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Plants 2022, 11(3), 458; <https://doi.org/10.3390/plants11030458> (https://doi.org/10.3390/plants11030458) - 07 Feb 2022



Abstract In this study we examine the occurrence of plants and their symbolic, economic, and intrinsic values in Slovenian folk songs. We have analyzed songs published by the ethnologist Karel Štrekelj between 1895 and 1912. Of the 8686 songs studied, plants occur in 1246 [...] [Read more](#).

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Isolation of the Novel Strain *Bacillus amyloliquefaciens* F9 and Identification of Lipopeptide Extract Components Responsible for Activity against *Xanthomonas citri* subsp. *citri* (2223-7747/11/3/457)

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Plants 2022, 11(3), 457; <https://doi.org/10.3390/plants11030457> (https://doi.org/10.3390/plants11030457) - 07 Feb 2022

Abstract Citrus canker, caused by *Xanthomonas citri* subsp. *citri* (*Xcc*), is a quarantine disease that seriously affects citrus production worldwide. The use of microorganisms and their products for biological control has been proven to be effective in controlling *Xanthomonas* disease. In this [...] [Read more](#).

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Combining Hyperspectral Reflectance Indices and Multivariate Analysis to Estimate Different Units of Chlorophyll Content of Spring Wheat under Salinity Conditions (2223-7747/11/3/456)

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Plants 2022, 11(3), 456; <https://doi.org/10.3390/plants11030456> (https://doi.org/10.3390/plants11030456) - 07 Feb 2022

Abstract Although plant chlorophyll (Chl) is one of the important elements in monitoring plant stress and reflects the photosynthetic capacity of plants, their measurement in the lab is generally time- and cost-inefficient and based on a small part of the leaf. This study examines [...] [Read more](#).

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UPLC-PDA-MS/MS Profiling and Healing Activity of Polyphenol-Rich Fraction of *Alhagi maurorum* against Oral Ulcer in Rats (2223-7747/11/3/455)

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Abstract Camelthorn, *Alhagi maurorum* Boiss, family Fabaceae has long been used in African folk medicine owing to its richness in pharmacologically active metabolites. The crude extract of *Alhagi maurorum* (PDA-MW) and its bioactive polyphenol fraction (PDA-MW-Poly) were investigated for [...] [Read more](#).

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Functional Antagonism of WR1 and TCP20 Modulates *GH3.3* Expression to Maintain Auxin Homeostasis in Roots (2223-7747/11/3/454)

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Plants 2022, 11(3), 454; <https://doi.org/10.3390/plants11030454> (https://doi.org/10.3390/plants11030454) - 07 Feb 2022

Abstract Auxin is a well-studied phytohormone, vital for diverse plant developmental processes. The *GH3* genes are one of the major auxin responsive genes, whose expression changes lead to modulation of plant development and auxin homeostasis. However, the transcriptional regulation of these *GH3* genes remains [...] [Read more](#).

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((2223-7747/11/3/452/pdf))

Antidiabetic Activity and In Silico Molecular Docking of Polyphenols from *Ammannia baccifera* L. subsp. *Aegyptiaca* (Willd.) Koehne Waste: Structure Elucidation of Undescribed Acylated Flavonol Diglucoside ((2223-7747/11/3/452))

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Eman S. Mostafa (https://sciprofiles.com/profile/1501188)

Plants 2022, 11(3), 452; https://doi.org/10.3390/plants11030452 (registering DOI) - 06 Feb 2022

Abstract Chemical investigation of the aerial parts of *Ammannia aegyptiaca* ethanol extract (AEEE) showed high concentrations of polyphenol and flavonoid content, with notable antioxidant activity. Undescribed acylated diglucoside flavonol myricetin 3-O-β-⁴C₇-(6"-O-galloyl glucopyranoside) 7-O [...] **Read more.** (This article belongs to the Special Issue **Polyphenols in Plants** (/journal/plants/special_issues/Polyphenols_Plants))

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Flax and Sorghum: Multi-Element Contents and Nutritional Values within 210 Varieties and Potential Selection for Future Climates to Sustain Food Security ((2223-7747/11/3/451))

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Plants 2022, 11(3), 451; https://doi.org/10.3390/plants11030451 (https://doi.org/10.3390/plants11030451) - 06 Feb 2022

Abstract The Dietary Guidelines for Americans recommends giving priority to nutrient-dense foods while decreasing energy-dense foods. Although both flax (*Linum usitatissimum*) and sorghum (*Sorghum bicolor*) are rich in various essential minerals, their ionomes have yet to be investigated. Furthermore, previous [...] **Read more.** (This article belongs to the Special Issue **Unraveling the Mechanisms of Zn Efficiency in Crop Plants: From Lab to Field Applications** (/journal/plants/special_issues/Zn_Efficiency))

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Plants 2022, 11(3), 450; https://doi.org/10.3390/plants11030450 (https://doi.org/10.3390/plants11030450) - 06 Feb 2022

Abstract Sulfur is a growth-limiting and secondary macronutrient as well as an indispensable component for several cellular components of crop plants. Over the years various scientists have conducted several experiments on sulfur metabolism based on different aspects of plants. Sulfur metabolism in seeds has [...] **Read more.** (This article belongs to the Special Issue **Plant Sulfur Network** (/journal/plants/special_issues/Plant_Sulfur))

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((2223-7747/11/3/449/pdf))

Monoterpene Synthase Genes and Monoterpene Profiles in *Pinus nigra* subsp. *laricio* ((2223-7747/11/3/449))

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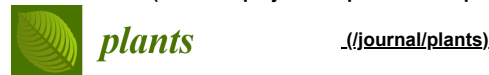
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Plants 2022, 11(3), 449; https://doi.org/10.3390/plants11030449 (https://doi.org/10.3390/plants11030449) - 06 Feb 2022

Abstract In the present study, we carried out a quantitative analysis of the monoterpenes composition in different tissues of the non-model conifer *Pinus nigra* J.F. Arnold subsp. *laricio* Palib. ex Maire (*P. laricio*, in short). All the *P. laricio* tissues examined showed [...] **Read more.** (This article belongs to the Section **Plant Genetics, Genomics and Biotechnology** (/journal/plants/sections/Plant_Genetics))

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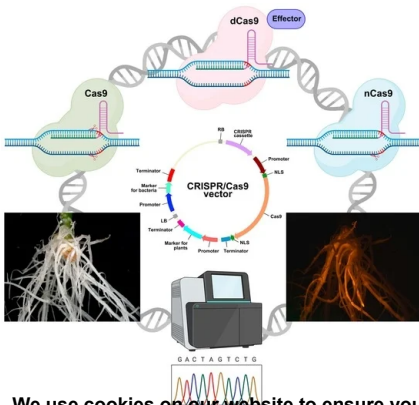
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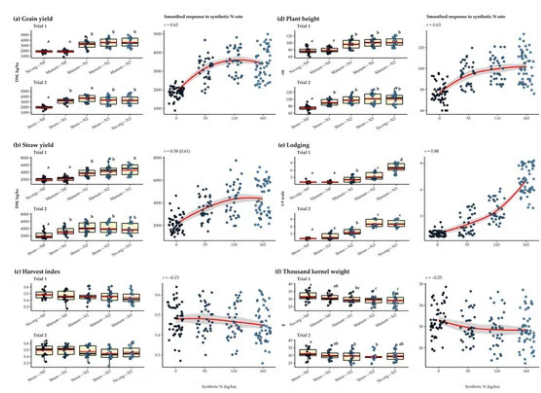


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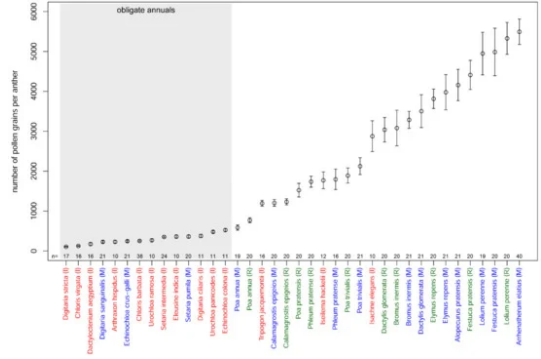
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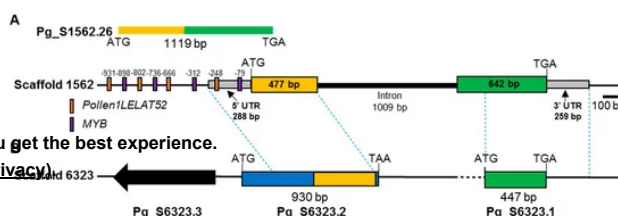
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Abstract

Cytochrome P450 (CYP) catalyzes a wide variety of monooxygenation reactions in plant primary and secondary metabolisms. Land plants contain CYP703, belonging to the CYP71 clan, which catalyzes the biochemical pathway of fatty acid hydroxylation, especially in male reproductive tissues. Korean/Asian ginseng (*Panax ginseng* Meyer) has been regarded as one of important medicinal plant for a long time, however the molecular mechanism is less known on its development. In this study, we identified and characterized a CYP703A gene in *P. ginseng* (*PgCYP703A4*), regarding reproductive development. *PgCYP703A4* shared a high-sequence identity (81–83%) with predicted amino acid as CYP703 in *Daucus carota*, *Pistacia vera*, and *Camellia sinensis* as well as 76% of amino acid sequence identity with reported CYP703 in *Arabidopsis thaliana* and 75% with *Oryza sativa*. Amino acid alignment and phylogenetic comparison of *P. ginseng* with higher plants and known *A. thaliana* members clearly distinguish the CYP703 members, each containing the AATDTS oxygen binding motif and PERH as a clade signature. The expression of *PgCYP704B1* was only detected in *P. ginseng* flower buds, particularly in meiotic cells and the tapetum layer of developing anther, indicating the conserved role on male reproduction with At- and Os- CYP703. To acquire the clue of function, we transformed the *PgCYP703A4* in *A. thaliana*. Independent overexpressing lines (*PgCYP703A4ox*) increased siliques size and seed number, and altered the contents of fatty acids composition of cutin monomer in the siliques. Our results indicate that *PgCYP703A4* is involved in fatty acid hydroxylation which affects cutin production and fruit size. [View Full-Text](https://doi.org/10.3390/plants11030383/htm) ([/2223-7747/11/3/383/htm](https://doi.org/10.3390/plants11030383/htm)).

Keywords: [cytochrome P450](#) ([/search?q=cytochrome%20P450](#)); [reproductive tissues](#) ([/search?q=reproductive%20tissues](#)); [PgCYP703A4](#) ([/search?q=PgCYP703A4](#)); [fatty acid](#) ([/search?q=fatty%20acid](#)); [reproduction](#) ([/search?q=reproduction](#)); [Panax ginseng](#) ([/search?q=Panax%20ginseng](#)).

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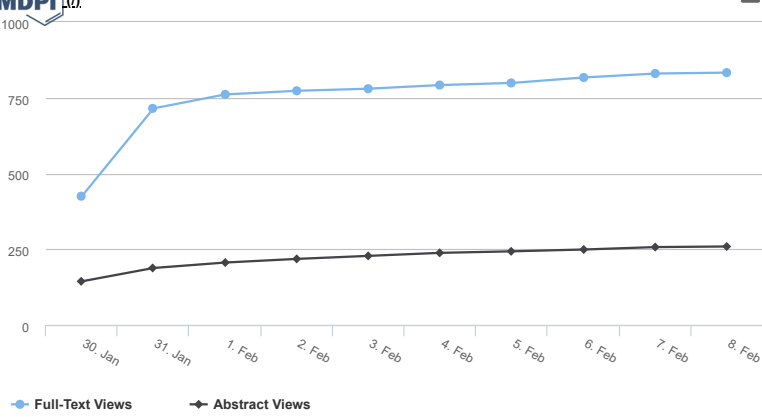
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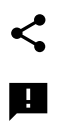

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Interests: role of compatible osmolytes in stress responses; plant metabolic profiling; regulation of carbon and nitrogen metabolism; effects of biostimulants on plant metabolism

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**Prof. Dr. Veronica De Micco *****Website** (<https://www.docenti.unina.it/#!/professor/5645524f4e4943414445204d4943434f444d43564e433737503634433439354d/avvisi>)**SciProfiles** (<https://sciprofiles.com/profile/829271>)*Section Associate Editor*

Department of Agricultural Sciences, University of Naples Federico II, 80055 Portici, NA, Italy

Interests: functional anatomical traits; linking structure and eco-physiology; plant hydraulics; wood formation; dendroecology; quantitative wood anatomy; stable isotopes; drought; ionizing radiation; altered gravity; crop biology in CEA; Mediterranean ecosystems; plant adaptive strategies in extra-terrestrial environments

* Section: Plant Response to Abiotic Stress and Climate Change

[Special Issues, Collections and Topics in MDPI journals](#)**Prof. Dr. Filippo Maggi *****Website** (https://www.researchgate.net/profile/Filippo_Maggi) **SciProfiles** (<https://sciprofiles.com/profile/190370>)*Section Associate Editor*

School of Pharmacy, University of Camerino, Camerino, Italy

Interests: medicinal and aromatic plants; essential oils; green extraction; phytochemistry; bioactivity

* Section: Phytochemistry

[Special Issues, Collections and Topics in MDPI journals](#)**Dr. Sotiris Tjamos *****Website** (http://efp.aua.gr/en/userpages_en/61) **SciProfiles** (<https://sciprofiles.com/profile/570198>)*Section Associate Editor*

Phytopathology Department, Agricultural University of Athens, 11855 Athens, Greece

Interests: biological control; epigenetics; microbial volatile organic compounds; plant-microbe interactions; soil-borne diseases; induced systemic resistance

* Section: Plant Protection and Biotic Interactions

[Special Issues, Collections and Topics in MDPI journals](#)**Dr. Christian Meyer *****Website** (<http://annuaire.inra.fr/afficherActivite.action?code=5133&type=AC>) **SciProfiles** (<https://sciprofiles.com/profile/1272496>)*Section Associate Editor*

Institut Jean-Pierre Bourgin, French National Institute for Agriculture, Food, and Environment (INRAE), Paris, France

Interests: role of the TOR kinase signalling pathway in plants; nitrate signalling

* Section: Crop Physiology and Crop Production

Advisory Board (2)

**Prof. Dr. Shuangxia Jin****Website** (https://www.researchgate.net/profile/Shuangxia_Jin) **SciProfiles** (<https://sciprofiles.com/profile/304371>)

College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China

Interests: plant biotechnology (genome editing, transgenic methods, chloroplast transformations); plant genome; genomics; Omics; big data and

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Prof. Dr. Iain Wilson

Website (<https://people.csiro.au/W/I/Iain-Wilson>) SciProfiles (<https://sciprofiles.com/profile/973596>)

CSIRO Agriculture and Food, Canberra, ACT 2601, Australia

Interests: cotton genomics; molecular understanding of cotton abiotic and biotic stress; cotton fuzz fibre development; plant genotyping; genomic selection

Editorial Board Members (727)

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Dr. Jason Able

Website (<https://researchers.adelaide.edu.au/profile/jason.able>) SciProfiles (<https://sciprofiles.com/profile/626950>)

School of Agriculture, Food and Wine, The University of Adelaide, Adelaide, Australia

Interests: breeding and commercialisation of cereal and pulses; micro RNAs (miRNAs) and their role in enhancing crop productivity (through either stress adaptation and/or reproductive fitness); understanding the molecular mechanisms that control meiosis in cereals

Special Issues, Collections and Topics in MDPI journals

Special Issue in [**Plants: Small RNAs in Crop Improvement and Breeding**](#) (/journal/plants/special_issues/small_RNAs_crop)



Dr. Rita Abranches

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Plant Cell Biology Laboratory, Instituto de Tecnologia Quimica e Biologica ITQB NOVA, Universidade Nova de Lisboa, Av Republica, 2780-157 Oeiras, Portugal

Interests: molecular farming; recombinant proteins; plant cell cultures; microalgae; cell biology; epigenetics

Special Issues, Collections and Topics in MDPI journals

Special Issue in [**Plants: Plant Molecular Farming**](#) (/journal/plants/special_issues/plant_molecular_farming)



Prof. Dr. Stefano Accoroni

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Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, via Brecce Bianche, 60131 Ancona, Italy

Interests: microalgae; microphytobenthos; phytoplankton; harmful algal blooms; environmental factors

Special Issues, Collections and Topics in MDPI journals

Special Issue in [**Plants: Systematics and Ecology of Algae and Marine Plants**](#) (/journal/plants/special_issues/algae_marine_plant)

Special Issue in [**Plants: Systematics and Ecology of Algae and Marine Plants II**](#) (/journal/plants/special_issues/Algae_Marine_Plants)

Special Issue in [**Geosciences: Atmospheric Deposition in Polar Regions**](#) (/journal/geosciences/special_issues/atmospheric_depositions)



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SciProfiles (<https://sciprofiles.com/profile/608169>)

Department of Entomology and Plant Pathology, North Carolina State University, 1575 Varsity Drive, VRB, Module # 6, Raleigh, NC 27695, USA

Interests: rice; wheat; strawberry and tomato diseases; integrated disease management; plant-pathogen interactions; genetic mapping, and

GWAS; RNA-seq analysis; genotyping-by-sequencing, and plant microbiomes

Special Issues, Collections and Topics in MDPI journals

Special Issue in [**Stresses: Stress Responses in Crops**](#) (/journal/stresses/special_issues/Stress_Responses_Crops)

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Department of Biosciences, Biotechnology and Biopharmaceutics, University of Bari, Bari, Italy

Interests: mitochondria; mitochondrial transporters; metabolism; TCA cycle-connected metabolism; organic acid metabolism; metabolic engineering



Dr. Mukhtar Ahmed

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- 1. Swedish University of Agricultural Sciences, Uppsala, Sweden
- 2. PMAS Arid Agriculture University, Rawalpindi, Punjab , Pakistan

Interests: agronomy; agroecosystems modeling; cropping systems; farm modeling; crop physiology; nutrients cycling; climate change; impact assessments; adaptation and mitigation

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Sustainability: Climate Resilient Sustainable Agricultural Production Systems***

(/journal/sustainability/special_issues/sust_agricult_prod_syst)

Special Issue in ***Plants: Agroecosystem Modeling*** (/journal/plants/special_issues/Agroecosystem_Modeling)

Special Issue in ***Plants: Plant Responses to Biotic and Abiotic Stresses: Crosstalk between Biochemistry and Ecophysiology***

(/journal/plants/special_issues/plant_Crosstalk)

Special Issue in ***Sustainability: Sustainable Agriculture Through Technological Intervention***

(/journal/sustainability/special_issues/sustainable_agri_tech_intervention)



Prof. Dr. Mi-Jeong Ahn

Website (<https://www.marketscreener.com/business-leaders/Mi-Jung-Ahn-0FWVF7-E/biography/>)

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Gyeongsang National University, Jinju, South Korea

Interests: Standardization of herbal medicines (Inner-morphological study and chemical profiles); Natural products chemistry; Metabolomics



Dr. Anna Aksmann

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Department of Plant Physiology and Biotechnology, Faculty of Biology, University of Gdansk, Wita Stwosza str. 59, PL-80-308 Gdansk, Poland

Interests: abiotic stress; anthropogenic pollutants (herbicides, pharmaceuticals); green algae response to stress factors; Chlamydomonas reinhardtii; plant physiology and biochemistry

Special Issues, Collections and Topics in MDPI journals

Topical Collection in ***Plants: Plant, Algae and Lichen Response to Abiotic Stress: from Molecules to Ecosystems***

(/journal/plants/special_issues/plant_algae_lichen_abiotic)



Dr. Josefa M. Alamillo

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Departamento de Botánica, Ecología y Fisiología Vegetal, Grupo de Fisiología Molecular y Biotecnología de Plantas, Campus de Excelencia Internacional Agroalimentario, CEIA3, Universidad de Córdoba, 1407 Córdoba, Spain

Interests: abiotic stress; drought tolerance; legumes; nitrogen fixation; purine nucleotides metabolism; ureides

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Drought Tolerance in Common Bean*** (/journal/plants/special_issues/Drought_Tolerance_Common_Bean)



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Prof. Dr. Emidio Albertini

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Department of Agricultural, Food and Environmental Sciences, University of Perugia, 06121 Perugia, Italy

Interests: plant reproduction; epigenetics; apomixis; stresses; tomato; grape

Special Issues, Collections and Topics in MDPI journals

Special Issue in **Plants: DNA Methylation in Plants** (/journal/plants/special_issues/DNA_methylation_plants).

Special Issue in **International Journal of Molecular Sciences: Molecular Analysis of Crop Diversity**.

(/journal/ijms/special_issues/omic_analysis_crop).



Prof. Dr. Robin G. Allaby

Website (<https://warwick.ac.uk/fac/sci/lifesci/people/rallaby/>)

School of Life Sciences, University of Warwick, Coventry CV4 7AL, UK

Interests: domestication; archaeogenomics; crop origins; crop evolution

Prof. Dr. Artur Alves

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CESAM-Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal

Interests: plant pathology; fungi; secondary metabolites; plant-microbe interactions

Special Issues, Collections and Topics in MDPI journals

Special Issue in **Microorganisms: Fungal-Plant Interactions under Climate Change**

(/journal/microorganisms/special_issues/fungal_plant_climate).



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School of Agriculture Forestry Food and, Environmental Sciences, Università della Basilicata, Viale dell'Ateneo Lucano 10, 85100 Potenza, Italy

Interests: plant roots; soil physics; soil-plant interactions; agronomy; geophysical methods for plant root research



Prof. Dr. Stephen O. Amoo

Website (<https://www.arc.agric.za/arc-vopi/Pages/Crop%20Science/Medicinal-Plants.aspx>)

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Agricultural Research Council-Vegetables, Industrial and Medicinal Plants, Private Bag X293, Pretoria 0001, South Africa

Interests: plant growth regulators; phytohormones; indigenous plant use; micropropagation; secondary metabolite production; biological activities;

medicinal plants; plant tissue culture; ethnopharmacology; antimicrobial activity; ethnobotany; plant biotechnology; biostimulants; plant production

Special Issues, Collections and Topics in MDPI journals

Special Issue in **Plants: Propagation and Cultivation of Medicinal Plants** (/journal/plants/special_issues/propagation_medicinal_plants)



Prof. Dr. Asunción Amorós

Website (<https://universite.umh.es/profesores/fichaprofesor.asp?NP=3846>) **SciProfiles** (<https://sciprofiles.com/profile/896934>)

Department of Applied Biology, Escuela Politécnica Superior de Orihuela (Miguel Hernández University of Elche), Ctra. Beniel Km 3.2, 03312

Orihuela, Spain

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Interests: ethylene; brassinosteroid; phenols; antioxidant activity; jujube; capper



Prof. Dr. Toyoaki Anai

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Department of Biological Resources, Faculty of Agriculture, Saga University, Saga 840-8502, Japan

Interests: soybean; mutant; genome analysis; transgenic plant; genetics and breeding; crop production; applied molecular and cellular biology; applied biochemistry; plant genetics and breeding



Dr. Naser A. Anjum

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Department of Botany, Aligarh Muslim University, Aligarh-202 002 U.P., India

Interests: plant-environment adaptation; plant stress physiology and biochemistry

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Advances in Adaptation of Plants to Climate Change: Agricultural to Molecular Approaches***
(/journal/plants/special_issues/Advances_Adaptation_plants)



Dr. Frederic Aparicio

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Department of Molecular and Evolutionary Plant Virology, Instituto de Biología Molecular y Celular de Plantas (IBMCP) (UPV-CSIC), Ingeniero Fausto Elio s/n, 46022 Valencia, Spain

Interests: plant virus–host factor interactions; RNA viruses; post-transcriptional modifications during virus infection

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Emerging Molecular Diagnostics for Plant Virology*** (/journal/plants/special_issues/Diagnostics_Virology)



Prof. Dr. Ismael Aranda

INIA, Ctr Invest Forestales CIFOR, Carretera Coruna Km 7,5, 28040 Madrid, Spain

Special Issues, Collections and Topics in MDPI journals

Topical Collection in ***Plants: Feature Papers in Plant Ecology*** (/journal/plants/special_issues/plant_ecology_fp)



Dr. Fabrizio Araniti

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Locality Feo di Vito, Department AGRARIA, University Mediterranea of Reggio Calabria, 89124 SNC Reggio Calabria, Italy

Interests: allelopathy; secondary metabolites; essential oils; weed management; plant nutrition; metabolomics; mode of action; chemical interaction; bio-herbicides

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Secondary Metabolites and Eco-friendly Techniques for Agricultural Weed/Pest Management***
(/journal/plants/special_issues/Secondary_Metabolites_Eco-friendly)

Special Issue in ***Plants: Mode of Action of Plant Natural Products*** (/journal/plants/special_issues/mode_action)

Special Issue in ***Agronomy: Natural Compounds as Bioherbicide for an Eco-Friendly Agriculture***

(/journal/agronomy/special_issues/compounds_bioherbicide)

Special Issue in ***Plants: Selected Papers from the 2nd International Electronic Conference on Plant Sciences***


(/journal/plants/special_issues/IECPS2021)

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Dr.iker Aranjuelo

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Agrobiotechnology Institute (IdAB-CSIC)-Gobierno de Navarra, Campus de Arrosadia, E-31192-Mutilva Baja, Spain



Interests: climate change; cereals; N2 fixers; resource use efficiency; photosynthesis; stable isotopes; sustainable agriculture; yield and quality traits

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Photosynthetic Metabolism under Stressful Growth Conditions***

(/journal/plants/special_issues/Photosynthetic_Metabolism)

Special Issue in ***Plants: Cereal Physiology and Breeding*** (/journal/plants/special_issues/Cereal_Physiology_Breeding)

Special Issue in ***Plants: Crop Cultivation and Low Carbon Agriculture*** (/journal/plants/special_issues/Carbon_Agriculture)



Dr. Vicent Arbona

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Departament de Ciències Agràries i del Medi Natural, Universitat Jaume I, Castelló de la Plana, Spain

Interests: abiotic stress; Arabidopsis; biochemistry; citrus; drought; flooding; metabolomics; plant physiology; tomato

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***International Journal of Molecular Sciences: Plant Metabolism in Crops: A Systems Biology Perspective***

(/journal/ijms/special_issues/plants_metabolism)



Prof. Dr. Carmen Arena

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University of Naples Federico II, Department of Biology, Naples, Italy

Interests: plant ecology; photosynthetic regulation mechanisms; antioxidant defences; plant-soil interactions; plants and abiotic stress; pollutants and photosynthesis

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Effects of Abiotic Stress on Plants 2020–2021*** (/journal/plants/special_issues/Effects_Abiotic_Stress)

Special Issue in ***Agriculture: Cropping Systems: Implications on Climate and Environment***

(/journal/agriculture/special_issues/cropping_systems)

Special Issue in ***Plants: Oxidative Stress, PolyADP(ribose)ylation and Antioxidant Defenses in Plants***

(/journal/plants/special_issues/Antioxidant_Defenses)



Prof. Dr. Fernando Ponz Ascaso

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Centro de Biotecnología y Genómica de Plantas (UPM-INIA), Campus Montegancedo, Autopista M40, km 38. Pozuelo de Alarcón, 28223 Madrid, Spain

Interests: plant-virus interactions; virus nanobiotechnology; plant molecular farming



Prof. Dr. Hagop Atamian

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Schmid College of Science and Technology, Chapman University, Orange, CA 92866, USA

Interests: understanding the molecular mechanisms of plant interactions with the environment; biotic interactions (insects, bacteria, fungi, nematodes); various biotic stresses (drought, cold, heat); high throughput sequencing; plant genotype and environment interactions



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Website (<https://www6.rennes.inra.fr/umreva>) **SciProfiles** (<https://sciprofiles.com/profile/138854>)

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Interests: nutrient use efficiency; plant nutrition; nitrogen and sulfur fertilization; plant responses to abiotic stress; plant senescence; seed quality; remobilization of nutrients; proteolytic mechanisms



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Special Issue in **[Plants: Advances in Plant Sulfur Research \(/journal/plants/special_issues/Sulfur_Metabolism\)](#)**



Dr. Germán Avila Sakar

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Department of Biology, University of Winnipeg, 599 Portage Ave., Winnipeg, MB R3B 2G3, Canada

Interests: plant–animal interactions; herbivory; tolerance; resistance; resource allocation; sexual systems of plants; dioecy; monoecy; pollination; evolution of plant responses to herbivores; evolution of plant mating systems

Special Issues, Collections and Topics in MDPI journals

Special Issue in **[Plants: Interaction Between Abiotic and Biotic Stresses in Plants \(/journal/plants/special_issues/plant-salt-stress\)](#)**

Special Issue in **[Plants: Interactions Between Abiotic and Biotic Stresses in Plants \(/journal/plants/special_issues/stress_plants\)](#)**

Special Issue in **[Plants: Plant Evolutionary Ecology \(/journal/plants/special_issues/Plant_Evolutionary_Ecology\)](#)**



Dr. Aziz Aziz

Website (https://www.univ-reims.fr/minisite_173/our-research-groups/immunity-and-beneficial-microorganisms/immunity-and-beneficial-microorganisms,22730,37873.html) **SciProfiles** (<https://sciprofiles.com/profile/250915>)

Lab RIBP 4707, University of Reims Champagne-Ardenne, SFR Condorcet FR-CNRS 3417, 51100 Reims, France

Interests: Plant-microbe interactions; beneficial microorganisms; Plant Immunity; signaling, metabolism; Induced resistance; plant defense; interactions between biotic and abiotic stresses



Dr. Christian Bachem

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Plant Breeding, Wageningen University and Research, Wageningen, The Netherlands

Interests: molecular signaling; plant organ development; sexual and vegetative reproduction; molecular environment-genotype interactions; abiotic stress; potato and Solanaceae biology



Prof. Dr. Tony Bacic

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1. Department of Animal, Plant and Soil Sciences, School of Life Sciences, La Trobe University, Bundoora VIC 3068, Australia

2. Department of Forestry, School of Forestry and Biotechnology, Zhejiang A & F University, Lin'an District, Hangzhou 311300, China

Interests: structure, function & biosynthesis of complex carbohydrates; cell walls; cell surfaces; mechano-sensing; plant cell and molecular biology; plant physiology; plant biochemistry; proteomics; metabolomics; glycomics



Prof. Dr. Martin Backor

Website (<http://martinbackor.science.upjs.sk/>) **SciProfiles** (<https://sciprofiles.com/profile/1028295>)

Department of Botany, Institute of Biology and Ecology, P. J. Safarik University in Kosice, Manesova 23, 041 67 Kosice, Slovakia

Interests: lichens; algae; mosses; abiotic stress; heavy metals; secondary metabolism of lichens; polar ecology of lower plants

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Special Issue in **[Plants: Secondary Metabolites from Lichens and Biological Activity](#)**

([/journal/plants/special_issues/secondary_metabolites_lichens_biological_activity](#))





Dr. Aneta Helena Baczewska-Dąbrowska

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Center for Conservation of Biological Diversity, Polish Academy of Sciences Botanical Garden, 02-973 Warsaw, 2 St. Prawdziwka, Poland

Interests: biotic and abiotic stress; trees; biomonitoring; environmental pollution

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Plants: Plants in Built-Up Areas*** (/journal/plants/special_issues/Plants_Built_Up)



Prof. Dr. Kwang-Hyun Baek

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Department of Biotechnology, Yeungnam University, Gyeongsan, Gyeongbuk 38451, Korea

Interests: antimicrobial agents; synergistic effects; nanoparticles; essential oils; secondary metabolites; plant extracts; bacteria; fungi; viruses; multidrug-resistant; microorganisms

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***Molecules: Advances of Metal and Metal Oxide Nanocomposites: Synthesis, Characterization and Biomedical Applications*** (/journal/molecules/special_issues/metal_nanocomposites_biomedical)

Special Issue in ***Plants: Impact of Metal and Metal Oxide Nanomaterials on Plant Research: Recent Advances and Challenges*** (/journal/plants/special_issues/metal_nanos)



Dr. Christophe Bailly

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Sorbonne Université, Institut de Biologie Paris-Seine (IBPS), UMR7622 "Biologie du Développement", Paris, France

Interests: seed; dormancy; germination; longevity; reactive oxygen species; transcriptome; RNA metabolism; abiotic stress

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***International Journal of Molecular Sciences: Physiological and Environmental Regulation of Seed Germination: From Signaling Events to Molecular Responses*** (/journal/ijms/special_issues/sdn)



Dr. Andrzej Bajguz

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Department of Biology and Plant Ecology, Faculty of Biology, University of Białystok, 15-245 Białystok, Poland

Interests: adaptation to heavy metal stress; brassinosteroids; phytoecdysteroids; phytohormones

Special Issues, Collections and Topics in MDPI journals

Special Issue in ***International Journal of Molecular Sciences: Hormones and Animal-Derived Compounds of Plants*** (/journal/ijms/special_issues/hormones_plant)

Special Issue in ***International Journal of Molecular Sciences: Metal Stress in Plants*** (/journal/ijms/special_issues/Metal_Stress_Plants)

Dr. Bénédicte Bakan

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SciProfiles (<https://sciprofiles.com/profile/334156>)

INRA, Biopolymers Interactions Assemblies Research unit, La Géraudière, CEDEX 3, 44316 Nantes, France

Interests: fruit cuticles; polysaccharides; polyester; cutin; cutin synthase; gdsI-lipase



Dr. Salma Balazadeh

Website (<https://www.universiteitleiden.nl/en/staffmembers/salma-balazadeh>)

Read more about Salma Balazadeh (<https://www.universiteitleiden.nl/en/staffmembers/salma-balazadeh>)

Institute of Molecular Plant Physiology, University of Potsdam and Max-Planck, Potsdam-Golm, Germany

Interests: transcription factors (TFs), gene regulatory networks (GRNs), leaf growth, senescence, abiotic stress, priming and memory

Special Issues, Collections and Topics in MDPI journals

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Prof. Dr. Raffaella Maria Balestrini

Website (<http://www.ipsp.cnr.it/researchers/balestrini-raffaella-maria/?lang=en>) **SciProfiles** (<https://sciprofiles.com/profile/453875>)

Institute for Sustainable Plant Protection National Research Council of Italy, IPSP-CNR, Turin, Italy

Interests: cell wall; genomics and fungal genomics of symbiotic fungi; mycorrhizal fungi; plant-microbe interactions; abiotic stresses

Special Issues, Collections and Topics in MDPI journals

Special Issue in [Agriculture: Plant-Microbe Interactions \(/journal/agriculture/special_issues/Plant-Microbe_Interactions\)](#)

Special Issue in [International Journal of Molecular Sciences: Cell-Specificity in Plants \(/journal/ijms/special_issues/plant_cell_specificity\)](#)

Special Issue in [Agronomy: Contribution of Arbuscular Mycorrhizal Symbiosis to Crop Growth](#)

[\(/journal/agronomy/special_issues/arbuscular_mycorrhizal_symbiosis_crop\)](#)

Special Issue in [Journal of Fungi: Cell Wall Stress Response \(/journal/jof/special_issues/cell_wall_stress_response\)](#)

Special Issue in [Journal of Fungi: Mycorrhizal Fungi and Plants \(/journal/jof/special_issues/Mycorrhizal_Plants\)](#)

Special Issue in [Plants: Biostimulants as Growth Promoting and Stress Protecting Compounds](#)

[\(/journal/plants/special_issues/Protecting_Compounds\)](#)

Special Issue in [Resources: Value-Added Compounds from Compost, Digestate and Agro-Industrial Waste](#)

[\(/journal/resources/special_issues/Value-Added_Compounds\)](#)

Special Issue in [International Journal of Molecular Sciences: Biochemical and Molecular Regulations of Priming: How Plants Enhance](#)

[Their Defence against Environmental Pressures \(/journal/ijms/special_issues/Plants_Defence\)](#)



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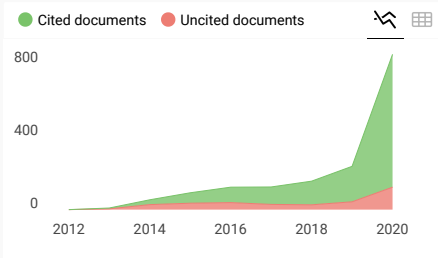
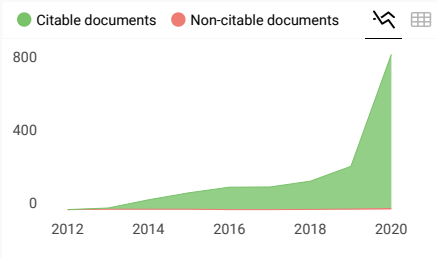
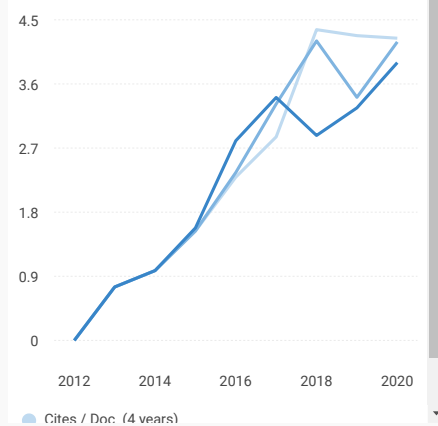
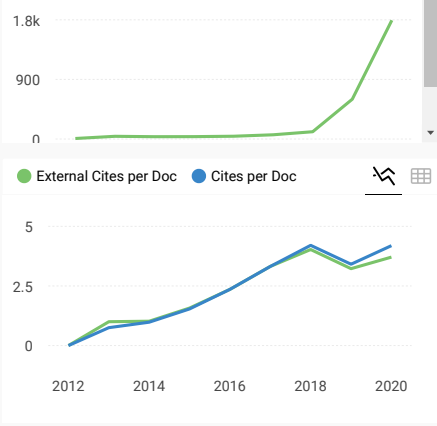
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Overexpression of the *Panax ginseng* CYP703 Alters Cutin Composition of Reproductive Tissues in *Arabidopsis*

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Abstract: Cytochrome P450 (CYP) catalyzes a wide variety of monooxygenation reactions in plant primary and secondary metabolisms. Land plants contain CYP703, belonging to the CYP71 clan, which catalyzes the biochemical pathway of fatty acid hydroxylation, especially in male reproductive tissues. Korean/Asian ginseng (*Panax ginseng* Meyer) has been regarded as one of important medicinal plant for a long time, however the molecular mechanism is less known on its development. In this study, we identified and characterized a CYP703A gene in *P. ginseng* (*PgCYP703A4*), regarding reproductive development. *PgCYP703A4* shared a high-sequence identity (81–83%) with predicted amino acid as CYP703 in *Daucus carota*, *Pistacia vera*, and *Camellia sinensis* as well as 76% of amino acid sequence identity with reported CYP703 in *Arabidopsis thaliana* and 75% with *Oryza sativa*. Amino acid alignment and phylogenetic comparison of *P. ginseng* with higher plants and known *A. thaliana* members clearly distinguish the CYP703 members, each containing the AATDTS oxygen binding motif and PERH as a clade signature. The expression of *PgCYP704B1* was only detected in *P. ginseng* flower buds, particularly in meiotic cells and the tapetum layer of developing anther, indicating the conserved role on male reproduction with At- and Os- CYP703. To acquire the clue of function, we transformed the *PgCYP703A4* in *A. thaliana*. Independent overexpressing lines (*PgCYP703A4ox*) increased silique size and seed number, and altered the contents of fatty acids composition of cutin monomer in the siliques. Our results indicate that *PgCYP703A4* is involved in fatty acid hydroxylation which affects cutin production and fruit size.

Keywords: cytochrome P450; reproductive tissues; *PgCYP703A4*; fatty acid; reproduction; *Panax ginseng*

1. Introduction

The cytochrome P450 (CYP) superfamily of enzymes, which catalyze diverse substrates through oxygenation and hydroxylation reactions, are found in all organisms [1]. Plant CYPs are involved in a variety of biochemical pathways that produce primary and

secondary metabolites, which constitute one of the largest families of enzymes in higher plants [2]. The diversification of land plant CYP families emerges during flowering plant evolution and specializes plant species with unique reactions [3]. The identification of CYP genes aids in understanding the evolution of various groups of enzymes and their conserved and diversified functions.

The *CYP703* gene family was found across the land plant taxa, suggesting that it encodes an essential function [4]. Land plants developed specialized cell layer to adapt to the environment, including cutin synthesis. As cutin cover in most plant organ of land plant, male reproductive organ of flowering plants is covered with a hydrophobic polymer barrier derived from fatty acids. The production of functional gametophytes leads to a successful proliferation in flowering plants [5]. Male reproduction is a complex and highly coordinated biological process that includes the development of the male reproductive organ: the stamen that contains the microspores and pollen. The study of male reproduction is important not only for increasing crop yield but for producing improved crops, such as superhybrid plants, through the use of male sterile lines [6].

The *CYP703* family is involved in the in-chain hydroxylation of mid-chain fatty acids, which is essential for the biopolymers of pollen exine, the outer wall of a pollen grain [7,8], and cutin, one of the most abundant lipid polymers and an important adaptive trait of plants to their terrestrial environment [9]. *A. thaliana* *CYP703A2* (*AtCYP703A2*) catalyzes the conversion of medium-chain saturated fatty acids to the corresponding monohydroxylated fatty acids, with a preferential hydroxylation of lauric acid at the C-7 position [8]. In comparison, *Oryza sativa* *CYP703A3* (*OsCYP703A3*) can only catalyze in-chain hydroxylation of lauric acid (C12), preferentially at position 7 [7]. The *A. thaliana* mutant, *cyp703a2*, exhibits impaired pollen development and a partial male sterile phenotype due to the lack of an exine [8]. *O. sativa* *CYP703A3* resulted in a complete male sterility with an abnormal anther epidermis, as well as defective pollen exine, indicating that the diversified function of *CYP703A* during evolution [7]. Both participated in a conserved pathway of in-chain hydroxylation of lauric acid that is required for male reproductive development. Some male-specific gene sequences that determine sex, where *CYP703* was found, have been identified in the *Phoenix* tree which belongs to dioecious species. [10]. Further studies in other plants will help elucidate the diversified *CYP703* function of fatty acid hydroxylation in plant reproductive development.

Panax ginseng is a perennial herb that has been cultivated for its highly valued root for medicinal purposes [11]. *P. ginseng* typically starts its reproduction at the third year of growth [12,13]. Attempts to increase the yield of *P. ginseng* and ginsenosides have been conducted by developing *P. ginseng* hybrids, and although they display heterosis, F1 hybrid plants exhibited male sterility that derived from pollen defects at the young microspore stage [13]. We previously studied and described the morphogenesis of the anther and carpel at a cytological level to understand and specify the reproductive developmental phases of *P. ginseng* [12,14] and identified the gene expression of *PgCYP703* in the anther tapetum layer [12]. Despite the importance of *P. ginseng* reproductive development, studies on functional gene analysis and molecular regulation remain scarce. In the studies presented here, we isolated and cloned the *CYP703A* gene from *P. ginseng*, *PgCYP703A*, which is highly expressed in flower buds during anther development. Surprisingly, in *A. thaliana*, overexpression of *PgCYP704B1* resulted in the enhanced in silique length, in terms of fruit size, which is potentially caused by the alteration of saturated fatty acids and hydroxy fatty acids in siliques.

2. Material and Methods

2.1. Plant Materials and Growth Conditions

The ginseng (*P. ginseng* Mayer) plant organs (root body, stem, leaf, flower bud, and fruit) were obtained from hydroponically cultured ginseng. Columbia ecotype (CS60000) of *A. thaliana* was used for gene overexpression. Sterilized seeds were sown on half-strength Murashige and Skoog medium (Duchefa Biochemie) containing 1% sucrose, 0.8% (*w/v*)

agar, and pH 5.7. Three-day-old cold-treated seeds were germinated under long-day photoperiods of 16-h light/8-h dark at 23 °C. The transformants were screened on hygromycin (50- μ g/mL)-selective medium plates. Ten-day-old seedlings were then transplanted to soil and cultivated for five weeks under the same light/dark conditions [15].

2.2. Identification of PgCYP703A4 Gene and Sequence Analysis

To obtain a coding sequence (CDS) of the *PgCYP703A4* gene, homologous sequences of *CYP703* was obtained based on *A. thaliana* sequence by homology-based PCR from *P. ginseng* flower cDNA. A complete genomic DNA sequence was obtained and analyzed from the database of the *P. ginseng* genome (<http://ginsengdb.snu.ac.kr>, accessed on 20 January 2022), and the putative ORF sequence was verified by sequencing after subcloning.

The predicted amino acid sequence of *PgCYP703A4* was used to search for homologous proteins via National Center for Biotechnology Information-Basic Local Alignment Search Tool (NCBI-BLASTX, <http://www.ncbi.nlm.nih.gov/BLAST/>, accessed on 18 January 2022). Sequence alignment was conducted using Clustal X V1.83, and a neighbor-joining tree was constructed using the MEGA4 software V.4.0.1, with the reliability of each node established by the bootstrap method. The subcellular localization for the N-terminus was predicted by PSORTdb (<http://www.psorth.org/psorth/>, accessed on 18 January 2022) [16], and the hydropathy value was calculated using the previously described method [17]. The 1000-bp sequence upstream of the ATG-coding site in the genomic DNA sequence of *PgCYP703* were used as promoters to predict Cis-acting elements by New PLACE (<http://www.dna.affrc.go.jp/PLACE/?action=newplace>, accessed on 20 December 2021) [18].

2.3. Vector Construction and A. thaliana Transformation

The full-length *CYP703* gene was amplified from *P. ginseng* flower cDNA and cloned into the *SalI* and *SpeI* sites of the pCAMBIA1390 vector containing the Cauliflower Mosaic Virus 35S promoter and yellow fluorescent protein. After nucleotide sequence verification, *A. thaliana* transformation was conducted using *Agrobacterium tumefaciens* C58C1 (pMP90) [19]. The insertion of transgenes into the transformants was confirmed via polymerase chain reaction (PCR). Heterozygous plants with a 3:1 segregation ratio on antibiotic plates which indicate the single gene insertion, were selected for additional analyses. Among the several T2 independent lines, two lines were selected for further statistical and metabolite analyses.

2.4. Gene Expression Analysis

Total RNA extraction from frozen samples was performed using the RNeasy Mini Kit (Qiagen, Valencia, CA, USA.), where 1- μ g of the total RNA was used as a reverse transcription template. For qRT-PCR, 100-ng cDNA in a 10- μ L reaction volume and SYBR[®] Green Sensimix Plus Master Mix (Quantace, Watford, England) were used. Specific primers for *PgCYP703A4* (F-5'-CTACGGGTGCAATGATGTTG-3' and R-5'-TGATGGAAAACGACTCAG-3') and a constitutively expressed *P. ginseng actin* gene (forward, 5'-AGAGATTCCGCTGTCCAGAA-3' and reverse, 5'-ATCAGCGATAACCAGGAACA-3') or *A. thaliana actin* gene (forward, 5'-GTGTGTCTTGTCTTATCTGGTTCG-3' and reverse 5'-AATAGCTGCATTGT CACCCGATACT-3') were used as an internal reference. qRT-PCR was conducted using a CFX Connect Real-Time PCR Detection System (BIO-RAD, Hercules, CA, USA) with the following program: 30 s at 95 °C, followed by 40 cycles of 95 °C for 3 s and 60 °C for 20 s. The threshold cycle (Ct) reflects the number of cycles where the fluorescence intensity at the original exponential stage of PCR amplification was significantly greater than the background fluorescence. To determine the relative fold differences in template abundance for each sample, the Ct value for *PgCYP703A4* was normalized to the Ct value for β -actin and calculated relative to a calibrator using the formula $2^{-\Delta\Delta Ct}$. Each qRT-PCR was technically repeated at least three times. Spatial expression of *PgCYP703* transcript in ginseng anther was analyzed by In situ hybridization, as reported previously [12].

2.5. Histological Analysis

Semi-thin sectioning was performed using anthers of mature flowers from 4-week-old plants. After fixing in FAA, the samples were dehydrated with an ethanol gradient (70%, 80%, 90%, and 100%) allowing 30 min for each step. Samples were then embedded in KULZER Technovit 7100 cold polymerizing resin by pre-infiltration, infiltration, and embedding at 45 °C, according to the previously described methods [20]. Samples were sectioned to a thickness of 4 µm in an Ultratome III ultramicrotome (LBK) and stained with 0.25% toluidine blue O (Chroma Gesellschaft Shaud). Bright-field photographs of the anther and silique sections were obtained using a Nikon ECLIPSE 80i microscope.

Scanning electron microscopy (SEM) was employed to analyze mature anthers that were fixed in FAA and dehydrated using 20–100% ethanol (10% increments) allowing 3 min for each step. The samples were then dried at the critical point temperature (Leica EM CPD300). A 5-nm-thick Aurum coating was paced on the samples with a Leica EM SCD050 ion sputter. The Aurum-coated samples were observed using a Hitachi S3400N SEM.

2.6. Analysis of Silique Fatty Acids

Cutin from the siliques of 5-week-old plants were examined as previously described [15,21]. Dried siliques (10–20 mg) were extracted in 2 mL of chloroform and spiked with 10 µg of tetracosane (Fluka) as the internal standard. Solvent was evaporated under a light stream of nitrogen, and the compounds containing free hydroxyl and carboxyl groups were transformed to trimethylsilyl ethers and esters using 20-µL bis-(N, N-trimethylsilyl)-trifluoroacetamine (Sigma-Aldrich, St. Louis, MO, USA) in 20-µL pyridine for 40 min at 70 °C. The monomers were identified from their electron ionization–mass spectrometry spectra (70 eV, m/z 50 to 700) after GC separation (column 30 mm × 0.32 mm × 0.1 µm film thickness [DB-1; J&W Scientific]). Gas chromatography–mass spectrometry (GC-MS) (Agilent gas chromatograph coupled with an Agilent 5973N quadrupole mass selective detector) and gas chromatography–flame ionization detection (GC-FID) (Agilent 6890 gas chromatograph) analyses were conducted. The means of three independent replicates were statistically analyzed and compared with control (* $p < 0.05$) using Student's *t*-test.

3. Results

3.1. Identification of CYP703 Gene in *P. ginseng*

CYP families often have many paralogs, but the CYP703 family was reported to be a single-gene-member family [8]. Analysis of the *P. ginseng* genome scaffold and CDS revealed that *P. ginseng* contains two scaffold sequences with high similarity to CYP703. Among the two scaffolds, scaffold 1562 contained a full-length CDS of CYP703 (Pg_S1562.26), which contained a two-exons and one-intron structure (Figure 1), similar to the *A. thaliana* gene structure. On the contrary, two CDS sequences, S6323.1 and S6323.2, present in scaffold 6323 were partial sequences of CYP703. Therefore, we concluded that the *P. ginseng* genome encodes just one PgCYP703 member, whereas the others are nonfunctional genes. The recent genome duplications of the *P. ginseng* genome [22] might explain the presence of two genes that can duplicated, in which one of the gene has retained the original sequence and function, whereas the other became a pseudogene. Similarly, CYP703A was noted as a single functional sequence in the poplar genome (*Populus trichocarpa*) [8].

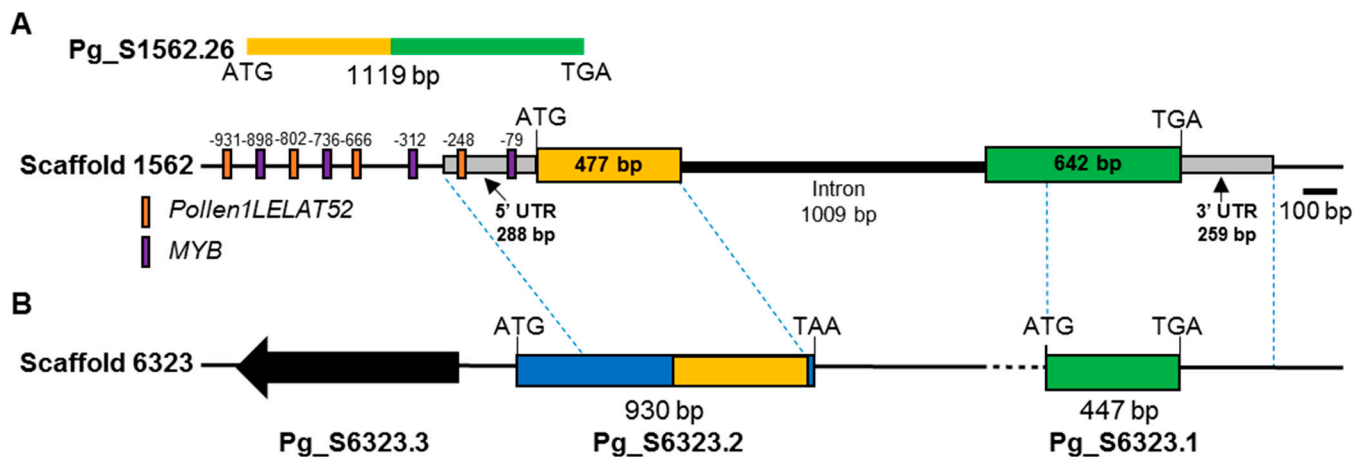


Figure 1. Analysis of gene and promoter structure of PgCYP703A4 and its pseudogene. Genomic sequence of scaffolds containing PgCYP703A4 and similar sequences were identified from the *P. ginseng* genome database (<http://ginsengdb.snu.ac.kr/> accessed on 20 January 2022). (A) PgCYP703A4 gene was confirmed as Pg_S1562.26 CDS, which encoded on Scaffold 1562. The coding regions (orange and green boxes) are interrupted by 1009 base pair (bp) intron. The upstream 1000-bp region from the translation start site has four POLLEN1LELAT52 binding-predicted sites and four MYBCORE binding-predicted sites. (B) A similar sequence structure was identified from Pg_scaffold6323 encoding two CDSs, assumed to be pseudogenes. The transcript was separated into two partial CDS sequences (Pg_S6323.2 and Pg_S6323.1). Dashed line indicates closed sequences between two scaffolds.

A putative ORF sequence, which had a length of 1119 bp and encoded 372 amino acids (Figure 1), was verified by sequencing, and an NCBI-BLAST search displayed the conserved superfamily CYP. There are three functionally reported genes: two CYP703A members registered in the Plant P450 Database (<http://erda.dk/public/vgrid/PlantP450/>, accessed on 10 December 2021) (CYP703A1 from a *Petunia hybrida* [23] and AtCYP703A2 [8]) and *O. sativa* CYP703A3 [7]. We named the CYP703 gene identified in *P. ginseng* as PgCYP703A4.

3.2. Sequence Alignment and Phylogenetic Analysis

CYP703 enzymes belong to the CYP71 clan, which includes the diverse families of P450 in plants [4,7]. To obtain information about the potential functions and evolutionary roles of PgCYP703A4, the full-length protein was used as a query to search for homologs in NCBI databases and the The *A. thaliana* Information Resource using NCBI-BLASTX. Highly similar homologs of PgCYP703A4 were detected in various dicot plant species whose genome sequences were available, although functional studies were limited. To see similarity of amino acids in various plant species, we selected the 10 closest sequences, and representative CYP71 members from *A. thaliana* were used to create a phylogenetic tree (Figure 2). Based on our phylogenetic comparison, PgCYP703A4 was placed in subfamily CYP703, separate from the other subfamilies of the CYP71 clan; CYP98, CYP73, CYP78, CYP84, CYP82, CYP81, CYP76, CYP61, CYP83, CYP705, and CYP701. CYP78 members hydroxylate short-chain fatty acids [24], CYP73 family members hydroxylate cinnamic acid [25], and CYP84 members are involved in lignin and flavonoid synthesis [26], thus indicating CYP71 clan subfamilies are not specific, rather showed various functions on metabolites.

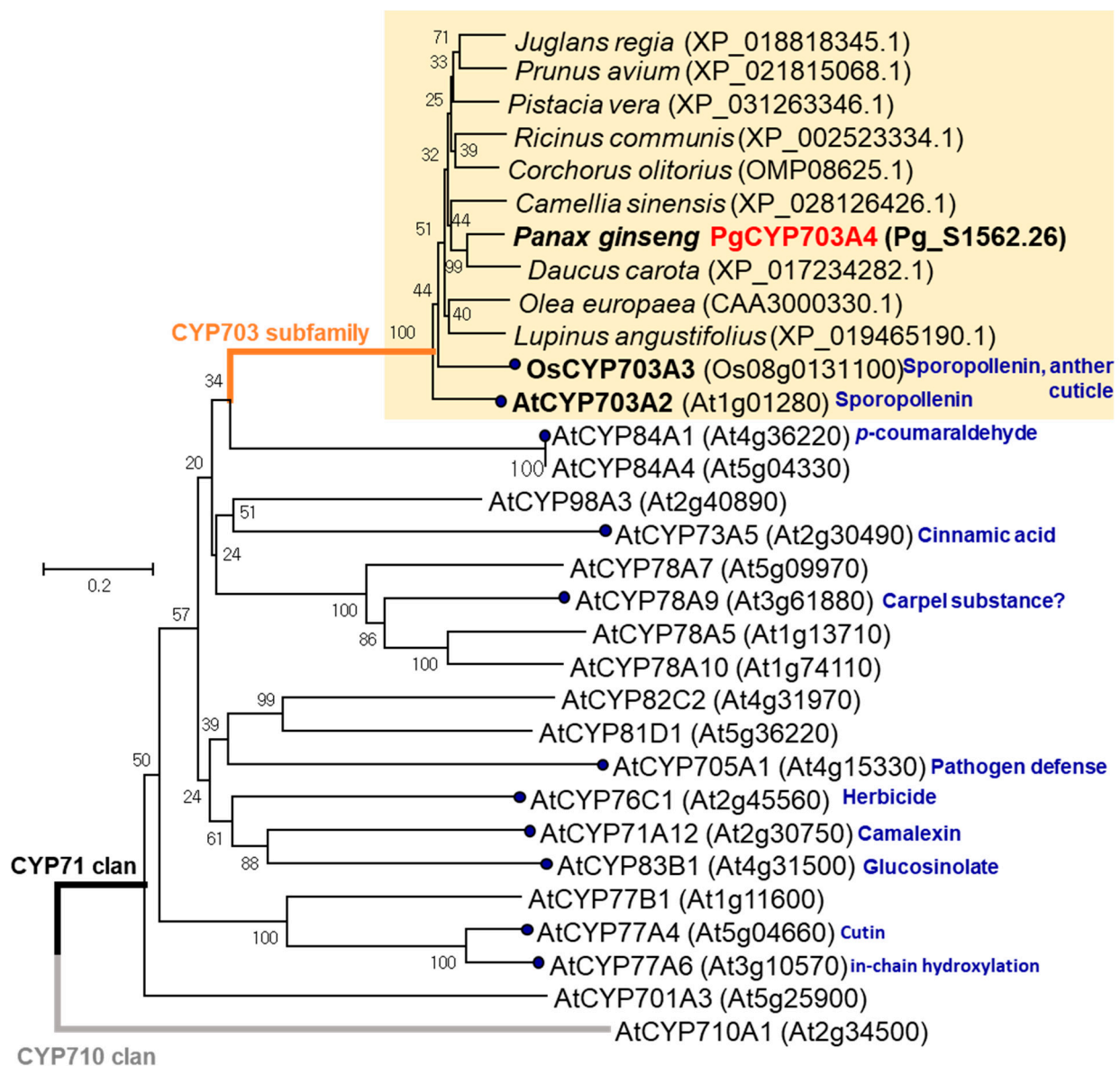


Figure 2. Phylogenetic analysis of PgCYP703. Neighbor-joining method analysis was conducted using the full-length amino acid sequences of PgCYP703A4 and closely related CYP703 subfamily members (Figure S1), in addition to the *A. thaliana* members of the CYP71 clan and outgroup of the CYP710 clan. The scale bar shows 0.2 amino acid substitutions per site. The reported CYP703A genes are distinguished by bold font with black dots. CYP703 subfamilies of the CYP71 clan are indicated by the yellow box. The functionally reported genes are indicated by circles and brief role in the right side. In figure, ‘At’ means *Arabidopsis thaliana*’s protein and ‘Os’ means *Oryza sativa*’s protein, and other plants are presented with full scientific name. NCBI accession numbers for other species and annotation numbers for *P. ginseng*, *A. thaliana* and *O. sativa* species are indicated inside bracket.

Multiple sequence alignment (Figure S1) revealed that the CYP703 proteins and Pg-CYP703A4 contain the conserved domains of the axial ligand for heme, the I-helix involved in oxygen binding, the Arg of the “PERF” consensus, and the E-R-R of the K-helix consensus (KETLR). Of these domains, only the cysteine of the heme-binding domain and the E-R-R triad are conserved in all plant cytochrome P450 sequences [27,28]. CYP703 members have a Phe–His substitution in the P(E)R(F) domain of CYP, known as a clade signature of the CYP703 family [28]. In addition, CYP703 members have an A-A-T-D-T-S motif (Figure S1) in the A/G-G-X-E/D-T-T/S domain, which is involved in oxygen binding

and activation [28]. Of the subfamilies in the CYP71 clan, substitution of A for the second G is unique to the CYP703 subfamily.

Plant P450s are usually bound to membranes, anchoring to the cytoplasmic surface of the endoplasmic reticulum (ER) through a short hydrophobic segment of their N-terminus [29]. The predicted transit peptide of PgCYP703A4 (indicated arrow in Figure S1) was shown to be positioned at its N-terminus with a cytoplasmic location [16] targeting ER with 69% certainty, predicted by PSORT (Prediction of Protein Localization Sites, version 6.4) Prediction program. Fatty acids are hydroxylated in the ER of plant cells through members of the CYP family [8,30,31]. The PgCYP703 hydrophobicity profile and those of its closest homologs indicated that both the N- and C-terminal regions, as well as the CYP703 motifs, are highly conserved (Figure S2).

3.3. Gene Expression Analysis of PgCYP703A4

To verify the conserved function of PgCYP703A4 in the male reproductive organ, as has been described for *A. thaliana* [8] and *O. sativa* [7], we conducted PgCYP703A4 expression analysis via qRT-PCR using *P. ginseng* tissues, such as the seed, root, stem, leaf, flower buds, and fruit at different age. PgCYP703A4 was specifically expressed in flower buds (Figure 3A).

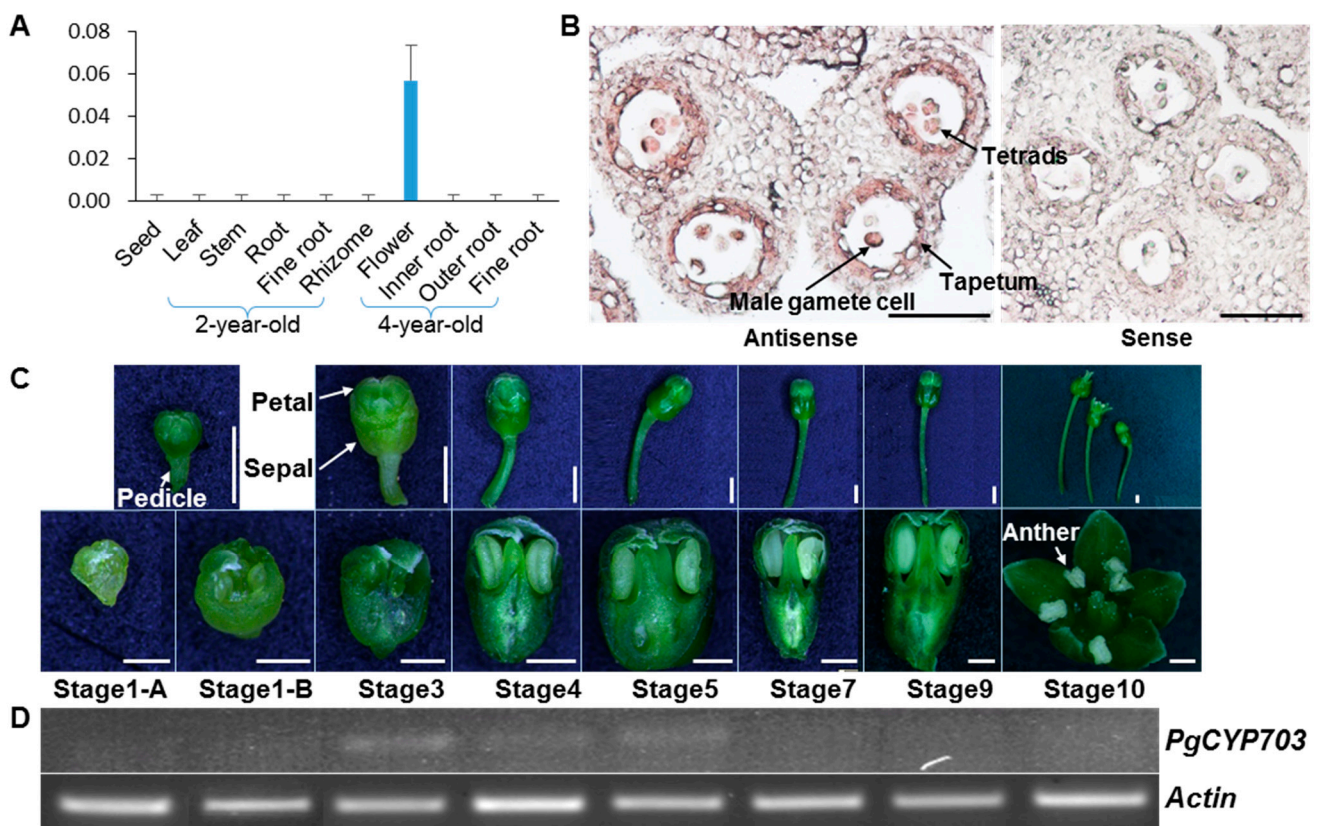


Figure 3. Tissue expression analysis of PgCYP703A4 in *P. ginseng*. (A) Quantitative expression analysis of PgCYP703A4 in various tissues at different age of *P. ginseng* plant. The expression levels were analyzed via realtime PCR, and PgActin served as the control. Values indicate mean of three technical replicates \pm SE. (B) In situ hybridization analysis of PgCYP703A4 in *P. ginseng* anther at stage 4 showing its expression (dark pink) in tapetal cells and microspores. Right image shows the anther with hybridized PgCYP703A4 sense probe, as control. Scale bars indicate 500 μ m. (C) Flower tissues of the *P. ginseng* at anther developmental stages [14] were used for RT-PCR. The scale bars of upper photo indicate 1 mm, and lower photo indicate 500 μ m. (D) RT-PCR gel images of PgCYP703A4 at seven stages of *P. ginseng* flowers show that PgCYP703A4 are expressed only during Stage 3 to 5. PgActin served as a control.

In situ hybridization experiments revealed that *PgCYP703A4* was expressed in the tapetal cell layer and tetrad cells (meiocytes after the second meiosis) in the anther (Figure 3B). The tapetum, the innermost layer of anther wall, plays a crucial role in pollen development by nursing and releasing the microspore [32]. During the developmental stage of anther, the *PgCYP703A4* expression was observed in meiosis to form young microspores (Figure 3C,D) [13].

To illuminate the regulation of gene expression, the 1000-bp upstream region from the coding sequence of *PgCYP703A4* was analyzed for cis-elements (Figure 1). The promoters contained various elements. Among them, we noted POLLEN1LELAT52 and MYBCORE, known as regulatory factors that are related to pollen and early pollen development, respectively [33,34]. These results indicated that MYBCORE and POLLEN1LELAT52 might bind to the promoters of *PgCYP703*, which leads to their specific expression during anther development.

3.4. Phenotype Analysis of *PgCYP3A4* Overexpressing *A. thaliana*

Due to difficulties in obtaining transgenic regenerated *P. ginseng* plants, we generated *PgCYP703A4* overexpressing transgenic Arabidopsis (*PgCYP703A4ox*) to examine its functional role in planta (Figure 4A–D). The stable incorporation of the *PgCYP703A4* gene and its heteroexpression was confirmed via RT-PCR (Figure 4B). *PgCYP703A4ox* produced slightly taller plants compared with the wild type, but not significant (Figure 4A). Notably, the siliques increased in size by 20% compared with the wild type and *PgCYP703A4ox* siliques contain higher number of seeds than wild type significantly (Figure 4C,D).

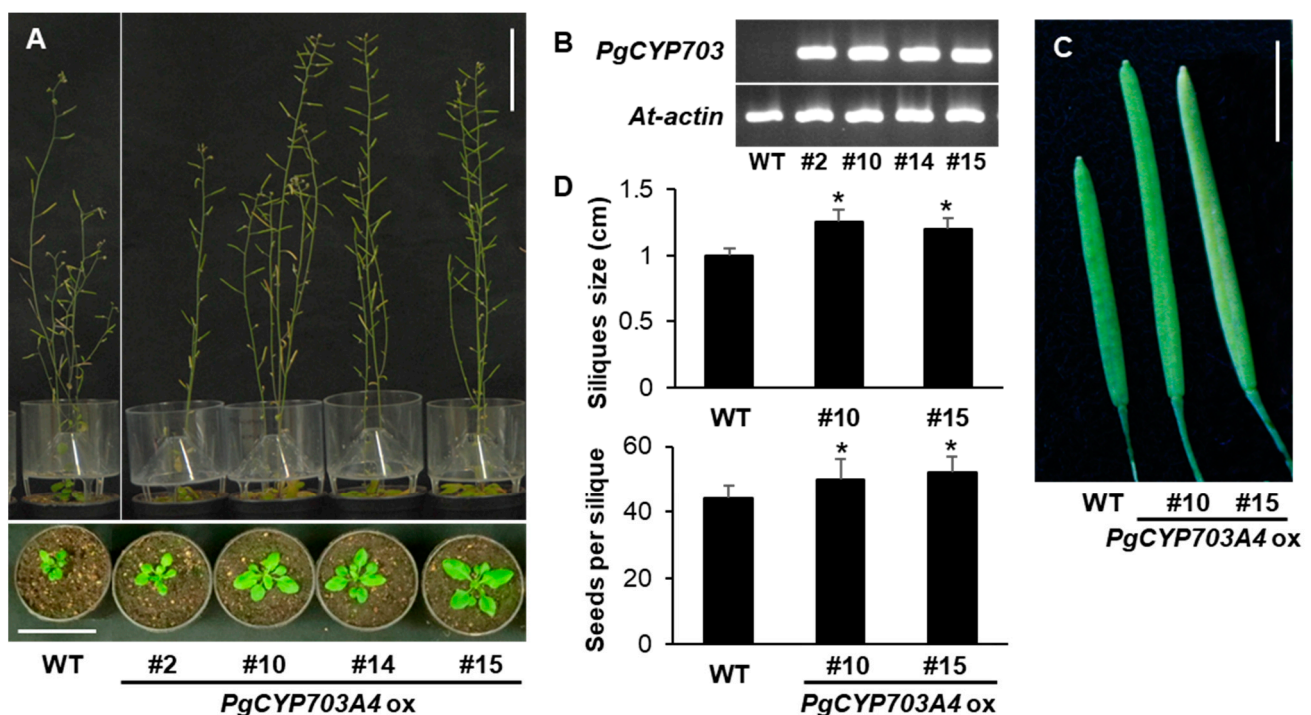


Figure 4. Phenotype analysis of *PgCYP703A4* overexpressing *A. thaliana*. (A) Growth phenotype of four different *PgCYP703A4* overexpression lines and wild type at 2 week- and 7 week- old. Scale bar indicates 5 cm. (B) Detection of *PgCYP703A4* transcription in transgenic *A. thaliana*'s rosette leaves. *At-actin* served as the control. (C,D) Silique size of *PgCYP703A4* overexpression lines. Scale bar indicates 5 mm. Values indicate mean of 20 biological replicates \pm SD. * $p < 0.05$.

A. thaliana *CYP703A3* mutant was reported to show impaired pollen walls lacking a normal exine layer, which leads to partial male sterility [8]. To determine how *PgCYP703A4* affects pollen wall formation, we observed the anthers and pollen phenotype by semi-thin cross-section and SEM (Figure S3). The anther, pollen, and pistil of *PgCYP703A4ox* appeared similar to the wild type, whereas *CYP703A3* exhibited aborted pollen without outer elegant

wall formation (Figure S3). Therefore, pollen viability and reproductive organ function was not altered by *PgCYP703A4* gene overexpression.

3.5. Fatty Acid Composition of *PgCYP703A4*-Overexpressing *A. thaliana*

The cuticle, a hydrophobic layer that coats the surface of the aerial organs, such as leaves, stems, flowers, and fruits, is a biopolymer that is composed of two classes of lipophilic constituents, namely, cutin and waxes [35,36]. Since the silique phenotype of *PgCYP703A4ox* is elongated and the exocarp is made of cutin, we further conducted GC-MS and GC-FID.

The overall sum of cutin monomers were not significantly different between wild type and *PgCYP703ox* lines. We found that two independent lines alter the composition of fatty acids, with some variation, which might explain complex fatty acids metabolism for the cutin polymer. For example, compared with the wild type, the *PgCYP703A4ox* #10 significantly increased saturated fatty acids of C18:0, C18:1, C26:1 and C28:0, (Figure 5A), dicarboxylic fatty acids of C18:0, C22:0, C24:0, and C26:0 (Figure 5C) and terminal-hydroxy fatty acids of C18:3, C22:0, and C24:0 (Figure 5D), and C28:0 alcohol type (Figure 5E). *PgCYP703A4ox* #15 increased C24:0, C25:0, and C26:0 saturated fatty acids (Figure 5A), and 2-hydroxyl fatty acids, such as C16:0, C23:0, C24:0, C25:0, C26:0 (Figure 5B). The dicarboxylic fatty acids of C22:0 and C24:0 were significantly increased in the *PgCYP703A4ox* lines (Figure 5C). The levels of the terminal-hydroxy fatty acid C22:0 was found to increase up to two times in *PgCYP703A4ox* in comparison with the wild type (Figure 5D). These data indicate that the *PgCYP703A4* overexpression in *A. thaliana* affects the fatty acid composition of cutin monomers in siliques.

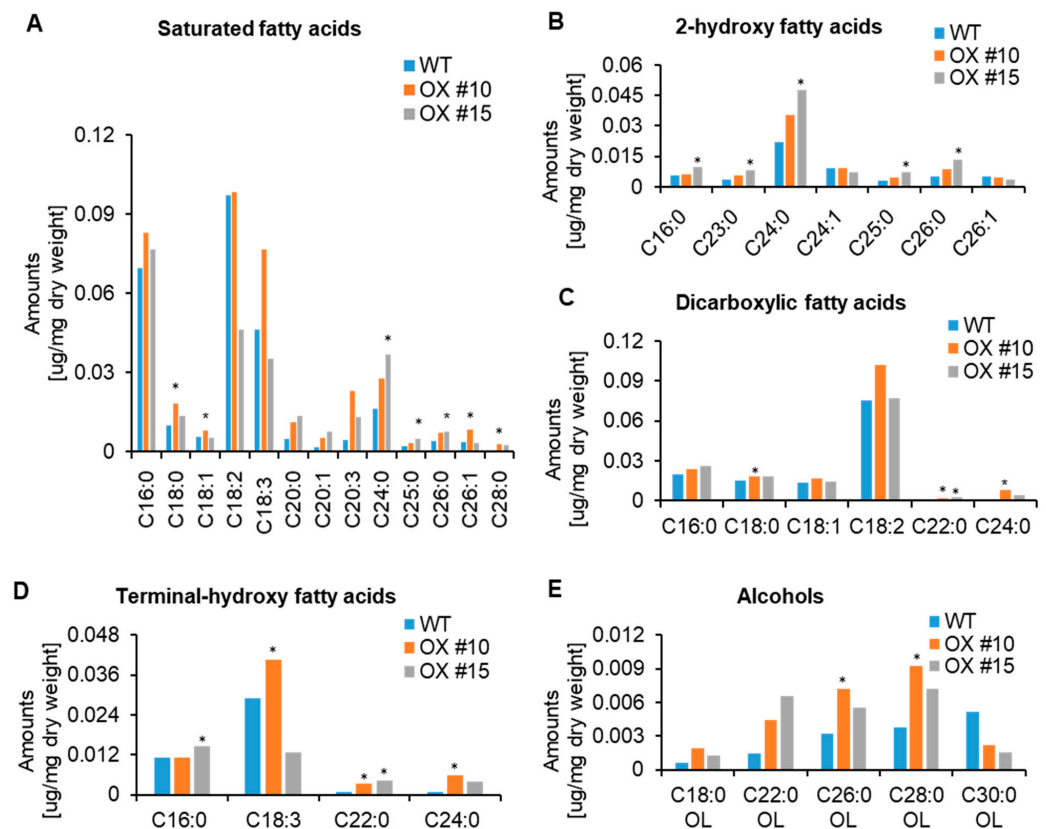


Figure 5. Chemical analysis of silique cutin monomers in wild type and *PgCYP703ox* lines via GC-MS and GC-FID. (A) Saturated fatty acids per milligram of dry weight ($\mu\text{g}/\text{mg}$). (B) 2-hydroxy fatty acids per milligram of dry weight ($\mu\text{g}/\text{mg}$). (C) Dicarboxylic fatty acids per milligram of dry weight ($\mu\text{g}/\text{mg}$). (D) Terminal-hydroxy fatty acids per milligram of dry weight ($\mu\text{g}/\text{mg}$). (E) Alcohols per milligram of dry weight ($\mu\text{g}/\text{mg}$). Values indicate mean of five biological replicates \pm SD. * $p < 0.05$.

4. Discussion

Plants have evolved a variety of enzymes for the in-chain α -, β -, and ω -hydroxylation of fatty acids. Hydroxylated fatty acids are the biosynthetic intermediates of plant biopolymers, such as cutin and suberin, which make up the barriers from land plant stress situations. Thus, fatty acid metabolic enzymes are critical for plants; however, the role of CYP members in controlling the development of *P. ginseng* has not been well studied. In this study, we characterized *PgCYP703A4* and its role in the fatty acid metabolism. The *PgCYP703A4* expression only detected at the flowering stage during microspore formation in the tapetum and gamete cells, which are active in sporopollenin synthesis. The overexpression of *PgCYP703A4* in *A. thaliana* increased silique size and seed production without affecting gamete cell, similar to *PgCYP704B1* [15].

CYPs constitute the largest family of enzymes in plant metabolism and represent plant evolution in terms of plant metabolism in development and adaptation, such as signaling, defense, and polymerization of complex chemical substances [37]. Among the 11 land plant clans, the CYP71 clan represents more than half of all CYPs in higher plants; consequently, a wide diversity of functions makes them more difficult to predict their preferred substrates than other clans [37]. In addition to CYP703, CYP77 family members, *AtCYP77A4* and *AtCYP77A6*, can in-chain-hydroxylate fatty acids to form precursors of cutin [9,38,39]. Looking at their phylogenetic relationship, CYP703 diversified prior to the emergence of CYP77s as spore protectors. CYP703 is an ancient gene family that is required for land plants, whereas CYP77 is required in only angiosperms [37]. However, both CYP703A and CYP77A function as in-chain hydroxylases, compared with most other enzymes that are end-chain (ω) hydroxylase [30].

In addition, a part of the CYP71 clan, the CYP78 subfamily genes exhibited fatty acid hydroxylation reactions, particularly for short chains [24]. Different from a single member of CYP703 (Figure 2), the CYP78 family contains several members in *A. thaliana* (Figure 2), indicating late gene duplication for the species. CYP78A family members regulate reproductive organ development but are more related to female organs. *A. thaliana* gene *CYP78A9* was reported to be involved in the control of carpel shape [40]. The overexpression of *CYP78A9* results in large, seedless fruit, although the metabolites have not been discovered [40]. *O. sativa* gene *OsCYP78A13* promotes seed growth by regulating the embryo and endosperm size, as well as spikelet hull development [41]. *PaCYP78A9* regulates fruit size in *Prunus avium*, showing increases in silique and seed size in *A. thaliana* by hetero-overexpression [42]. In addition to the above studies of the CYP71 clan other functions include glucosinolate production [43], p-coumaraldehyde hydroxylation [44], and pathogen defense function [45], as indicated in Figure 2. It is clear that the CYP71 clan has a large diversity of functions, but only CYP703 and CYP78 families of this clan, have the conserved PERF consensus, and both subfamilies are involved in plant reproductive development. Further studies are required to identify its positive relationship with biological function.

In *P. ginseng*, reproductive development and functional studies are scarce. We previously identified a functional ortholog of *AtCYP704B1*, termed *PgCYP704B1* [15]. The CYP704B family, which belongs to the CYP86 clan, is involved in the ω -hydroxylation of long-chain fatty acids. Altered exine in the pollen wall was detected in mutant of *A. thaliana cyp704B1* [46], *Brassica napus CYP704B1* [47], and *O. sativa CYP704B2* [36]. However, *O. sativa CYP704B2* also had an undeveloped anther cuticle and sterile male phenotype [36]. It is similar to CYP703A, although it is in a separate clan. Similarly, CYP701A and CYP88A, which belong to the CYP71 and CYP85 clans, respectively, act sequentially in the same pathway as ent-kaurene oxidase and kaurenolic acid oxidase, respectively [48]. With the early evolution of CYPs, CYP703 and CYP704 could be involved in cutin biopolymer synthesis, particularly for pollen wall polymers, for in-chain and ω -hydroxylation, respectively. This study was limited by the difficulty of obtaining flowers from transgenic *P. ginseng*. However, further studies on *P. ginseng* development is required to develop hybrid and male sterile system for breeding.

Taken together, PgCYP703A4, a member of CYP703A in the CYP71 clan, and Pg-CYP704B1 [22], in the CYP86 clan, are similarly expressed in the *P. ginseng* tapetum and meiotic cells, and overexpression in *A. thaliana* affects fatty acid metabolism in siliques. Previous studies on *A. thaliana* and *O. sativa* examined knockout mutants displaying partial or full male sterility [7,9,36,46] and therefore did not further investigate the phenotype regarding fruit development. This requires further investigation to determine the role of hydroxylated fatty acids in sporopollenin synthesis and the development of the silique cuticle.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/plants11030383/s1>, Figure S1: Multiple alignment of PgCYP703 with homologous proteins from other plant species. Figure S2: Superimposed hydrophobicity profile predictions for PgCYP703A4 and selected homologs from the 703A4 family. Figure S3: Cytological analysis of an *Arabidopsis* mutant and the PgCYP703A4 overexpression line.

Author Contributions: Y.-J.K. and D.Z. conceived and design the project and experiments. J.S. (Jeniffer Silva) and J.K. conducted the experiments and data arrangements. C.P., Y.K., N.P. and J.S. (Johan Sukweenadhi) contributed for bioinformatic analysis and plant growth. C.-O.H. and K.K.K. provide critical comments for metabolite analysis. J.Y. contributed for cytological analysis and J.S. (Jianxin Shi) performed the wax and cutin analysis. H.-J.S., H.C.P. and K.M.L. contributed for manuscript revision. Y.-J.K. and J.K. co-write the manuscript. All authors have read and agreed to the published version of the manuscript.

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