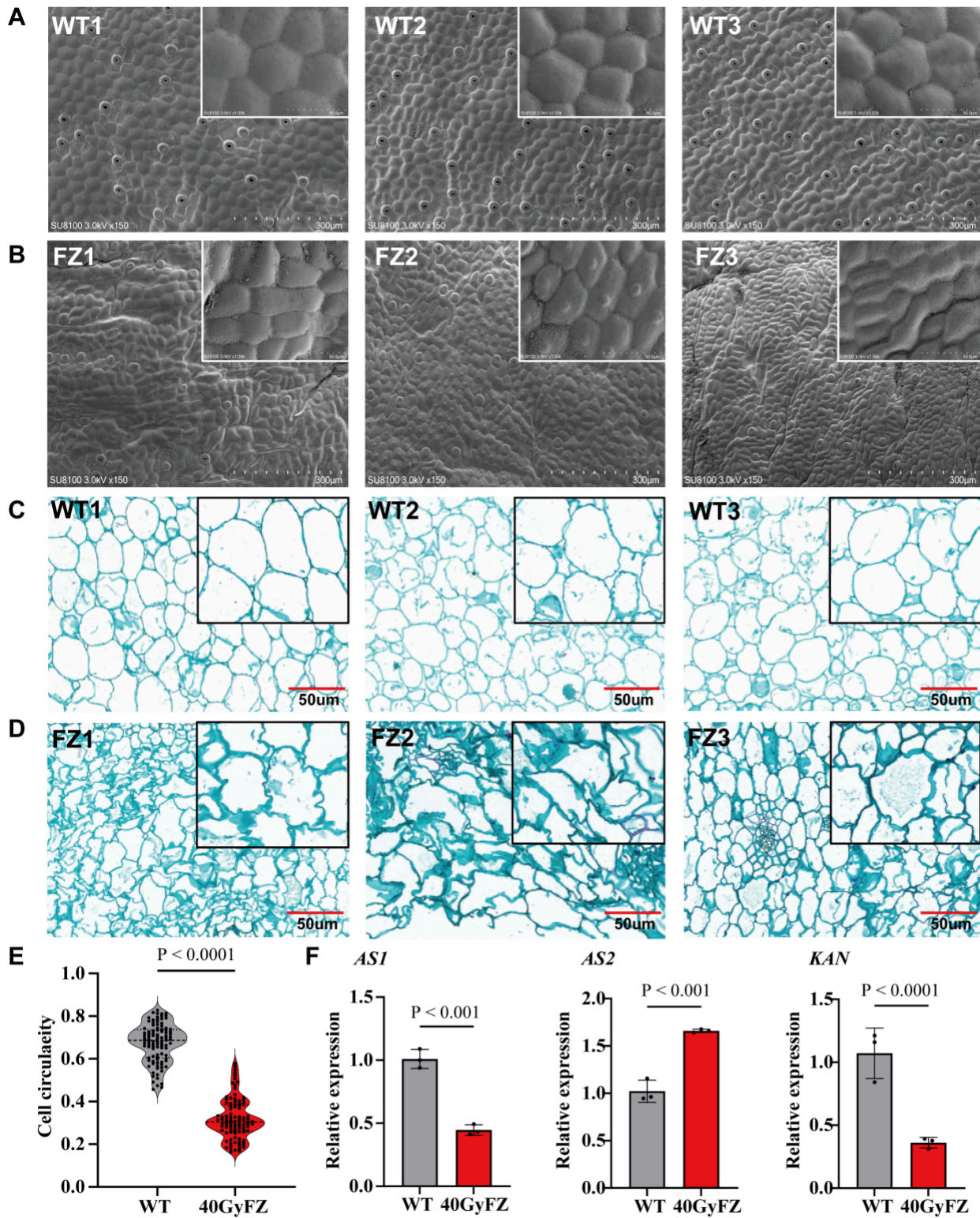


Figure 2

Cytological characteristics and polarity gene expression in WT and 40 Gy-treated leaves. (A, B) SEM images of epidermal cells. (C, D) Paraffin cross-sections. (E) Cell circularity. (F) Relative expression of *PeKAN2*, *PeAS1*, and *PeAS2*.

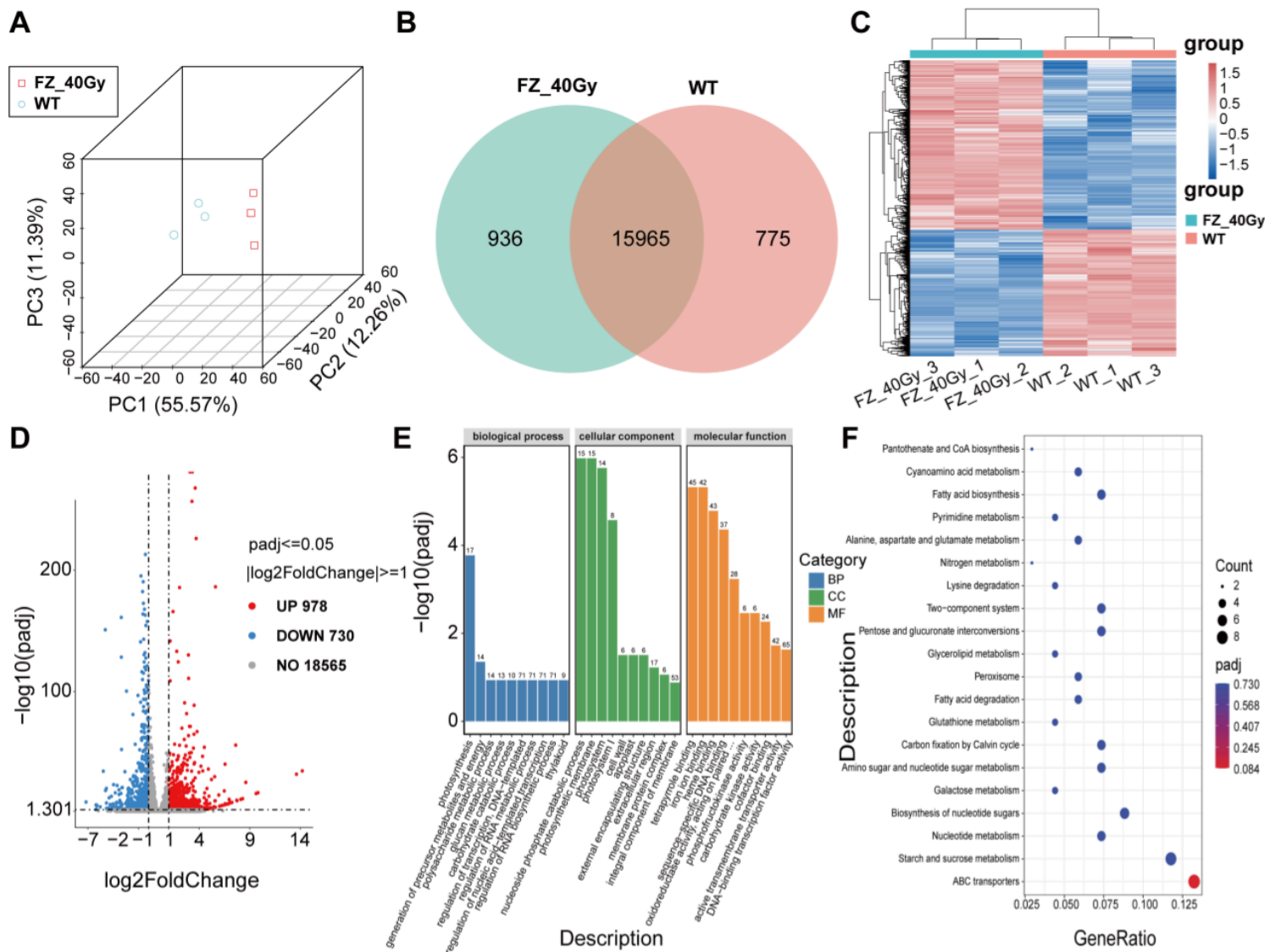


Figure 3

Transcriptome analysis of WT and irradiated leaves. (A) PCA plot. (B) Venn diagram of expressed genes. (C) Heatmap of DEGs. (D) Volcano plot of DEGs. (E) GO enrichment analysis. (F) KEGG pathway enrichment analysis.

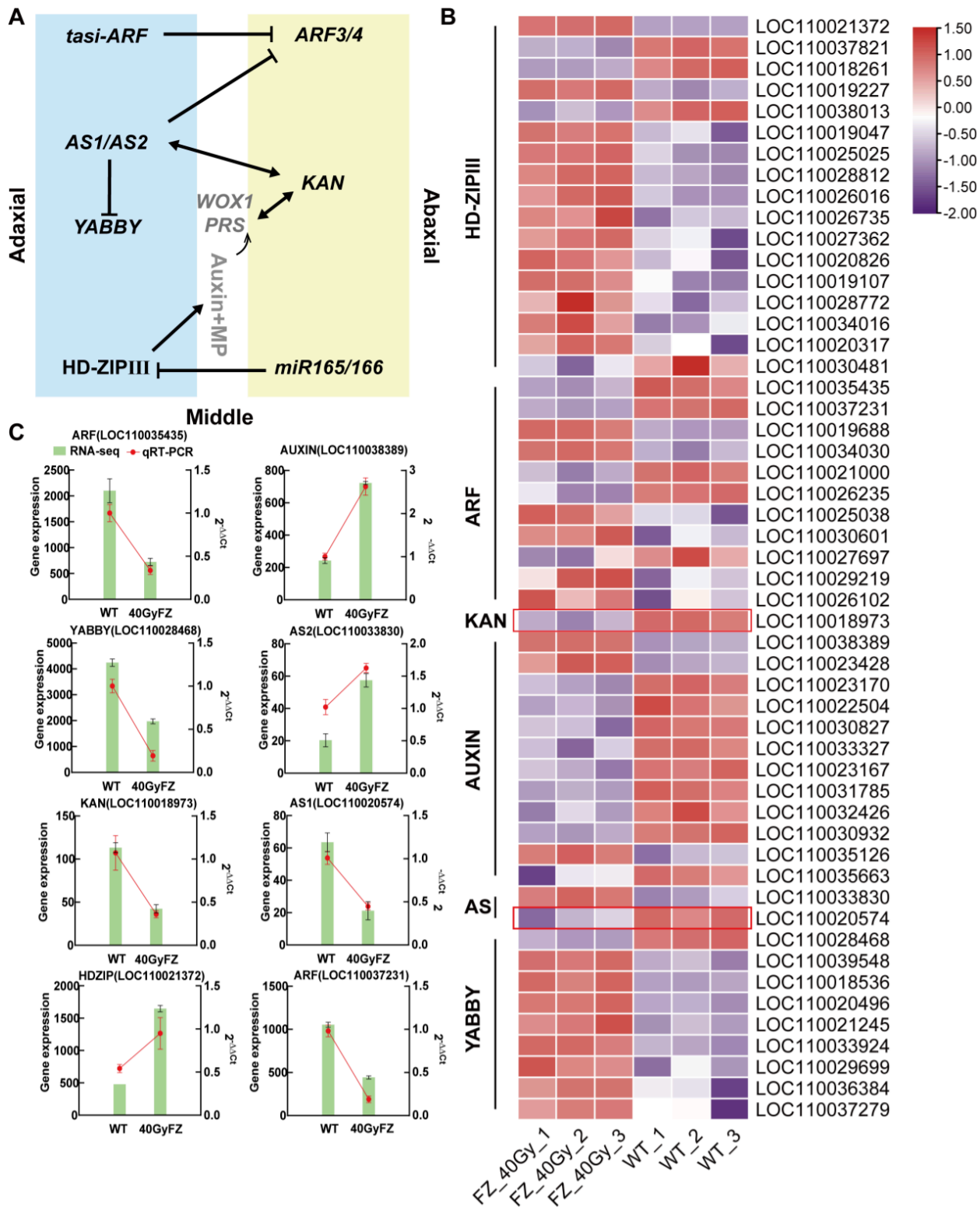


Figure 4

Expression profiles of adaxial–abaxial polarity-related genes. (A) Regulatory network of leaf polarity. (B) Heatmap of polarity DEGs. (C) qRT-PCR verification of key genes.

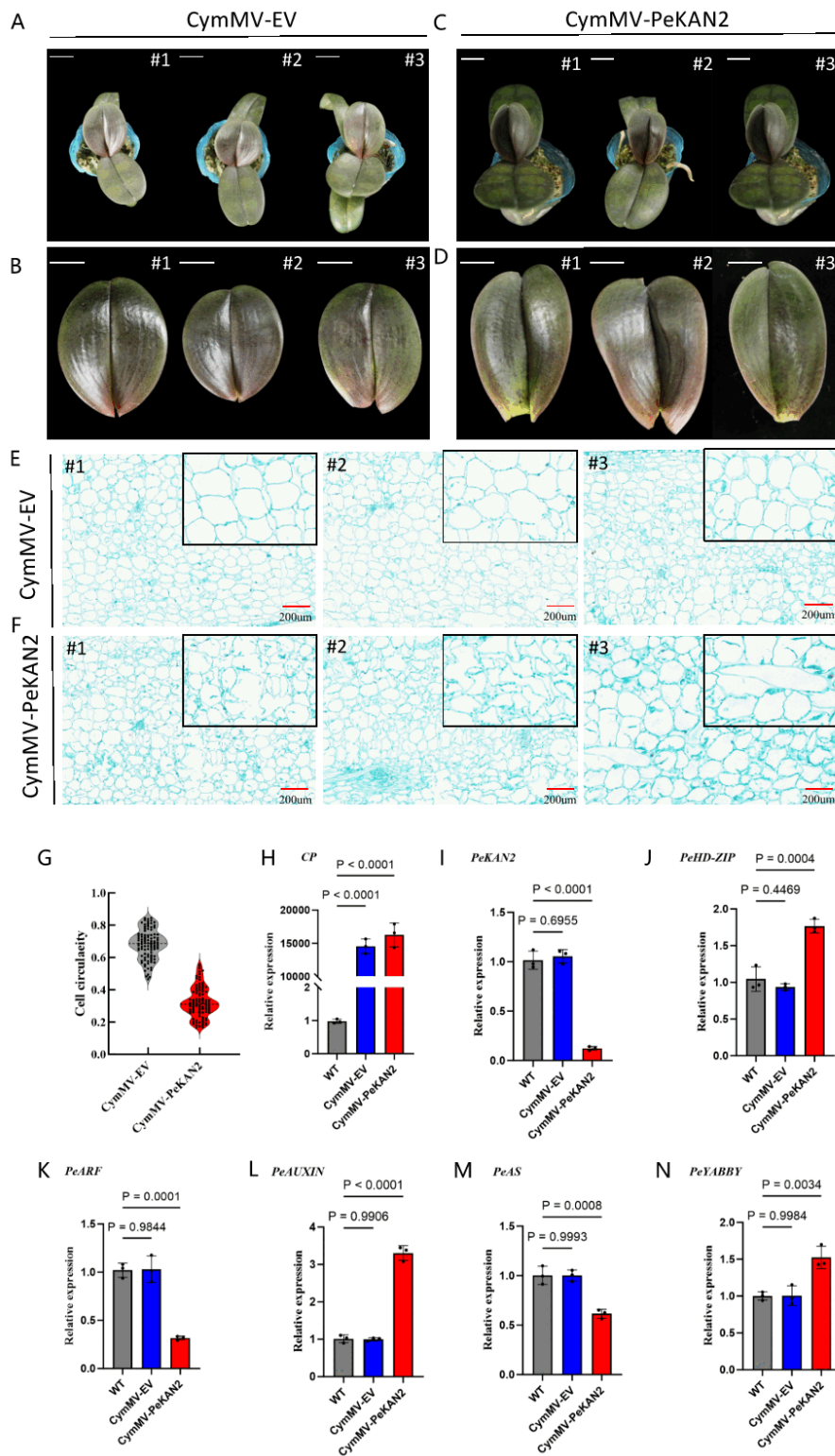


Figure 5

Functional analysis of PeKAN2 by VIGS. (A-D) Leaf morphology. (E, F) Paraffin sections. (G) Cell circularity. (H) CP gene expression. (I) PeKAN2 silencing efficiency. (J-N) Expression of other key polarity-related genes

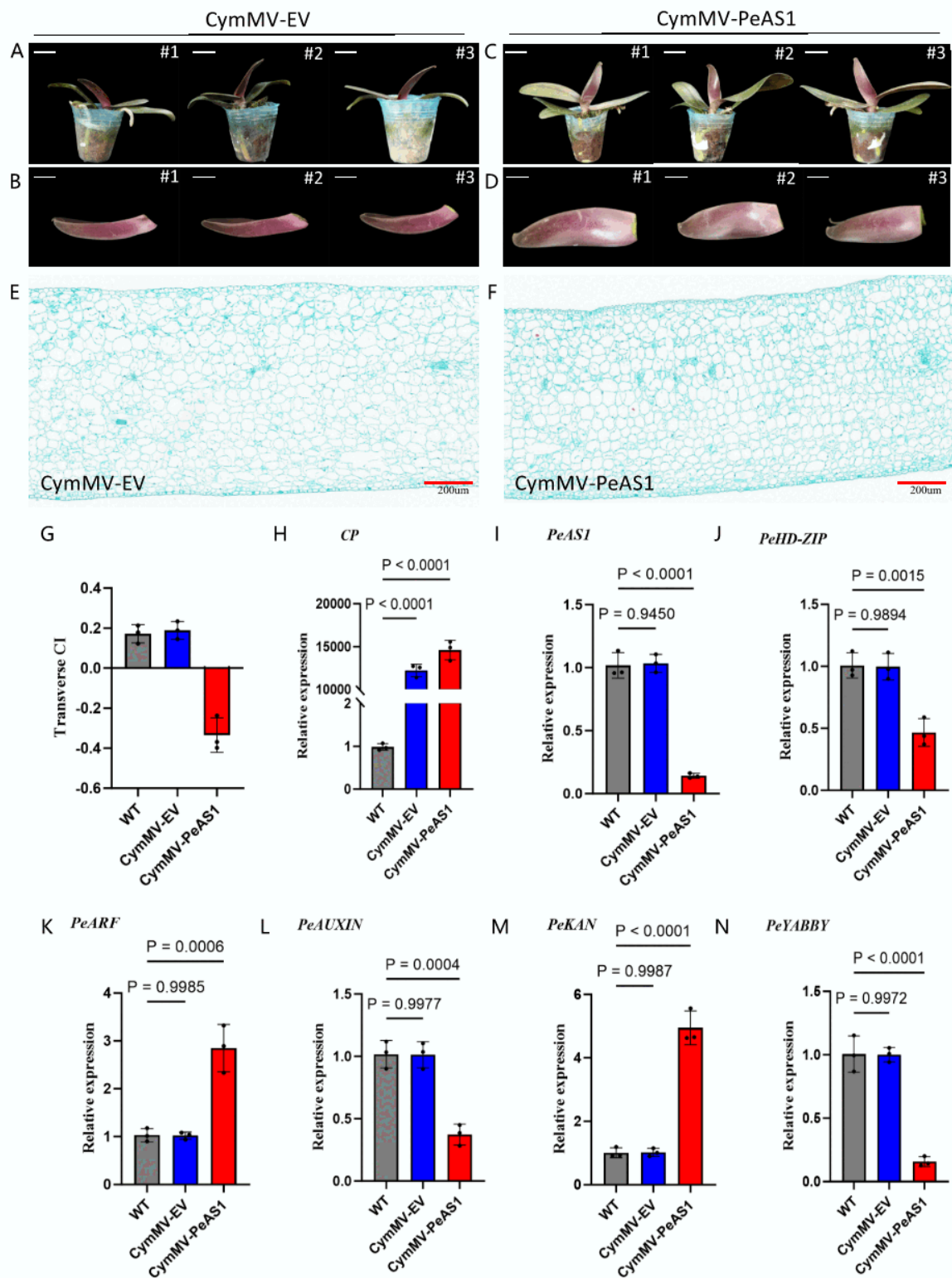


Figure 6

Functional analysis of PeAS1 by VIGS. (A-D) Leaf morphology. (E, F) Paraffin sections. (G) Transverse curvature index (CI). (H) CP gene expression. (I) PeAS1 silencing efficiency. (J-N) Expression of other key polarity-related genes.

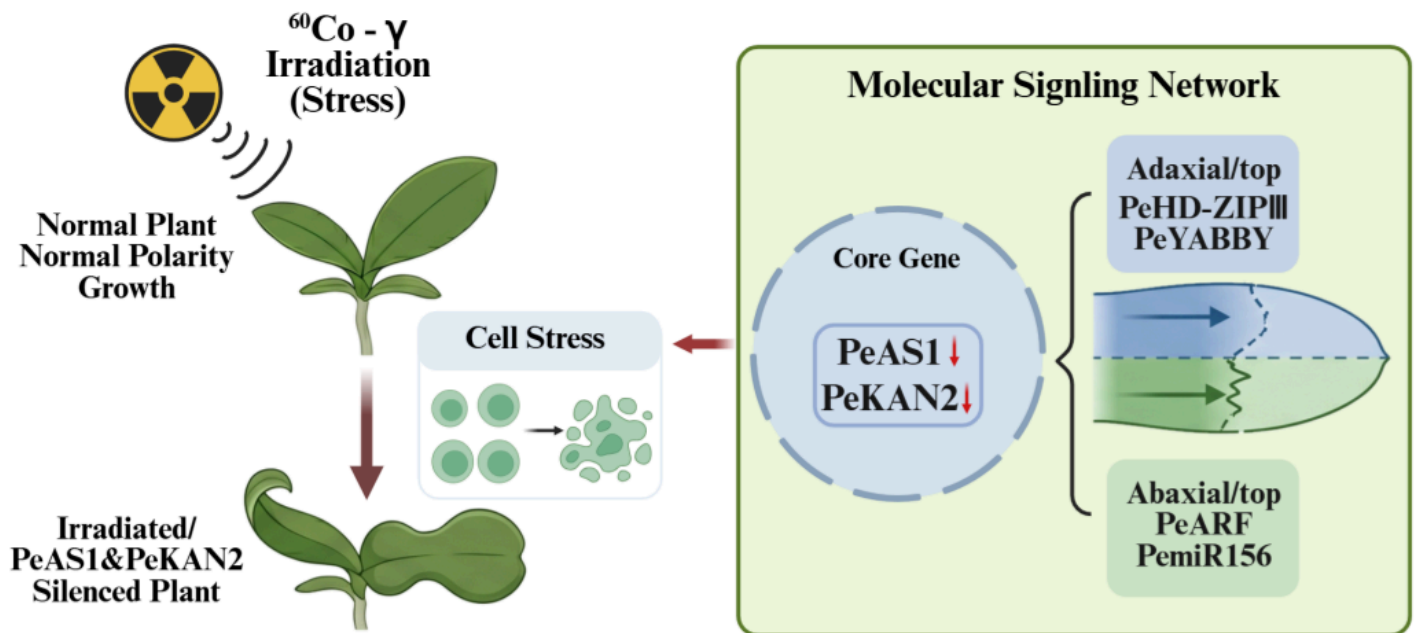


Figure 7

A hypothetical model illustrating the mechanism by which ^{60}Co - γ irradiation induces polarity growth in *Phalaenopsis* leaves.

Supplementary Files

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- [SupplementaryFigureBMCPPlantBiology.docx](#)
- [SupplementaryTableS1S2.docx](#)