

Article

RhSCL3 and *RhSCL33* (SCARECROW-LIKE) Regulate the Adventitious Root Formation of *Rosa hybrida* Responding Auxin

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Abstract

Adventitious root (AR) formation is critical for the successful establishment and survival of rose (*Rosa hybrida*) cuttings. *SCARECROW-LIKE* (*SCL*) genes are known to regulate plant growth and development; however, their functions in rose AR formation remain poorly understood. In this study, the rooting rate of rose cuttings declined, whereas AR number increased with increasing concentrations of exogenous indole-3-butyric acid (IBA) and N-1-naphthylphthalamic acid (NPA). Most of the 36 identified *RhSCL* genes were significantly up-regulated during AR formation. Notably, the expression level of *RhSCL3* and *RhSCL33* was positively associated with AR formation under low concentrations of exogenous IBA and NPA. Both genes were expressed at higher levels in roots than in other organs and encoded nuclear-localized proteins with transcriptional activation activity. Heterologous expression of *RhSCL3* and *RhSCL33* in tobacco increased primary root length under exogenous IBA treatment, enhanced AR number and length, and promoted dry matter accumulation, accompanied by increased starch degradation and soluble sugar production. Compared with wild-type plants (WT), transgenic plants showed reduced indole-3-acetic acid (IAA) levels, more pronounced changes in gibberellic acid (GA₃) content, and higher activities of superoxide dismutase (SOD), peroxidase (POD), polyphenol oxidase (PPO), catalase (CAT), and indole-3-acetic acid oxidase (IAAO). These findings suggest that overexpression of *RhSCL3* and *RhSCL33* facilitates rooting under low-auxin conditions, and *RhSCL33* acting earlier during AR development, and *RhSCL3* functioning mainly at later stages. This regulatory module may provide useful genetic targets for improving vegetative propagation efficiency in rose and other horticultural or crop species.

Keywords: rose; SCARECROW-LIKE; adventitious root formation; plant hormone; heterologous expression; reactive oxygen species



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1. Introduction

Adventitious roots (ARs) are a common root type that provide structural support for aboveground plant organs and facilitate the uptake of mineral nutrients and water essential for normal growth and development [1]. Under environmental stresses such as mechanical injury, darkness, flooding, or nutrient deficiency, plants initiate ARs from organs or tissues including calluses, wounds, internodes, stems, and leaves [2,3]. AR formation generally progresses through three stages: reprogramming of initial cells into

procambium-like cells (AR primordia), formation of ARs from these cells, and subsequent root elongation [4]. Elevated auxin concentrations near cambial wound sites trigger stem cell fate and reprogramming, thereby promoting AR initiation [5].

Cutting propagation is a common method for rose propagation as it maintains desirable plant characteristics and is currently one of the most widely used approaches for propagating elite plant germplasm resources [6]. However, the rooting of roses remains a persistent challenge for growers, as the rooting capacity varies considerably among genotypes and is frequently influenced by fluctuating environmental conditions [7]. In most rose varieties, AR induction requires exogenous hormones, particularly auxin [7]. Studies on *R. 'Grand Parade'* demonstrated that supplementing the culture medium with 100 mg·L⁻¹ IBA and 300 mg·L⁻¹ naphthaleneacetic acid (NAA) optimized AR formation [8].

During plant AR formation, endogenous hormones, macromolecular substances, and reactive oxygen species (ROS) levels change significantly. During AR development in *R. 'Chinese Red'*, endogenous IAA and GA₃ contents were positively correlated with cutting survival rates [8]. Furthermore, carbohydrate levels vary markedly across different sections of rose cuttings: higher levels in cuttings from the upper branch promote rooting, whereas lower levels in the lower branch restrict AR formation [9]. The rooting process of *R. 'Dorothy Perkins'* is closely associated with high starch content [10]. Soluble sugars serve as the primary carbon source, and their decomposition rate critically determines rooting efficiency in roses [11]. During the rooting process of cuttings from two climbing rose cultivars, 'Alchymist' and 'Handel', the POD activity showed an increase-decrease-increase-decrease pattern, with high POD activity required for callus induction and AR elongation. High PPO activity also promotes callus development, thereby facilitating AR induction and formation, while PPO activity declines as ARs elongate [12].

AR formation is governed by numerous genes and transcription factors, including AP2/ERF (APETALA2/ethylene responsive factor) [3], ARFs (Auxin response factor) [13], LBDs (Lateral organ boundaries domain) [14], WOXS (WUSCHEL-related homeobox) [15] and GRAS [16,17]. Among these, SCL (Scarecrow-Like), a sub-family of GRAS, plays a pivotal regulatory role in plant growth and development [18]. Overexpression of *AtSCL28* promotes cell division and suppresses cell elongation of *Arabidopsis thaliana* roots [19]. *PdbSCL1* of *Populus davidiana* × *P. bolleana* simultaneously improves drought tolerance and plant growth through acetylation-dependent mechanisms [20]. miR171-targeted *CsnSCL2* and *CsnSCL3* regulate somatic embryogenesis in *Citrus sinensis* [21]. In addition to playing a role in stem development, *AtSCL23* is also a key gene in root development. It is expressed in cells of the AR endothelial layer, promoting the formation of ARs [22,23]. In *Pinus radiata* and *Castanea sativa*, *PrSCL1* and *CsaSCL1* are induced by exogenous auxins, with their expression increasing during the initial stage of AR primordia formation [24]. In our previous study, overexpression of *RhSCL2* promoted AR formation of tobacco [4]. However, the regulatory functions of other *SCL* genes in rose AR formation remain unclear, and the mechanisms underlying their responses to auxin-induced AR formation are also unknown.

This study investigated how rose *SCL* genes respond to auxin and participate in AR formation during cutting propagation, with particular emphasis on the functions of *RhSCL3* and *RhSCL33* in regulating AR formation. This research aims to lay a foundation for elucidating the mechanism by which *SCL* genes regulate auxin-responsive AR formation in modern roses.

2. Materials and Methods

2.1. Plant Materials and Treatments

R. hybrida cv. 'The Fairy' was cultivated in a greenhouse without supplemental lighting at Northeast Agricultural University (Harbin, China, 126.7° E, 45.7° N), under a relative

humidity of 65–75%, and a temperature of 20–28 °C. Four-week-old *Nicotiana benthamiana* plants for transient expression and *N. tabacum* plants for genetic transformation were grown under long-day conditions (16 h light/8 h dark) at 24 °C.

Single-node rose cuttings of 3–4 cm were cut from three-year-old post-flowering mother plants grown in the greenhouse. After disinfection with 8% NaClO for 10 min and rinsing five times with sterile water, the cuttings were placed on sterile Murashige and Skoog (MS) medium containing 30 g·L⁻¹ sucrose and 7 g·L⁻¹ agar (pH = 5.8). Different concentrations of IBA (0, 0.25, 0.5, 0.75 mg·L⁻¹) or NPA (0, 0.05, 0.1, 0.15 mg·L⁻¹) were independently supplemented to the MS medium. The cuttings were cultured under long-day conditions (16 h light/8 h dark) at 25 °C. After 30 d of treatment, rooting rate, average AR length, and average AR number were recorded.

2.2. Real-Time qPCR

The basal portions of rose cuttings treated with 0.25 mg·L⁻¹ IBA or 0.1 mg·L⁻¹ NPA were collected at 0, 10, and 20 d, corresponding to the initial stage, AR primordium formation stage, and AR elongation stage, respectively [4], and were immediately frozen in liquid nitrogen. Total RNA was extracted from basal portions of rose cuttings using the FastPure Plant Total RNA Isolation Kit (Vazyme, Nanjing, China). RNA quality, concentration, and integrity were evaluated by 1% agarose gel electrophoresis and a micro spectrophotometer (K 5800, KAIAO, Beijing, China). For each 20 µL of first-strand cDNA synthesis reaction, 1 µg of RNA was reverse-transcribed using the HiScript II Q RT SuperMix for qPCR (+gDNA wiper) kit (Vazyme, Nanjing, China). Amplification reactions were performed using a qTOWER³G Real-Time Fluorescent Quantitative PCR System (Analytik jena, Jena, Germany). Each qPCR reaction contained 10 µL of 2 × ChamQ Universal SYBR qPCR Master Mix (Vazyme, Nanjing, China), 1 µL of cDNA template, 0.5 µL of forward primer (10 µM), 0.5 µL of reverse primer (10 µM), and 8 µL of ddH₂O. The program consisted of pre-denaturation at 95 °C for 30 s, followed by 40 cycles of 95 °C for 10 s and 60 °C for 30 s. Finally, a melt curve was generated by increasing the temperature from 65 to 95 °C to confirm reaction specificity. *RhGAPDH* was used as the reference gene. Gene expression levels were quantified using the 2^{-ΔΔCT} method [25], and primer sequences are listed in Table S1. The complete coding sequences of rose *SCLs* were downloaded from the GDR database (<https://www.rosaceae.org/>).

2.3. Subcellular Localization of RhSCL3 and RhSCL33

The full-length coding sequences *RhSCL3* and *RhSCL33* (excluding stop codons) were cloned into the pCambia1300-sGFP vector between the *Kpn* I and *Bam*H I sites using the pEASY[®]-Uni Seamless Cloning and Assembly Kit (TransGen, Beijing, China) to construct recombinant plasmids, respectively. These plasmids were introduced into the *Agrobacterium tumefaciens* strain GV3101. The transient transformation of *A. tumefaciens* was subsequently performed on four-week-old *N. benthamiana* leaves following a previously described method [5]. The OD₆₀₀ of *A. tumefaciens* containing either pGambia1300-*RhSCL3*-sGFP, pGambia1300-*RhSCL33*-sGFP, or pGambia1300-sGFP plasmid was adjusted to around 0.6 using a resuspended solution (200 mM of acetosyringone, 10 mM of 2-morpholinoethanesulphonic acid, and 10 mM of MgCl₂). Each infection solution was placed in the dark for 3 h and then injected into the subepidermal cells of four-week-old *N. benthamiana* leaves using a syringe. Five leaves were injected with *A. tumefaciens* containing different plasmids. After 2 d of dark incubation at 23 °C, the infected leaves were placed on a confocal laser scanning microscope (FV3000, Olympus, Shinjuku, Japan) to visualize the fluorescence signal of GFP protein at 488 nm. Primer sequences are listed in Table S1.

2.4. The Yeast Activation Assays

The full-length coding sequences of *RhSCL3* and *RhSCL33* were inserted into the *EcoR* I and *Nde* I sites of the pGBKT7 (BD) vector using the pEASY[®]-Uni Seamless Cloning and Assembly Kit (TransGen, Beijing, China) to generate the recombinant constructs, respectively. The resulting recombinant vectors were transformed into AH109 yeast competent cells (WeiDi, Shanghai, China). After 2 d of cultivation at 28 °C, yeast colonies were selected and cultured in SD/-Trp/-His liquid yeast medium at 28 °C and 200 rpm. The yeast was centrifuged at 4000 rpm for 1 min to collect the yeast cells. The AH109 yeast containing the recombinant plasmid was resuspended in sterile water until its OD₆₀₀ reached 0.2. The suspended culture was diluted to 1×, 10×, and 100× concentrations, and then was plated on SD/-Leu/-His/X-a-gal medium supplemented with 20 g·L⁻¹ sugar (Coolaber, Beijing, China), and incubated at 28 °C for 48–60 h. The pGBT9 (T9) and BD vectors served as positive and negative controls, respectively. Primer sequences are listed in Table S1.

2.5. The Generation of Transgenic Plants

The plasmids pCAMBIA1300-*RhSCL3*-sGFP and pCAMBIA1300-*RhSCL33*-sGFP were introduced into *N. tabacum* via the leaf disk method, respectively [4]. Putative transformants were screened on a medium containing 25 mg·L⁻¹ hygromycin. Subsequently, integration of the transgenes was verified by PCR amplification of the GFP sequence, and RT-qPCR was employed to quantify the relative expression levels of the target genes (*RhSCL3* or *RhSCL33*) for the identification of positive transgenic lines. Three independent T₁ lines exhibiting stable expression were selected for further analysis. Surface-sterilized T₁ transgenic seeds were germinated on 1/2 MS medium supplemented with 30 g·L⁻¹ sucrose and 7 g·L⁻¹ Agar, and either 0.25 mg·L⁻¹ IBA or 0.1 mg·L⁻¹ NPA. 10 d post-sowing, the root length and number were measured. Then, the seedlings were transferred to fresh medium of the same composition after excision of the primary roots. After a 30-d treatment period, phenotypic parameters were recorded, including adventitious rooting rate, AR length, AR number, fresh weight, and dry weight.

2.6. Phenotypic Observation and Determination of Key Indicators

2 cm section of the basal part of tobacco stem cuttings was collected after the removal of the primary roots at 0, 10, and 20 d, respectively. All samples were quickly frozen in liquid nitrogen and then stored at −80 °C for the determination of key indicators. The starch (AKSU015M) and soluble sugar (AKPL008M) contents, as well as SOD (AKAO001M), POD (AKAO005M), PPO (AKAO004M), and IAAO (AKPL022M) activity, were determined using relative assay kits (Boxbio, Beijing, China). The contents of IAA and GA₃ were determined by high-performance liquid chromatography (HPLC) [26]. The weight of each sample was prepared according to the instructions. All experiments were conducted with three biological replicates.

2.7. Statistical Analysis

Experimental data were organized and statistically analyzed using Excel. Analysis of variance was performed with SPSS v10.0 software, and data analysis and graphing were conducted using GraphPad Prism 8.02. All experiments included three independent biological replicates, and the results are expressed as the mean ± standard deviation. Statistical significance was assessed using the least significant difference test of ANOVA, with significance thresholds set at $p < 0.05$.

3. Results

3.1. Exogenous IBA and NPA Altered ARs of Rose

Low concentrations of exogenous auxin were positively correlated with AR formation in rose (Figure 1a). As IBA concentration increased, the growth potential of rose ARs first increased and then decreased, and the rooting rate reached a maximum of 96.7% at $0.25 \text{ mg} \cdot \text{L}^{-1}$ of IBA (Figure 1b). The average AR length progressively decreased, with the longest average length (38.25 mm) observed in the medium without IBA. The average number of ARs showed a continuous increasing trend, peaking at 11 roots at $0.75 \text{ mg} \cdot \text{L}^{-1}$ of IBA (Figure 1c).

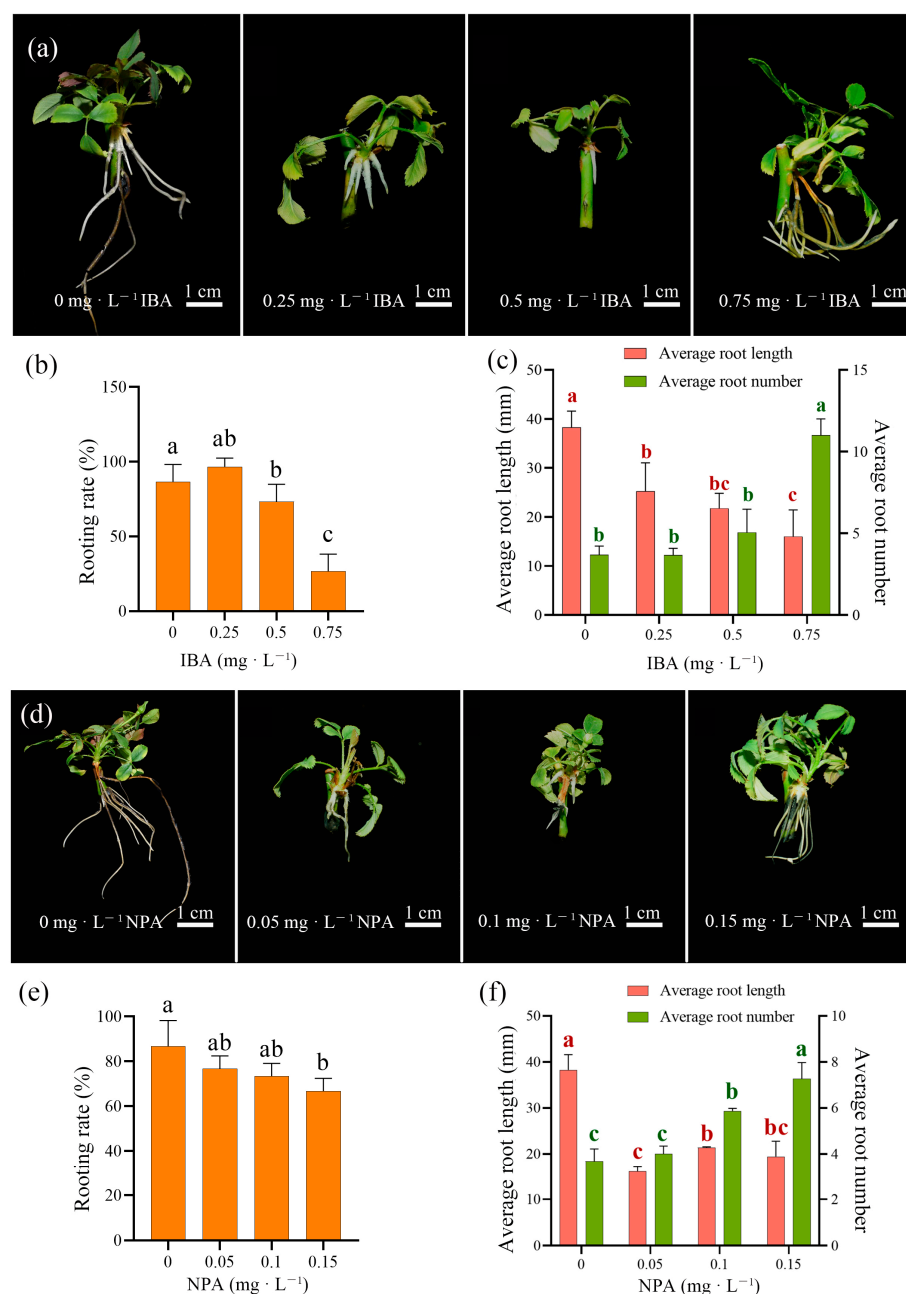


Figure 1. Adventitious roots (ARs) of rose cuttings treated with different concentrations of exogenous IBA and NPA. Phenotype (a,d), rooting rate (b,e), average AR length and average AR number (c,f) after treatment with IBA (a–c) and NPA (d–f), respectively. The experimental data are presented as the mean $\pm$ standard error, $n = 30$. Different lowercase letters represent significant differences between treatments within the group, $p < 0.05$.

As NPA concentration increased, the growth potential of rose ARs also first increased and then decreased (Figure 1d). The rooting rate gradually declined, reaching a minimum of 66.7% at $0.15 \text{ mg}\cdot\text{L}^{-1}$ of NPA (Figure 1e). The average AR number presented a continuous increasing trend, reaching a maximum of 7.27 roots at $0.15 \text{ mg}\cdot\text{L}^{-1}$ of NPA (Figure 1f). The average length of ARs was the longest (38.24 mm) in the medium without NPA. These results indicate that $0.25 \text{ mg}\cdot\text{L}^{-1}$ IBA exerted a more significant promoting effect on the formation of ARs in roses, and 0.1 NPA exhibited an inhibitory effect on rooting, while this inhibitory effect disappeared with the increase in NPA concentration.

3.2. Exogenous Application of Auxins and Auxin Inhibitors Affected RhSCLs Expression Level During ARs Formation

The 36 RhSCLs were divided into five major categories based on their relative expression level during ARs formation in *R. hybrida* cuttings supplemented with $0.25 \text{ mg}\cdot\text{L}^{-1}$ IBA or $0.1 \text{ mg}\cdot\text{L}^{-1}$ NPA (Figure 2).

RhSCL7, *RhSCL13*, *RhSCL17*, and *RhSCL29* responded to exogenous NPA during AR elongation. Under CK (without any exogenous hormone) and IBA treatments, all four genes showed up-regulated expression during root formation. Compared with the CK group, their expression levels were significantly reduced at 20 d after NPA treatment, which may contribute to the inhibition of root formation. Among them, *RhSCL13* and *RhSCL17* exhibited relatively high expression levels on the 20th day under IBA treatment.

Exogenous IBA treatment activated the expression of *RhSCL2*, *RhSCL19*, *RhSCL20*, *RhSCL23*, *RhSCL24*, *RhSCL26*, *RhSCL27*, and *RhSCL28*. During AR formation, the expression levels of these eight genes reached their highest at 20 d under IBA treatment and were significantly higher than those in other groups. Since IBA treatment promoted AR formation in plants, these genes may respond to IBA during AR elongation. In the CK group, these genes were also significantly up-regulated at 20 d compared to 0 and 10 d, indicating that they play more prominent roles during the late stage of AR formation.

RhSCL31 and *RhSCL34* showed similar expression patterns. Although their expression levels increased during AR formation, their relative expression levels at 20 d under IBA treatment were significantly lower than those under NPA and CK treatments.

RhSCL4, *RhSCL5*, *RhSCL6*, *RhSCL8*, *RhSCL9*, *RhSCL10*, *RhSCL11*, *RhSCL12*, *RhSCL14*, *RhSCL15*, *RhSCL16*, *RhSCL21*, *RhSCL22*, *RhSCL32* and *RhSCL36* all showed significantly higher expression levels at 20 d than at 0 and 10 d under all treatments. This indicates that these genes play important roles in the AR elongation stage.

RhSCL1, *RhSCL3*, *RhSCL7*, *RhSCL15*, *RhSCL18*, *RhSCL25*, *RhSCL33*, and *RhSCL35* exhibited similar expression patterns. Their expression levels gradually increased with AR initiation and elongation. Although exogenous hormones reduced the expression levels of these genes, the overall trend of gradual up-regulation during AR formation remained. *RhSCL3* and *RhSCL33* were therefore selected for further analysis of their roles in AR development.

3.3. RhSCL3 and RhSCL33 Are Nuclear Proteins with Self-Activation Activity

Analysis of gene expression in different rose tissues showed that *RhSCL3* and *RhSCL33* had the highest expression levels in roots and the lowest in petals, suggesting that both genes may be associated with root morphogenesis (Figure 3a,b). The green fluorescent signal of the pCAMBIA1300-*RhSCL3/33*-sGFP fusion proteins was detected exclusively in the nucleus, whereas the fluorescent signal of the pCAMBIA1300-sGFP control was diffusely distributed throughout the cell (Figure 3c). Transcriptional activation assays showed that both *RhSCL3* and *RhSCL33* proteins possessed weak transcriptional activation activity (Figure 3d). Collectively, these results indicate that *RhSCL3* and *RhSCL33* are nucleus-localized proteins with self-activation activity and may play important roles in AR formation.

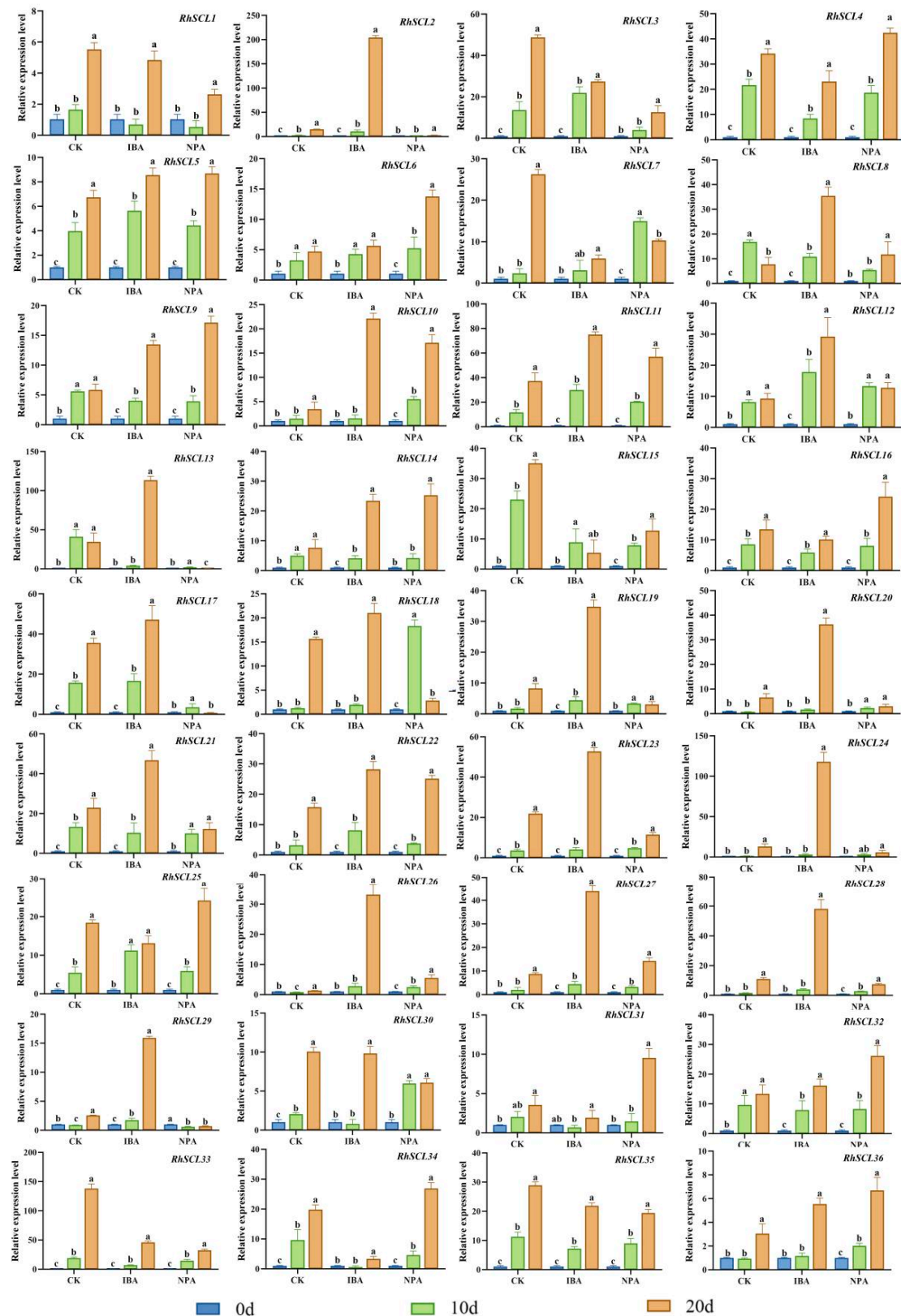


Figure 2. Relative expression levels of 36 RhSCL genes during AR formation under exogenous IBA and NPA treatments. The experimental data are presented as the mean $\pm$ standard error, $n = 30$. Different lowercase letters represent significant differences between treatments within the group, and $p < 0.05$.

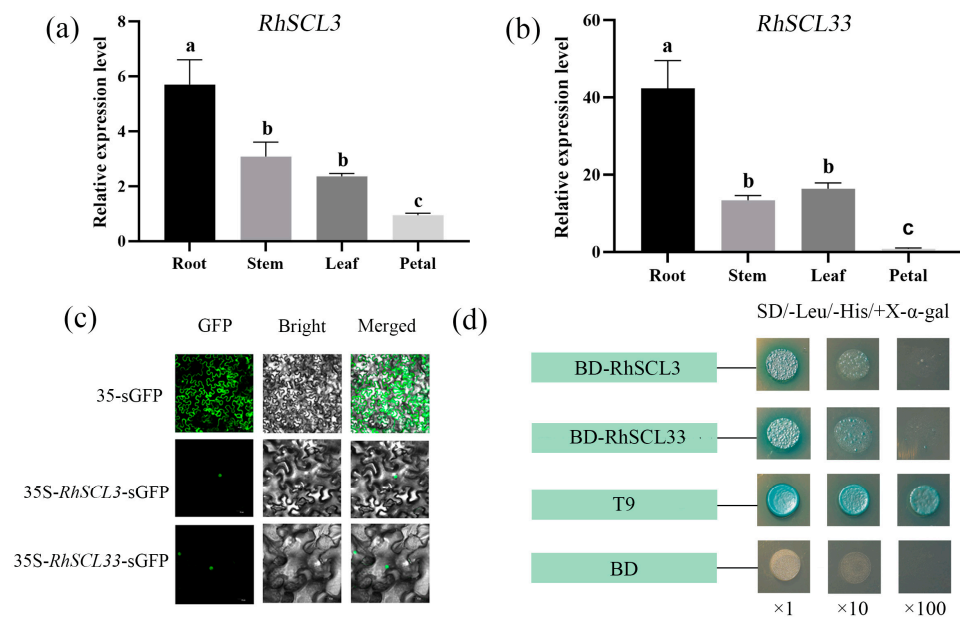


Figure 3. The characteristics of RhSCL3 and RhSCL33 transcription factors. (a,b) *RhSCL3* and *RhSCL33* expression in different tissues of rose. (c) Subcellular localization of RhSCL3 and RhSCL33. (d) Transcriptional activation assay of RhSCL3 and RhSCL33. pGT9 was used as a positive control, and BD was used as a negative control. The experimental data are presented as the mean $\pm$ standard error, $n = 10$. Different lowercase letters represent significant differences between treatments within the group, $p < 0.05$.

3.4. *RhSCL3* and *RhSCL33* Positively Regulated Plant Adventitious Root Formation

Overexpression of both *RhSCL3* and *RhSCL33* genes promoted the formation and growth of primary roots (PRs) and ARs in tobacco (Figures 4 and 5). Compared with WT, *RhSCL3* and *RhSCL33* overexpression lines produced longer and more numerous PRs (Figure 4a,d). The combination of exogenous IBA and overexpression of these two genes resulted in the strongest root-promoting effect. Specifically, the average root length and root number of *RhSCL3* OE lines were approximately 26.86 mm (Figure 4b) and 2 (Figure 4c), respectively. For *RhSCL33* OE plants, these values were approximately 25.95 mm (Figure 4e) and 2.2 (Figure 4f), respectively, which were significantly higher than those of WT plants without IBA treatment, which exhibited an average root length of approximately 13.12 mm and a root number of 1.8. Furthermore, overexpression of *RhSCL3* and *RhSCL33* alleviated the inhibitory effect of exogenous NPA on root elongation, although its effect on root number was limited.

The average AR length in WT was 62.8 mm, significantly shorter than that in *RhSCL3* and *RhSCL33* OE lines, which reached 83.2 mm and 77.0 mm, respectively (Figure 5a–c). The AR number in WT was 18.3, significantly lower than the 26.7 and 24.3 recorded for the *RhSCL3* and *RhSCL33* OE lines (Figure 5d,e). Overexpression of the two *RhSCLs* also increased both fresh and dry weight. The dry weight of WT was 0.0119 g, while *RhSCL3* and *RhSCL33* OE lines reached 0.0181 g and 0.0172 g, respectively (Figure 5f,g). Furthermore, transgenic tobacco plants had more leaf number than WT, indicating consistency between aboveground and underground growth. This promotion was also evident during AR formation in rose cuttings (Figure 1). Collectively, these results suggest that *RhSCL3* and *RhSCL33* may promote root development via auxin signaling or transport pathways.

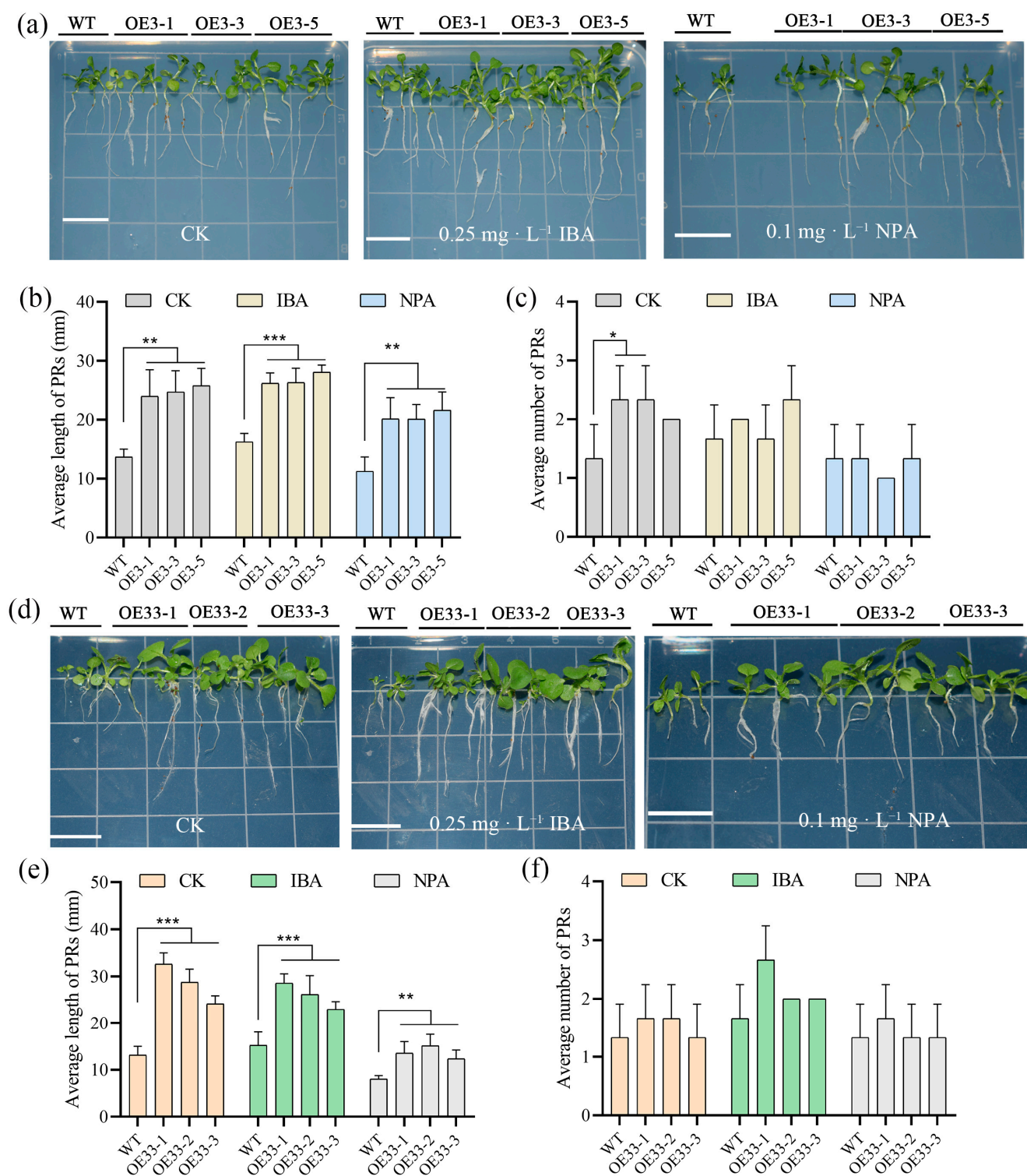


Figure 4. PR growth of overexpression *RhSCL3* and *RhSCL33* transgenic tobacco under IBA and NPA treatments. (a) Phenotype, (b) average length, (c) average number of primary roots of *RhSCL3* OE lines. (d) Phenotype, (e) Average length, (f) average number of *RhSCL33* OE lines. The data are presented as the mean $\pm$ standard error, $n = 10$. * represents $p < 0.05$, ** represents $p < 0.01$, *** represents $p < 0.001$.

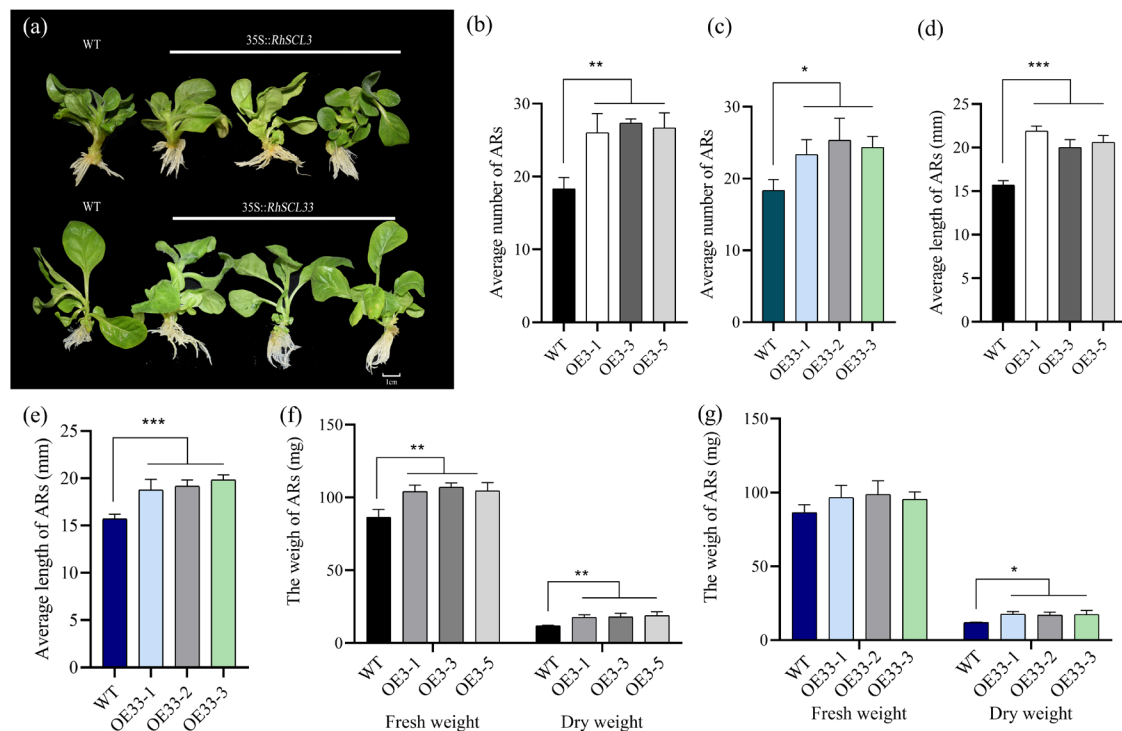


Figure 5. AR growth of overexpression *RhSCL3* and *RhSCL33* transgenic tobacco. (a) Phenotype, (b,c) average length, (d,e) average number, (f,g) fresh and dry weight of ARs of *RhSCL3* and *RhSCL33* OE lines. The data are presented as the mean $\pm$ standard error from at least three independent biological replicates. * represents $p < 0.05$, ** represents $p < 0.01$, *** represents $p < 0.001$.

3.5. *RhSCL3* and *RhSCL33* Promoted AR Development by Regulating Endogenous Hormones and Carbon Metabolites

Hormones and nutrients are involved in AR formation. During AR formation, the IAA content in tobacco showed a trend of first increasing and then decreasing. The IAA content in *RhSCL3* OE lines was significantly lower than that in WT at both 10 d and 20 d, indicating that overexpression of *RhSCL3* reduced the auxin content for AR formation in tobacco (Figure 6a). *RhSCL33* OE lines had lower IAA content than WT at 10 d after cutting, suggesting that *RhSCL33* has a time-specific effect on reducing the auxin content for AR formation (Figure 6e). The change in GA₃ content in WT was opposite to that in OE lines: WT showed a decrease followed by an increase, whereas *RhSCL3* OE lines showed an increase followed by a decrease, and *RhSCL33* OE lines showed a continuous increase. Moreover, the GA₃ content in *RhSCL33* OE lines was $19.2 \mu\text{g} \cdot \text{g}^{-1}$, significantly higher than that in WT ($16.9 \mu\text{g} \cdot \text{g}^{-1}$) and *RhSCL3* OE lines ($6.1 \mu\text{g} \cdot \text{g}^{-1}$) (Figure 6b,f). These results indicate that although the two genes share similarities in regulating AR formation, they differ significantly in their regulation of IAA and GA₃ levels.

During AR primordia formation and root elongation, the soluble sugar content in *RhSCL3* and *RhSCL33* OE lines was consistently higher than that in the WT. In particular, at 10 d after cutting, the soluble sugar content in the OE lines was $20.1 \text{ mg} \cdot \text{g}^{-1}$ and $16.1 \text{ mg} \cdot \text{g}^{-1}$, respectively, significantly higher than the $11.6 \text{ mg} \cdot \text{g}^{-1}$ observed in WT (Figure 6c,g). The trend in starch content during AR formation was opposite to that of soluble sugars, and the content of starch in *RhSCL3* and *RhSCL33* OE lines remained lower than that in WT (Figure 6d,h). These results indicate that overexpression of *RhSCL3* and *RhSCL33* promoted the accumulation of soluble sugars, thereby providing an energy supply that supported the formation of longer and more numerous ARs.

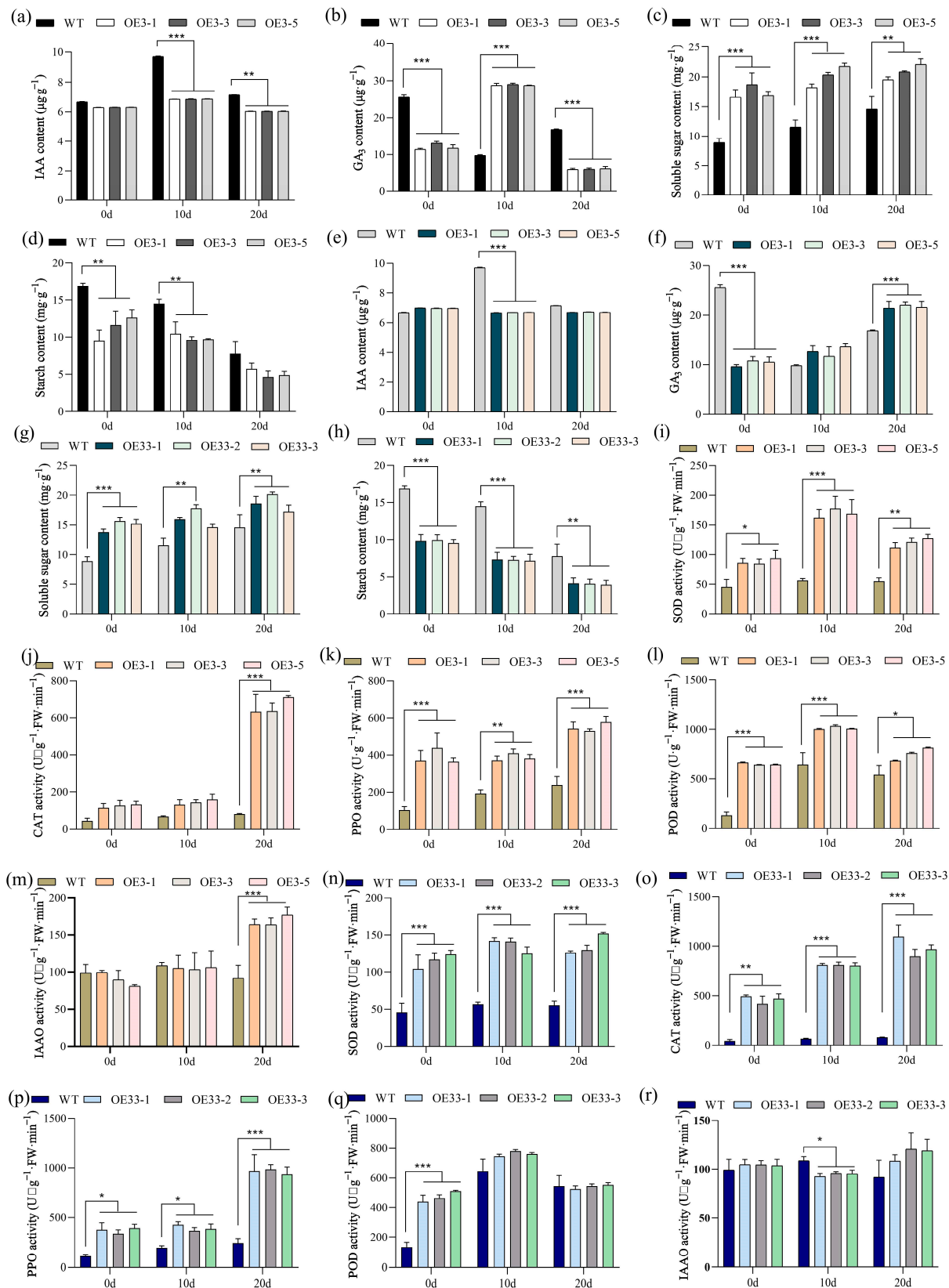


Figure 6. Endogenous hormones, nutrient content, and enzyme activities during AR formation of *RhSCL3* and *RhSCL3* transgenic tobacco. The content of (a,e) IAA, (b,f) GA_3 , (c,g) soluble sugar, (d,h) starch of *RhSCL3* and *RhSCL3* OE lines. The Enzyme activities of (i,n) SOD, (j,o) CAT, (k,p) PPO, (l,q) POD, and (m,r) IAAO of *RhSCL3* and *RhSCL3* OE lines. The data are presented as the mean $\pm$ standard error $n = 30$. * represents $p < 0.05$, ** represents $p < 0.01$, *** represents $p < 0.001$.

3.6. Antioxidant-Related Enzyme Participate in ROS Removal During AR Formation

The SOD activity of *RhSCL3* and *RhSCL33* OE lines was significantly higher than that in WT at 0, 10, and 20 d after cutting, with the most pronounced difference observed at 10 d (Figure 6i,n). At 20 d, the CAT activity of WT was $81.03 \text{ U} \cdot \text{g}^{-1} \text{ FW} \cdot \text{min}^{-1}$, significantly lower than that in *RhSCL3* and *RhSCL33* OE lines, which reached 660.20 and $988.86 \text{ U} \cdot \text{g}^{-1} \text{ FW} \cdot \text{min}^{-1}$, respectively (Figure 6j,o). Moreover, the PPO activity of *RhSCL3* and *RhSCL33* OE lines reached $550.9 \text{ U} \cdot \text{g}^{-1} \text{ FW} \cdot \text{min}^{-1}$ and $962.9 \text{ U} \cdot \text{g}^{-1} \text{ FW} \cdot \text{min}^{-1}$, respectively, and were consistently higher than that in WT, which reached $239.2 \text{ U} \cdot \text{g}^{-1} \text{ FW} \cdot \text{min}^{-1}$, with the greatest discrepancy detected at 20 d (Figure 6k,p).

The POD activity of *RhSCL3* OE lines was significantly higher than that in WT at 0, 10, and 20 d. and OE *RhSCL33* only had a higher POD activity than WT before cutting (Figure 6l,q). The IAAO activity of *RhSCL3* OE lines was significantly higher than that of the WT at 20 d, which may have contributed to the reduced IAA content in *RhSCL3* OE lines. In *RhSCL33* OE lines, both IAAO activity and IAA content were lower than those in WT at 10 d. This might be due to reduced auxin synthesis caused by *RhSCL33* overexpression, which maintained IAA content at a low level even when IAAO activity was inhibited (Figure 6m,r).

These results demonstrate that *RhSCL3* and *RhSCL33* were similar in their oxidative stress responses during cutting-induced wound stress and significantly enhanced plant stress resistance. However, they differ in their regulatory functions during AR morphogenesis. *RhSCL3* mainly functions during AR elongation, while *RhSCL33* appears to participate primarily in the regulation of AR primordia formation.

4. Discussion

4.1. Exogenous Auxins Promote AR Formation Within an Appropriate Concentration Range

Auxin plays a crucial role in promoting the development of ARs and lateral roots. In this study, a low concentration of IBA ($0.25 \text{ mg} \cdot \text{L}^{-1}$) promoted AR formation in *R. 'The Fairy'*, whereas a low concentration of NPA ($0.05 \text{ mg} \cdot \text{L}^{-1}$) inhibited it. As the concentrations of these two exogenous regulators increased, the frequency of AR formation decreased significantly, AR length became shorter, and AR number increased (Figure 1). Treatment of roots with IBA significantly increases new root growth, budbreak, and new shoot dry weight, and replaces the chilling requirement for these responses in apple roots [27]. The IBA requirement for AR formation differs among plant species. A high concentration of IBA inhibits root growth and elevates lignin accumulation in maize roots, whereas a low concentration of IBA stimulated root growth but did not affect lignin content [28]. In *Cinnamomum bodinieri*, rooting rates and root number under 1.5 mg/L IBA treatment are significantly higher than those under 0, 0.5, 1.0, or 2.0 mg/L IBA treatments [29]. In conclusion, plants adopt different response strategies to different auxin concentrations. An appropriate auxin concentration is beneficial for AR formation, whereas excessively low or high auxin concentrations may alter cellular differentiation at the wound site of the cuttings, promote root number, and slow root elongation. and slow root elongation. Moreover, hormones or small molecules such as chlormequat chloride [30], brassinosteroids [14], jasmonic acid, and phytoalexin [31] regulate plant AR formation through the auxin signaling pathway.

4.2. Some SCL Genes Respond to Auxin During AR Formation

SCL genes are extensively involved in plant development, hormone signal transduction, and abiotic stress responses. In rose, most *RhSCL* genes were implicated in AR elongation, with expression levels significantly higher at 20 d post-cutting compared to 0 and 10 d, including *RhSCL2*, *RhSCL5*, and *RhSCL9*. During AR formation in *Juglans regia*,

the key *SCL* gene was identified during the transformation of cambial cells into root primordia initial cells [32]. In *A. thaliana*, *SCL6-II*, *SCL6-III* and *SCL6-IV* play critical regulatory roles in flower and root development [33]. In *Pinus radiata*, AR formation involves the coordinated participation of multiple genes, including *PrSCL2*, *PrSCL6*, *PrSCL7*, *PrSCL10* and *PrSCL12* [34]. In *Larix kaempferi*, the *LaSCL6* gene is regulated by miR171 to control somatic embryogenesis [35]. In *Vitis vinifera*, elevated miR171d expression down-regulates *VvSCL15* and *VvSCL17*, thereby affecting AR formation [36]. In *P. davidiana* × *P. bolleana*, overexpression of *PdbSCL1* enhances plant drought resistance and growth rate, whereas knockout of this gene reduces drought tolerance and growth capacity [20]. In *Glycine max*, *GmSCL* mediates aluminum tolerance by regulation of miR170 [37].

The *SCL* gene family responds to multiple hormones and hormone signal transduction pathways, thereby regulating plant growth, development, and adaptation to abiotic stress. Exogenous IBA exerted specific regulatory effects on the expression of distinct *RhSCL* genes, resulting in two distinct outcomes: promotion and inhibition. Specifically, IBA induced the expression of 21 *RhSCLs* while reducing that of six genes, including *RhSCL3* and *RhSCL33*. NPA, an auxin transport inhibitor, influenced gene expression by disrupting polar auxin transport, promoting 12 *RhSCLs*, including *RhSCL3* and *RhSCL33*, and inhibiting 15 others (Figure 2). AR formation in *P. radiata* and *C. sativa* depends on exogenous auxin application and is associated with increased transcript levels of *PrSCL1* and *CsSCL1* [24]. Furthermore, *AtSCL3* negatively regulates GA signal transduction and interacts with DELLA proteins to modulate downstream gene expression [38].

4.3. Effect of *RhSCL3* and *RhSCL33* Overexpression on AR Formation

RhSCL3 and *RhSCL33* function as positive regulators of AR formation. The average root lengths of *RhSCL3*- and *RhSCL33*-overexpressing tobacco were significantly greater than those of WT (Figures 4 and 5). In addition, tobacco treated with exogenous IBA had longer roots than those without hormone application. This indicates that the combination of overexpression combined with exogenous hormone application has a stronger root-inducing effect than overexpression alone. Overexpression of *LcERF1* resulted in significantly longer roots and larger leaf areas than WT under 5 µM IBA [39]. Overexpression of *RhSCL3* and *RhSCL33* was accompanied by a significant increase in soluble sugar content and a marked increase in starch consumption (Figures 6 and 7). The *AtSCL3* subfamily, a branch of the GRAS family, plays a crucial role in root elongation [40,41], consistent with our finding that *RhSCL3* functions during the late stage of AR formation. As energy-supplying substances, soluble sugars and starch reflect the energy demand of plant cuttings. Overexpression of the *RhSCL2* gene promoted AR elongation in tobacco, with lower soluble sugar and starch contents at 3, 5, and 10 d compared with WT [4].

During PR and AR formation, the morphological and physiological traits of tobacco overexpressing *RhSCL33* closely resembled those of *RhSCL3*-overexpressing lines. However, *RhSCL3* OE lines exhibited longer and more abundant roots, along with a stronger promoting effect. Furthermore, increases in soluble sugar content and starch consumption were more pronounced in *RhSCL3* OE lines than *RhSCL33* OE lines. Although both genes displayed similar physiological trends, *RhSCL3*-overexpressing tobacco showed higher POD activity, suggesting that *RhSCL3* plays a more critical role than *RhSCL33* in responding to cutting-induced stress (Figure 6). From the perspective of IAAO dynamics, *RhSCL33* OE lines exhibited higher enzyme activity during early AR formation, whereas *RhSCL3*-overexpressing tobacco showed significant enzyme activity at later stages of AR formation. This suggests that *RhSCL33* functions earlier in AR development, while *RhSCL3* acts primarily at later stages. As a transcription factor, *RhSCL33* may also participate in the auxin regulatory pathway, warranting further investigation (Figure 7).

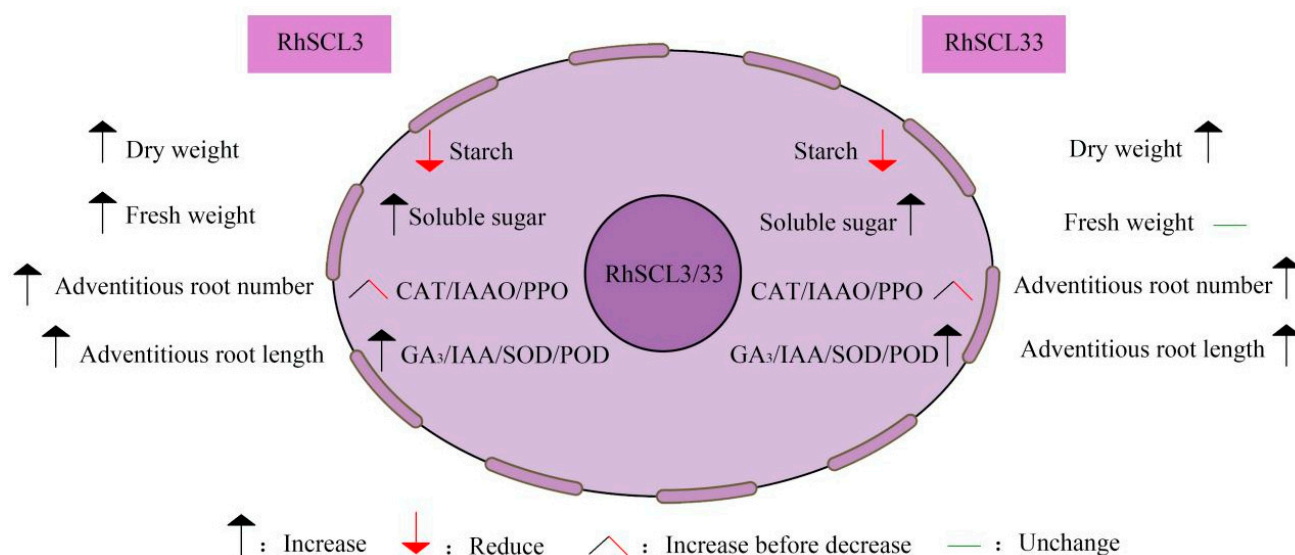


Figure 7. The working model diagram of *RhSCL3/33* regulating ARs

The formation and development of ARs constitute a complex biological process precisely regulated by multiple factors, among which plant hormones, particularly auxin, play a central role. Auxin establishes a concentration gradient through polar transport and subsequently regulates downstream gene expression to initiate AR primordium formation and promote root elongation and development. This study proposes that *RhSCL3* and *RhSCL33*, as transcription factors, participate in the auxin-mediated regulatory network of AR formation. In *A. thaliana*, certain GRAS family transcription factors interact with ARFs, modulating their transcriptional activation or repression of target genes and thereby influencing plant growth and development [42]. Given that *SCL3/33* belong to the GRAS family of transcription factors, they likely engage in auxin signal transduction to regulate AR development.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12080959/s1>, Table S1: primers list.

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