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Letter

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Snowwhite: a rapid genetic tool for sweet potato functional genomics

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Dear Editor,

Albinism, a naturally occurring lethal genetic mutation in plants, disrupts photosynthesis by blocking chlorophyll biosynthesis. Albino seedlings serve as valuable tools for ornamental breeding and functional studies, particularly in investigating photosynthesis, phytohormone regulation, and environmental responses. While diploid species such as rice and maize readily develop homozygous recessive albino phenotypes, this trait remains largely undocumented in polyploid crops, including the hexaploid sweet potato (*Ipomoea batatas*, 2n = 6x = 90). This study successfully developed and characterized the sweet potato albino mutant "Snowwhite," revealing that *IbMYB70* plays a key role in its albino phenotype. The absence of chloroplasts and thin cell walls in Snowwhite contribute to its exceptional callus induction and root regeneration, high explant transformation rates, and superior protoplast isolation capacity, thus establishing Snowwhite as an auxiliary platform for functional validation of development-, quality-, and stress-related genes, as well as for assessing gene-editing efficiency and dissecting molecular mechanisms in sweet potato.

Sweet potato possesses thickened cell walls and contains abundant phenolic compounds, which rapidly oxidize into cytotoxic quinone derivatives upon wounding, suppressing cell division and making callus induction from root, stem, and leaf tissues extremely challenging. Moreover, protoplast isolation from sweet potato exhibits low efficiency. Current genetic transformation primarily employs technically challenging and time-consuming apical meristem-derived suspension cell lines or stem-based methods such as the cut-dip-budding delivery system (Cao et al. 2022) or one-step *Agrobacterium*-mediated transformation system (Zhang et al. 2023), which frequently produce chimeric plants and suffer from limited gene-editing efficiency and high land requirements. Furthermore, the asexual propagation of sweet potato complicates the identification of chimeras and the recovery of stable, non-chimeric plants. Developing novel, highly efficient auxiliary genetic validation tools is therefore imperative for advancing functional genomics in sweet potato. Here, we established a stable albino mutant "Snowwhite" through somaclonal variation. This study evaluates its utility for functional genomics applications.

We previously obtained a salt-tolerant and disease-resistant mutant, LM1 (renamed ND98), through gamma-ray-induced mutation (Zhang et al. 2017, 2020). Shoot apical meristems excised from ND98 were used to establish an embryogenic cell suspension line, from which plants were regenerated to induce somaclonal variation. Among approximately 9,000 cell aggregates, a single soft albino mutant (designated "Snowwhite') was obtained (Fig. S1a). It exhibited stable survival under in vitro culture with intense illumination for 13 yr (2012 to 2025), displaying white and small leaves, and pale green stems compared to ND98 (Fig. 1a; Fig. S1b and S1c).

Paraffin section analysis revealed that Snowwhite leaves exhibited loosely arranged spongy and palisade mesophyll cells with reduced cell layers and thinner leaf blades compared to ND98 (Fig. S2a and S2c). In stems, both xylem and phloem were underdeveloped in

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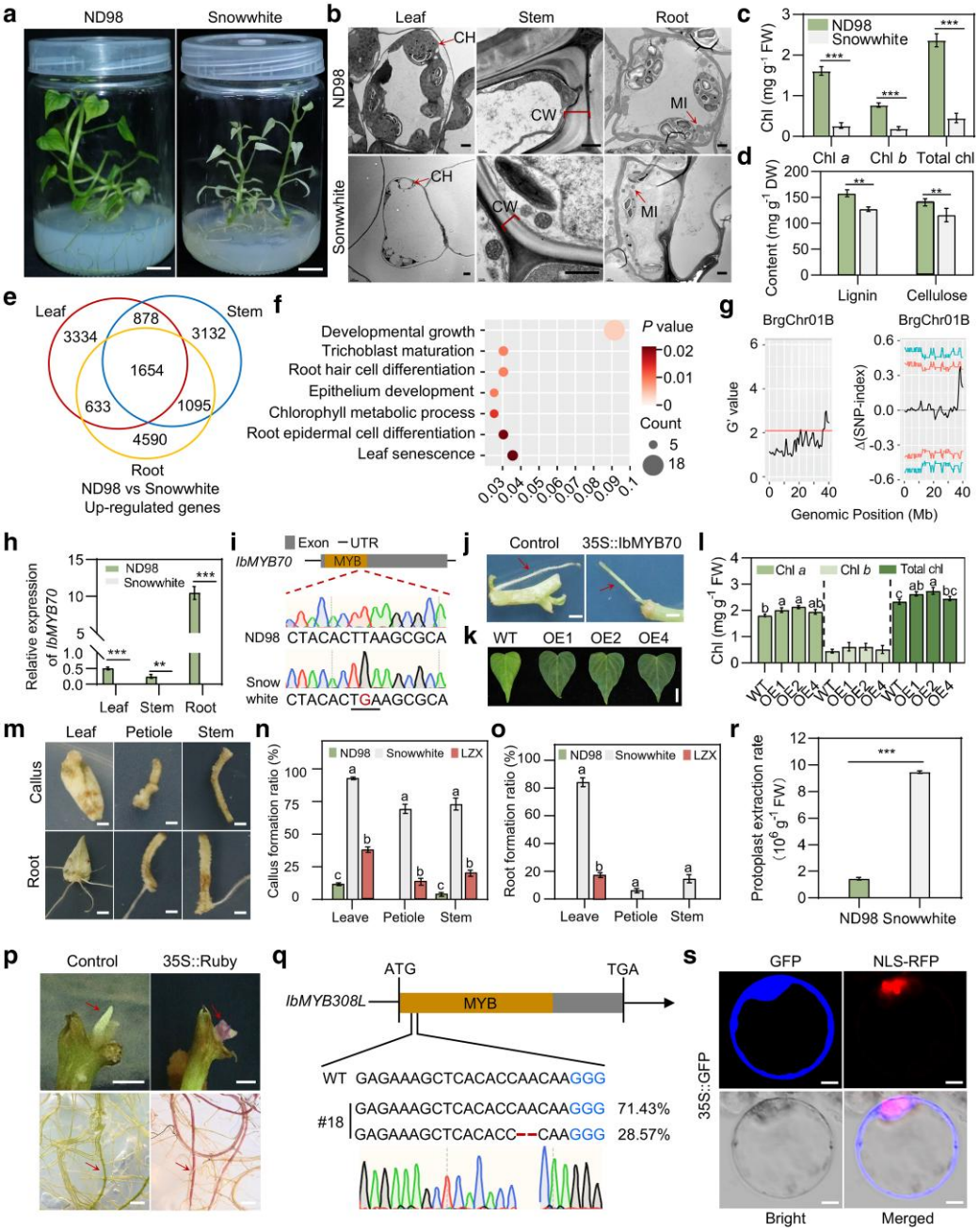

Figure 1 Snowwhite is a rapid genetic tool for sweet potato functional genomics. **a)** Plant morphology of 1-mo-old ND98 and Snowwhite plants. Bars = 1.5 cm. **b)** TEM observation of leaves, stems, and roots in 1-mo-old ND98 and Snowwhite. CH, chloroplast; CW, cell wall; MI, mitochondria; Bars = 1 μm. **c)** Chlorophyll content in leaves. Chl *a*, Chlorophyll a; Chl *b*, Chlorophyll b; Total chl, total Chlorophyll. **d)** Lignin and cellulose contents in stems. **e)** Venn diagram showing 1,654 DEGs commonly upregulated in leaves, stems, and roots of ND98 compared to Snowwhite. **f)** GO enrichment analysis of the 1,654 DEGs. **g)** SNP-index diagram showing variation location on the chromosome 1B. The red horizontal line indicates the threshold for significant association. The black curve shows the Δ(SNP-index) calculated using a sliding window approach. The red and blue curve indicate the 95% and 99% confidence intervals under the null hypothesis, respectively. **h)** Relative expression of *IbMYB70* of leaves, stems, and roots in ND98 and Snowwhite. **i)** Sanger sequencing validation of SNPs in ND98 and Snowwhite. **j)** Regenerated roots in Snowwhite stems infected with K599-35S::IbMYB70. The red arrows represent regenerated roots. Bars = 0.3 cm. **k)** Leaf phenotype of *IbMYB70*-overexpressing (*IbMYB70*-OE) plants and WT plants. Bars = 0.5 cm. **l)** Chlorophyll content in leaves of WT and *IbMYB70*-OE plants. **m)** Regenerated roots from different tissues after K599-35S::GFP infection. Bars = 0.3 cm. **n)** Callus formation rates in leaves, petioles, and stems of ND98, Snowwhite, and Lizixiang. (LZX). Three biological replicates consisting of 40 explants were presented. **o)** Root regeneration efficiency in leaves, petioles, and stems of ND98, Snowwhite, and LZX. Three biological replicates consisting of 32 explants were presented. **p)** Regenerated buds and roots infected with K599-35S::RUBY. The red arrows represent regenerated buds or roots. Bars = 0.3 cm. **q)** CRISPR-Cas9 editing at the exon of *IbMYB308L* in Snowwhite explant. The PAM sequence was indicated by blue, respectively. **r)** Protoplast extraction rate in ND98 and Snowwhite. **s)** Subcellular localization of pCAMBIA1300-GFP. Bars = 10 μm. All data in c, d, h, l, n, o, and r presented as mean ± SD (n = 3); $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$ (2-tailed Student's *t*-test). Different letters indicated statistically significant differences (1-way ANOVA followed by post hoc Tukey test; $P < 0.05$).

Snowwhite (Fig. S2b). Snowwhite roots displayed irregularly arranged xylem vessels with reduced density (Fig. S2a and S2d). Transmission electron microscopy (TEM) further demonstrated aberrant chloroplast development in Snowwhite leaves, significantly thinner cell walls in its stems, as well as abnormal mitochondrial cristae architecture in its roots compared to ND98 (Fig. 1b). Consistent with these structural observations, Snowwhite showed significantly lower chlorophyll a and b and total chlorophyll content in leaves (Fig. 1c) and reduced lignin and cellulose accumulation in stems compared to ND98 (Fig. 1d).

To investigate the genetic mechanisms underlying albinism, we performed comparative transcriptomic and genomic analyses of Snowwhite and ND98 (Materials and methods; table S1–S4). A total of 1,654 differentially expressed genes (DEGs; $|\log_2 FC| \geq 1$, $P < 0.05$) were significantly upregulated in ND98 compared to Snowwhite across root, stem, and leaf tissues (Fig. 1e; Table S1). Gene Ontology (GO) enrichment analysis revealed that these DEGs were enriched in pathways such as developmental growth (GO:0048589), chlorophyll metabolic process (GO:0015994), and leaf senescence (GO:0010150) (Fig. 1f; Table S2). Comparative genomic analysis of high-coverage resequencing data (Snowwhite, 200×; ND98, 50×) identified a 5.32 Mb quantitative trait locus (QTL) on chromosome 1 (Chr01B: 35,877,298 to 40,193,319). To prioritize causal genes, we defined a 500 kb candidate interval (Chr01B: 37,850,263 to 38,850,263) centered on the peak G′ statistic locus (Chr01B:38,350,263; $P < 1 \times 10^{-5}$), encompassing 149 annotated protein-coding genes (Fig. 1g; Table S3). Notably, the intronless gene *Ibat.Brg_v3.01BG038880*, encoding a MYB transcription factor IbMYB70 with the highest homology to AtMYB70 in *Arabidopsis* (Fig. S3a; Wan et al. 2021), exhibited undetectable expression levels in Snowwhite but was constitutively expressed in ND98 roots, stems, and leaves (Table S1; Fig. 1h). Sanger sequencing of *IbMYB70* coding regions revealed a truncation mutation (a premature stop codon in the exon, TTA to TGA) within the conserved MYB DNA-binding domain of Snowwhite (Fig. 1i; Fig. S3b). To investigate the functional implications, we overexpressed *IbMYB70* in Snowwhite. Green regenerated roots derived from callus cultures of Snowwhite stem segments were observed (Fig. 1j). TEM observations demonstrated that the overexpression of *IbMYB70* restored the chloroplast structure in leaves, cell wall thickness in stems, and mitochondrial morphology in roots to that of the ND98 wild-type (WT) phenotype (Fig. 1b; Fig. S4). Furthermore, we overexpressed *IbMYB70* in the easily transformable, green-leafed cultivar Lizixiang and obtained 3 *IbMYB70*-OE lines (Fig. S5a). Stably transformed *IbMYB70*-OE plants exhibited visibly darker green leaves compared to WT (Fig. 1k), with significantly increased chlorophyll a, chlorophyll b, and total chlorophyll content (Fig. 1l). Paraffin section analysis revealed that overexpression of *IbMYB70* increased the number of xylem vessels in the roots (Fig. S5b).

To elucidate the regulatory mechanism of *IbMYB70*, we analyzed the transcriptome of Snowwhite and identified several DEGs involved in chlorophyll biosynthesis, cell wall metabolism, lignin biosynthesis, and ROS metabolism (Fig. S6a), all of which contain MYB-binding sites within their 2,000 bp upstream promoter sequences (Fig. S6b). ChIP-qPCR and EMSAs confirmed that IbMYB70 directly binds to the promoters of the chlorophyll biosynthesis-related gene *IbHEMA* (encoding glutamyl-tRNA reductase; Zeng et al. 2020), the cell wall metabolism-related gene *IbXET* (encoding xyloglucan endotransglucosylase; Rose et al. 2002), the lignin biosynthesis-related gene *IbC4H* (encoding cinnamate 4-hydroxylase; Boerjan et al. 2003), and the ROS metabolism-related gene *IbRBOH* (encoding respiratory burst oxidase homolog; Felix et al. 2024; Fig. S6c to S6j). Furthermore, RT–qPCR and Dual-LUC assays demonstrated that IbMYB70 strongly activates the expression of *IbHEMA*, *IbXET*, *IbC4H*, and *IbRBOH* (Fig. S6k to S6o).

After 2 wk of *Agrobacterium rhizogenes*-mediated transformation, we observed remarkably high callus induction rates (69.33% to 92.66%) from leaf, petiole, and stem explants from Snowwhite. In contrast, Lizixiang showed rates of 13.50% to 39.80%, while ND98 showed only 0% to 12.33% (Fig. 1m and 1n). After 1 wk of culture, adventitious roots gradually developed from the Snowwhite callus. The leaf-derived callus exhibited a root regeneration rate of 83.66%, whereas the rates for Lizixiang and ND98 were 18.92% and complete failure, respectively (Fig. 1o; Fig. S7a and S7b). Subsequently, we introduced the *35S::RUBY* construct into Snowwhite. Within 3 wk, we successfully obtained red-pigmented stable transgenic buds (achieving a 10.69% transformation efficiency) and red transgenic roots (14.12% efficiency) via *A. rhizogenes*-mediated transformation, whereas no positive transgenic events were detected in ND98 (Fig. 1p; Fig. S7c to S7e). Furthermore, we employed *A. rhizogenes*-mediated transformation to validate the efficacy of the "Snowwhite" system for CRISPR-Cas9 gene editing. We obtained 26 CRISPR-Cas9 positive transgenic lines (49.06% positive efficiency, Fig. S7f), including 3 *IbMYB308L* gene-editing lines (11.54% efficiency, Fig. S7f). Sanger sequencing of these edited lines revealed deletions or substitutions in 16.67%, 28.57%, and 100% of the sequenced alleles for Lines #21, #18, and #20, respectively (Fig. S8, Fig. 1q). Notably, all mutations were localized to the sgRNA1 target site, with no editing detected at the sgRNA2 site. These results suggest that the editing events occurred in 1, 2, or all 6 homologous alleles of the hexaploid genome. These results demonstrate that the albino Snowwhite-based transformation system is rapid and efficient, offering broad application prospects for the functional characterization of candidate genes governing root development, quality traits (eg, carotenoids, anthocyanins), and stress tolerance (eg, salinity, drought) in sweet potato breeding.

Furthermore, given Snowwhite's thin cell walls and nearly absent chloroplasts, its protoplast extraction rate was 9.52×10^6 g^{-1} FW, markedly higher than ND98's 1.68×10^6 g^{-1} FW (Fig. 1r). The extracted protoplasts were successfully used in subcellular localization and Dual-LUC experiments. Green fluorescent signals appeared in both the nucleus and plasma membrane, indicating successful expression and localization of pCAMBIA1300-GFP (Fig. 1s). Dual-LUC assay in Snowwhite protoplasts showed that transcription factor IbMYB70 significantly activated the expression of *IbHEMA*, a gene encoding glutamyl-tRNA reductase in the chlorophyll biosynthesis pathway (Zeng et al. 2020), which was among the 1,654 DEGs significantly downregulated in Snowwhite (Table S1; Fig. S7g). These results highlight the utility of Snowwhite protoplasts for molecular mechanisms validation and gene-editing efficiency test in sweet potato functional genomics.

In summary, our study successfully developed and characterized the sweet potato albino mutant "Snowwhite", revealing that IbMYB70 plays a key role in its albino phenotype. The absent chloroplasts and thin cell walls in Snowwhite contribute to its exceptional callus induction and root regeneration, high explant transformation rates, and superior protoplast isolation capacity, thus establishing Snowwhite as an auxiliary platform for functional validation of development-, quality-, and stress-related genes, as well as for assessing gene-editing efficiency and dissecting molecular mechanisms in

sweet potato. Furthermore, this hexaploid albino mutant holds significant potential for advancing research in ornamental breeding, source-sink dynamics, photosynthetic regulation, phytohormone signaling, and environmental adaptation studies.

Supplementary material

Supplementary material is available at *Plant Physiology* online.

Author contributions

H. Zhang and S.H. conceived and designed the research. K.P. and Y.B. analyzed the data. K.P., Y.B., Z.D., J.Z., and M.S. performed the experiments. H. Zhang, K.P., and Y.B. wrote the paper. Q.L., H. Zhai, N.Z., and S.G. revised the paper. All authors read and approved the final version of the paper.

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Conflicts of interest

The authors declare no competing interests.

Data availability

The resequencing and RNA-seq data of ND98 and Snowwhite are available in the NCBI database under accession code PRJNA1244576. Supporting data for this study can be found in the supplemental materials.

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