



## Suberin: Chemistry and Applications

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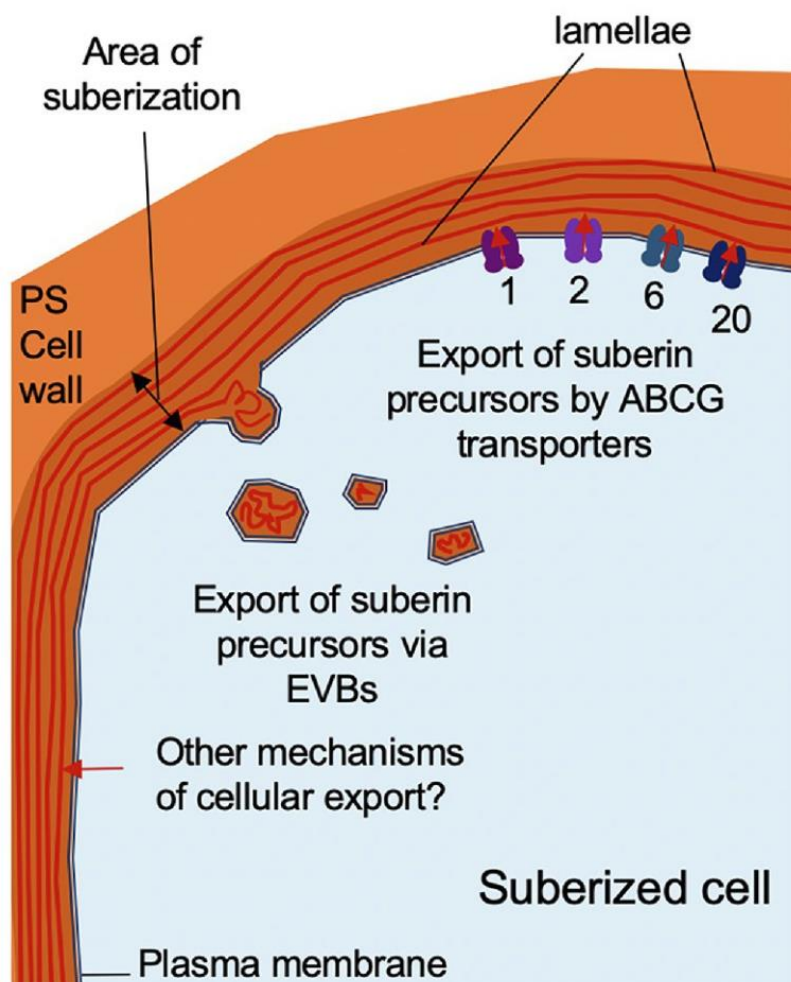
**Abstract:** Animals evolved to form protective barriers in the form of biopolymeric proteins (collagens) or modified sugars (chitin). Meanwhile, plants evolved to feature polymerized lipid-like precursors forming cutin and suberin. Suberin is a lipophilic polyester composed of glycerol, fatty acids, and aromatics that impart structural support in the cell walls (predominantly in exodermis and endodermis) of plants. It is biosynthesized and deposited as a hydrophobic layer along the periphery of the cellular plasma membrane and primary cell wall leading to the formation of an insulated and specialized (suberized) cell wall. Suberin is protective against stresses, both abiotic and biotic, and resistant to some extraneous factors that may damage or deform the plant cell. This review aims to discuss the general nature and structure of suberin, the monomeric precursors and enzymes involved in suberin biosynthesis, the chemical nature of suberin reactions, and some common applications of suberin outside its natural environment.

## 1. Introduction

Lignin is a structural biopolymer in the plant cell wall and contributes to the stiffness of vascular plants, making it possible to let them grow higher, as evident in trees. Lignified cell walls provide mechanical and chemical resistance to degradation, but the outer plant tissues responsible for protection against external factors are not simply made of lignocellulosic materials. It needs reinforcement in the form of suberin. Suberin is biosynthesized and deposited as a hydrophobic layer between the plasma membrane and primary cell wall of the plant, leading to the formation of a suberized cell wall, as shown in [Figure 1](#). The cork cells in the periderm, the exodermis in plant roots, and the Casparian strips on the endodermis are known plant parts where suberin is deposited. Thus, it is a polymer found in the cell walls of various plant tissues, including roots, stems, leaves, and fruits. This polymer is known for its exceptional ability to resist both physical and biological degradation, making it a critical component of the plant's protective barrier against the environment.

Suberin is an insoluble poly(acylglycerol) polyester, whose monomeric components can be released by treatments involving ester-breaking depolymerization in solution ([Serra & Geldner, 2022](#)). This polyester molecule contains the aliphatic domain containing the fatty acids and the oxidized

derivatives, glycerol and ferulic acid, linked by ester bonds. Meanwhile, the polyphenolic domain is made up of polyaromatics, comparable to the polyaromatic monolignols making up lignin. Suberin has been extensively studied over the years, and its chemistry has been the subject of numerous researches. Some of the physiological and ecological importance and relevance of suberization has been covered by great reviews and publications over the years (Barberon, 2017; Campilho *et al.*, 2020; Holbein *et al.*, 2021; Serra *et al.*, 2022).

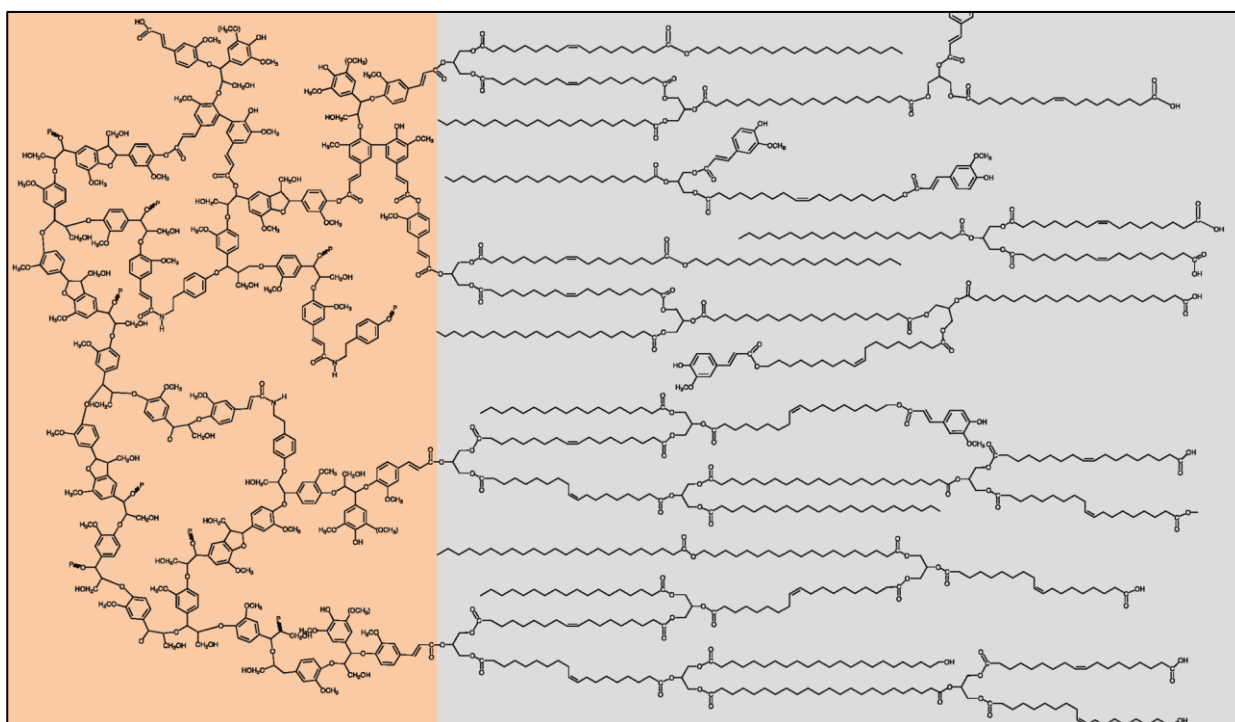


**Figure 1.** Schematic of the location of suberized layers formed between the primary cell wall and plasma membrane of plant cells (Philippe *et al.*, 2022).

## 2. Suberin structure

The structure of suberin can be divided into two primary components: the polyaromatic domain and the aliphatic domain. The polyaromatic domain of suberin is composed of phenolic compounds, such as ferulic acid, *p*-coumaric acid, and cinnamic acid, the same monolignols comprising lignin (Figure 2). These compounds are linked together through ester bonds to form a highly cross-linked network that provides the polymer with remarkable resistance to biodegradation. The phenolic compounds in suberin are typically arranged in a highly ordered, crystalline structure, which is thought to contribute to the polymer's strength and rigidity. On the other hand, the aliphatic domain of suberin is composed of a variety of long-chain fatty acids, hydroxy fatty acids, dicarboxylic acids (C<sub>14</sub>-C<sub>20</sub>), fatty alcohols (C<sub>18</sub>-C<sub>30</sub>), and waxes. The fatty acids in suberin are typically in the form of  $\omega$ -hydroxy acids, such as 16-hydroxy palmitic acid and 18-hydroxy oleic acid. The alcohols in suberin are typically long-chain

primary alcohols, such as 1-octanol and 1-hexanol. The waxes in suberin are typically long-chain esters, such as octadecyl octadecanoate and hexadecyl hexadecanoate. The aliphatic domain of suberin is responsible for the polymer's hydrophobic properties, which play a critical role in its ability to prevent water loss and protect the plant from environmental stresses (Harman-Ware *et al.*, 2021).

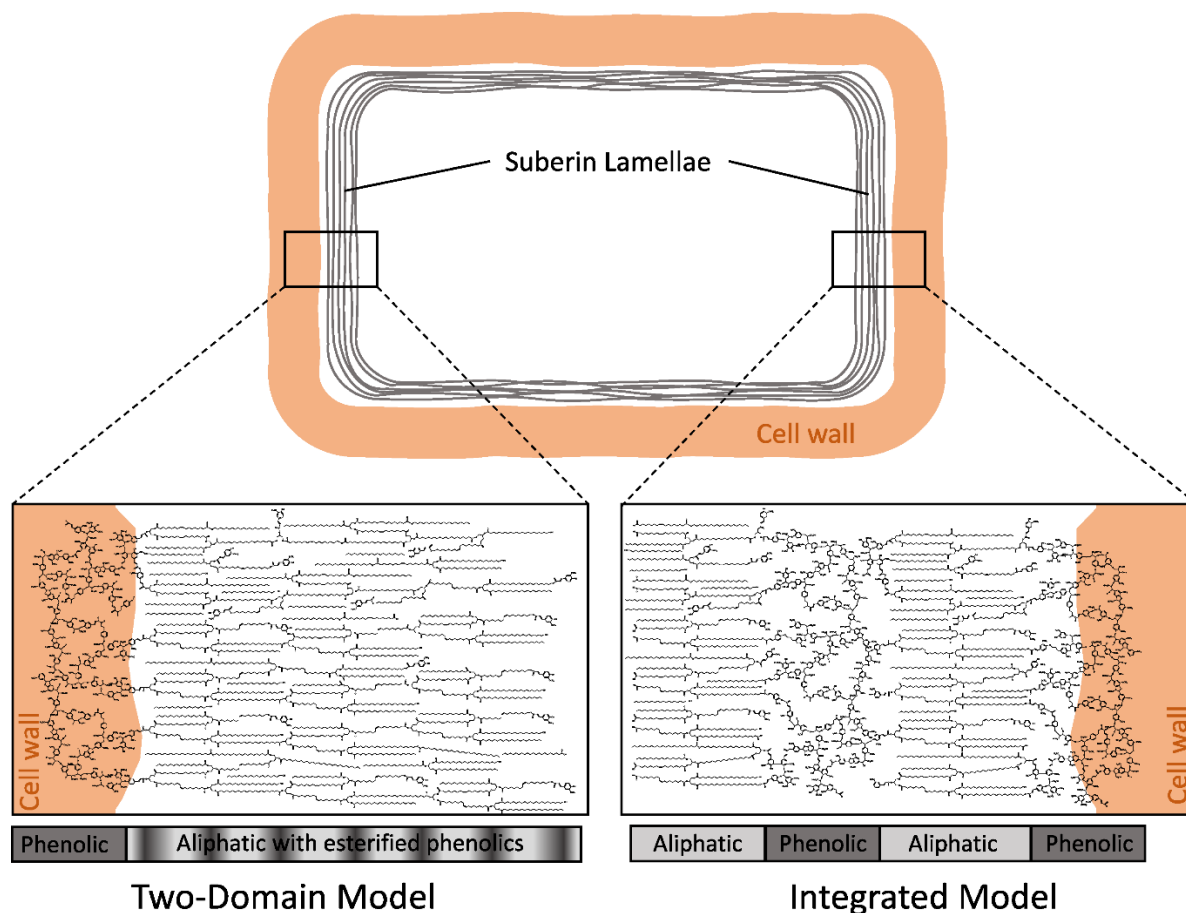


**Figure 2.** The monolignols in suberin (orange) are like lignin in terms of linkages, but the 9'-OH groups remained unlinked. Suberin forms esters with long-chain fatty acids and hydroxy fatty acids (gray). The carboxylic acid esters provide connections between the monolignol units in some portions of the structure (Woolfson *et al.*, 2022).

Suberin has been described differently by various researchers, with some going with a polyester-based polymer with an aliphatic domain associated with a polyphenolic (aromatic) domain (integrated model), and as a polymer composed of distinct poly(aliphatic) and poly(phenolic) domains (two domain model). These two views regarding suberin are based on the idea that suberized cells contain both poly(aliphatic) and poly(phenolic) polymers, but the process in which they are assembled and arranged is unknown. The integrated model of the structure of suberin was first proposed on the premise that the polymers are formed with alternating phenolic and aliphatic layers, as shown in Figure 3, and was inspired by the unique lamellar bands observed by TEM (Graça, 2015; P. E. Kolattukudy, 1980). Partial depolymerization of suberin yielded fragments that contain both aliphatic and phenolic compounds linked by ester bonds. In this integrated model, “suberin” refers to a largely poly(aliphatic) polymer with associated phenolics. However, the complete removal of the aliphatic components yields a poly(phenolic) rich residue that contains phenolic monomers (e.g., sinapic acid-derived phenolics) not found in the aliphatic portion of the polymer (Mattinen *et al.*, 2009).

Meanwhile, the two-domain model is supported by metabolic and gene expression data demonstrating a temporal difference in phenolic and aliphatic metabolism during induced suberization (Woolfson, 2018; Woolfson *et al.*, 2018; Yang & Bernards, 2007), the presence of both phenolic and aliphatic components in ectopically deposited suberin (Kosma *et al.*, 2014), and the failure of suberin deposition in endodermal tissue with compromised phenylpropanoid metabolism (Andersen *et al.*,

2021). Both models are not mutually exclusive. The difference between the models is mainly in the degree of integration of the aliphatic and phenolic domains into the suberin structure.



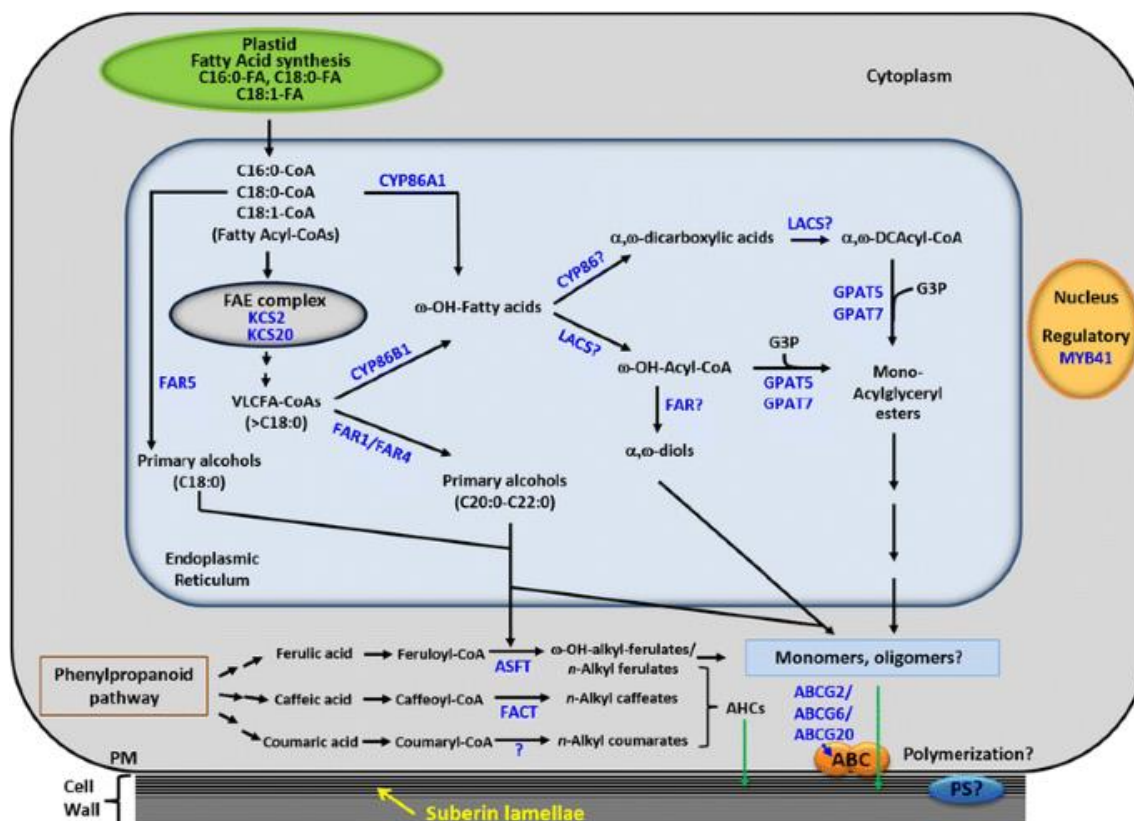
**Figure 3.** Comparison of two models of suberin structure, namely the two-domain and integrated models (Woolfson *et al.*, 2022).

### 3. Biosynthesis of suberin

The biosynthesis of suberin is a complex process that involves multiple enzymatic pathways, as shown in **Figure 4**. Model organisms such as *Arabidopsis thaliana* and potato (*Solanum tuberosum* L.) served as genomic resources for the elucidation of the functions of numerous suberin biosynthetic genes (Beisson *et al.*, 2012; Li-Beisson *et al.*, 2013). Genetic approaches and analysis of mutant genes led to the identification and characterization of the genes responsible for encoding enzymes involved in the biosynthesis of suberin. The initial steps of suberin biosynthesis involve the activation of fatty acids and the synthesis of  $\omega$ -hydroxy fatty acids. This process is catalyzed by a family of enzymes known as fatty acid hydroxylases, which introduce hydroxyl groups into the fatty acid chains (Woolfson *et al.*, 2022). The hydroxylation of fatty acids is critical for the subsequent polymerization and cross-linking reactions that occur during suberin biosynthesis. Once the  $\omega$ -hydroxy fatty acids are synthesized through encoding by the genes StCYP86A33 (Serra *et al.*, 2009), AtCYP86A1 (Höfer *et al.*, 2008), and AtCYP86B1 (Compagnon *et al.*, 2009), the aliphatic suberin feruloyl transferases that transfer from feruloyl-CoA to  $\omega$ -hydroxy acids and fatty alcohols, (encoded by StFHT and AtASFT genes) are incorporated into suberin through a series of enzymatic reactions (Molina *et al.*, 2009). The first step in this process involves the acylation of the hydroxy group with different chain-length primary fatty alcohols producing fatty acids with varying lengths, such as palmitic acid or stearic acid. This



reaction is catalyzed by enzymes collectively known as fatty acyl-CoA reductases, specifically encoded by the genes *AtFAR1*, *AtFAR4*, and *AtFAR5* (Domergue *et al.*, 2010). The resulting compound, a fatty acid ester, is then incorporated into the suberin polymer through ester linkages.



**Figure 4.** Enzymatic pathways of suberin biosynthesis (Vishwanath *et al.*, 2015)

The aromatic components of suberin are synthesized through a separate pathway that involves the activation of phenolic compounds and their subsequent incorporation into the polymer. The activation of phenolic compounds is catalyzed by a family of enzymes known as phenylpropanoid enzymes and hydroxycinnamoyl transferases (HCT), which convert the phenolic compounds into activated forms that can be incorporated into the suberin polymer. Once activated, the phenolic compounds are incorporated into the polymer through the same ester linkages to the aliphatic fatty acids (Gou *et al.*, 2009).

#### 4. Functions of suberin

The survival of terrestrial plants is dependent on the ability to control water loss, transport of solutes, insulation from environmental and climate extremes, and protection against pathogens (Harman-Ware *et al.*, 2021). One of the primary functions of suberin is to act as a waterproofing barrier in plants. The hydrophobic nature of suberin makes it an excellent barrier to water loss, preventing excessive transpiration and ensuring that the plant retains sufficient water for survival (Graça, 2015). Suberin is particularly important in plant roots, where it forms the Casparian strip, a barrier that prevents water and solutes from moving freely between the root and the soil. The Casparian strip is composed of lignin and suberin and is critical for regulating the uptake of water and nutrients by the plant (Shabala & Mackay, 2011). In addition to its waterproofing function, suberin also plays a critical role in providing a physical barrier against external stresses, such as pathogens and herbivores. The polyaromatic domain of suberin contains phenolic compounds, such as ferulic acid, that have been shown to have

antimicrobial and antifungal properties (de Morais *et al.*, 2021). The cross-linking of these phenolic compounds into a highly compact structure provides suberin with exceptional strength and rigidity, making it difficult for pathogens to penetrate the plant's protective barrier.

Suberin also acts as a chemical barrier against external stresses, such as toxins and pollutants. The aliphatic domain of suberin contains fatty acids and alcohols, which are highly hydrophobic and can effectively help in acquiring water and nutrients from the surrounding soil and at the same time sequester hydrophobic toxins. This sequestration function is particularly important in the roots of plants, where the uptake of pollutants from the soil can be a significant problem (Chen *et al.*, 2022). The ability of suberin to sequester these harmful compounds and pathogens is critical for the survival of plants in contaminated environments.

Suberin has also been shown to play a critical role in the interactions between plants and microorganisms. Plants can defend themselves against microbial attacks with physical and chemical barriers. Plant cells are equipped with thick walls, with specialized features on the external parts of the plants which are usually covered with cutin or suberin. The leaves of terrestrial plants have superficial waxes. Also, there is the bark, which acts as a physical barrier. The size, shape, and location of stomata can also affect pathogen entry into the plant cell wall. Plants contain a range of low-molecular-weight antimicrobial compounds (phytoanticipins) that are inhibitory against the growth and development of microorganisms, including phenols and quinones, long-chain aliphatic and olefinic compounds, aldehydes, cyanogenic glucosides, saponins, terpenoids, stilbenes, glucosinolates, cyclic hydroxamic acids and related benzoxazolinone compounds, tannins, lysozyme, proteinase inhibitors, polygalacturonase-inhibiting proteins (PGIPs), defensins, anti-microbial proteins, peptides, and low-molecular-weight compounds (Panti *et al.*, 2014; Ragasa *et al.*, 2013; Tongco *et al.*, 2014; Tongco *et al.*, 2016). The low availability of nutrients to the pathogen also contributes to defense. Further, most plants are in some state of basal defense most of the time, as the innate immunity of plants, though rapid and transient, is constantly being activated since plants are continuously encountering bacteria, fungi, and damage in the rhizosphere and phyllosphere (Boddy, 2016). Suberin also features unique biochemical features and its presence in some biomass feedstock such as sugarcane forage, leads to recalcitrance and ultimately affects biomass digestibility (Figueiredo *et al.*, 2016).

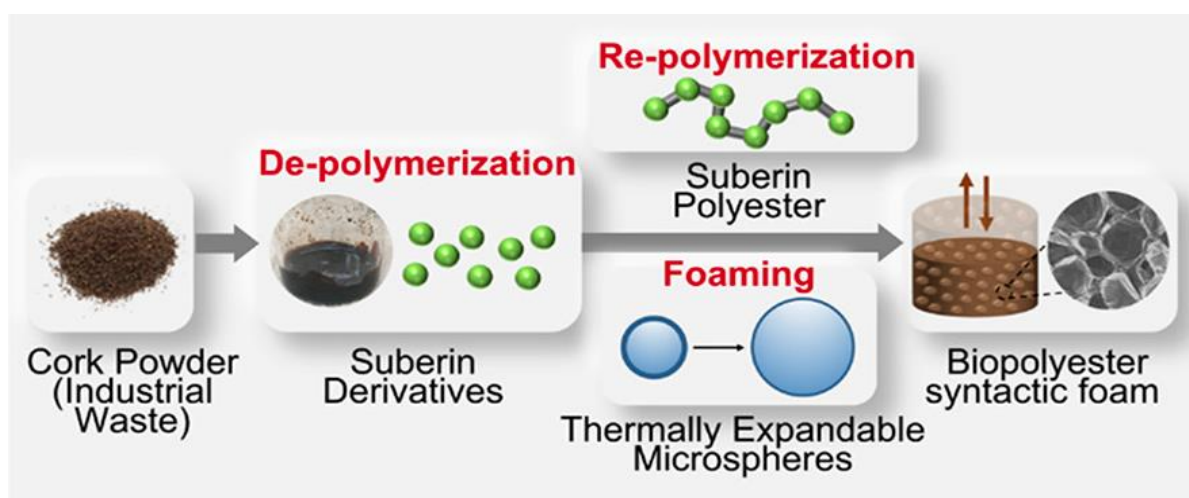
## 5. Reactions of suberin

### 5.1. Hydrolysis

The polyaromatic domain of suberin is particularly susceptible to hydrolysis (reaction of water with the polymer to break it down into its constituent components), as the ester bonds linking the phenolic compounds can be easily cleaved by water. Hydrolysis of suberin can release nutrients, such as phenolic compounds and fatty acids, which can be utilized by microorganisms or taken up by the plant. The release of these nutrients can also lead to changes in the soil microenvironment, as the breakdown products can alter the pH and nutrient availability of the soil. Hydrolysis of suberin releases phenolic compounds and fatty acids. This breakdown of suberin can alter the permeability of the cell wall, potentially affecting the uptake of nutrients and water by the plant.

The hydrolysis of suberin can be affected by a range of factors, including pH, temperature, and the presence of enzymes (Beaulieu *et al.*, 2016). Hydrolysis is typically more rapid at higher temperatures and in more acidic or basic environments (Mission & Cocero, 2022). Enzymes, such as esterases, can also accelerate the hydrolysis of suberin, leading to faster breakdown of the polymer. The hydrolysis of suberin can also be affected by the chemical composition of the polymer. The presence of more ester bonds, particularly in the polyaromatic domain, can make suberin more susceptible to hydrolysis.

Suberin that contains more hydroxyl groups, such as acetylated suberin, may be less susceptible to hydrolysis due to the increased stability of the ester bonds. Suberin can also be hydrolyzed by using supercritical extraction or ionic liquid-based methods (Correia *et al.*, 2020; Mission & Cocero, 2022). The breakdown products of suberin, such as phenolic compounds and fatty acids, can be utilized as an inhibitor of certain microorganisms. In addition, the release of these hydrolysis products can alter the soil microenvironment, potentially improving soil fertility through soil organic carbon release and reducing the need for synthetic fertilizers (Harman-Ware *et al.*, 2021). Suberin hydrolysis can also be utilized in the production of biodegradable materials. Suberin can be isolated from plant tissues and hydrolyzed to release its constituent components (monomers). These monomers can then be used as building blocks to produce biodegradable plastics and films (Bento *et al.*, 2021; Garcia *et al.*, 2014). **Figure 5** shows a schematic for the formation of biopolyester foam sourced from the hydrolysis products of suberin.



**Figure 5.** Schematic showing the depolymerization of suberin through alkaline hydrolysis and subsequent re-polymerization to form biopolyester foam (Cho *et al.*, 2022).

## 5.2. Oxidation

Suberin is naturally resistant to oxidative and acid treatments, but given unfavorable conditions, the reaction can push through. Oxidation is a process in which a molecule loses electrons and becomes more positive in charge. In the context of suberin, oxidation typically refers to the reaction of suberin with oxygen, resulting in the formation of reactive oxygen species (ROS). ROS can include free radicals such as superoxide, hydroxyl radical, and singlet oxygen, as well as non-radical species such as hydrogen peroxide. Suberin contains phenolic compounds that are susceptible to oxidation reactions, which can lead to the formation of quinones and other reactive compounds (Boddy, 2016; Denaxa *et al.*, 2022). These reactive compounds can participate in redox reactions with other molecules, such as amino acids and proteins, leading to the formation of covalent bonds and potentially causing damage to the plant cell. However, studies have suggested that the formation of quinones and other reactive compounds may also play a role in plant defense against pathogens (Fones & Preston, 2012). The polyaromatic domain of suberin is particularly susceptible to oxidation, as the phenolic compounds it contains are highly reactive toward ROS. The oxidation of suberin can be initiated by a range of factors, including exposure to light, temperature, soil conditions, and salinity (Jan *et al.*, 2021). Once oxidation is initiated, it can propagate rapidly through the polymer, leading to extensive damage. Another specific example is the oxidation of suberin with alkaline nitrobenzene liberating *p*-hydroxybenzaldehyde,

vanillin, and minor amounts of syringaldehyde as determined by gas chromatography/mass spectrometry (Cottle & Kolattukudy, 1982).

The oxidation of suberin can have a range of effects on the plant itself and the surrounding environment. ROS generated during the oxidation process can lead to oxidative stress in the plant, potentially damaging cellular components such as lipids, proteins, and nucleic acids. This oxidative stress can also lead to programmed cell death, which is an important defense mechanism in plants. The oxidation of suberin can also have effects on the soil microenvironment. The origin of carbon stabilized in soil as mineralized carbon or soil organic matter has been linked to cutin or suberin found in plant roots (Rasse *et al.*, 2005). ROS generated during oxidation can alter the pH and nutrient availability of the soil, potentially affecting plant growth and microbial populations. The breakdown products of oxidized suberin can also serve as an inhibitor for microorganisms, potentially altering the composition of the soil microbiome (Berrios & Rentsch, 2022). The oxidation of suberin can be affected by different factors, including the presence of antioxidants, the chemical composition of the polymer, and environmental conditions. Antioxidants, such as alkyl hydroxycinnamates, and ferulic and coumaric acids can scavenge ROS and protect suberin from oxidation (Domergue & Kosma, 2017). The presence of more phenolic compounds, particularly those with electron-donating groups, can make suberin more susceptible to oxidation. In contrast, suberin that contains more hydroxyl groups, such as acetylated suberin, may be less susceptible to oxidation due to the increased stability of the phenolic compounds. Environmental conditions can also affect the oxidation of suberin. Light exposure can increase the production of ROS, while microbial activity can generate ROS as a byproduct of metabolism and inflammatory signaling (Forrester *et al.*, 2018). High temperatures and drought stress can also increase the susceptibility of suberin to oxidation. The breakdown products of oxidized suberin, such as phenolic compounds and fatty acids, have antioxidant and antimicrobial properties and can be utilized in the development of natural preservatives and disinfectants.

### 5.3. Cross-Linking Reactions

Cross-linking is a chemical reaction in which two or more polymer chains are linked together by covalent bonds. In the context of suberin, cross-linking refers to the formation of covalent bonds between different suberin molecules or between suberin and other polymers or compounds. Cross-linking can occur through a range of chemical reactions, including oxidation, condensation, and addition reactions. Suberin contains both phenolic compounds and long-chain fatty acids and alcohols, which can participate in cross-linking reactions (Kolattukudy, 1981). Cross-linking involves the formation of covalent bonds between different components of suberin, leading to the formation of a polyester network consisting of both aliphatic and aromatic domains. The cross-linking of phenolic compounds in the polyaromatic domain can increase the strength and rigidity of suberin, making it more resistant to physical and biological degradation. The cross-linking of long-chain fatty acids and alcohols in the aliphatic domain can also increase the hydrophobicity of suberin, making it more effective as a waterproofing barrier. The most common chemical agents used for cross-linking of suberin are glycerol, epoxides, and isocyanates (Graça & Pereira, 1997). Cross-linking can be carried out in the presence or absence of a catalyst, depending on the reaction conditions. A specific example is the cross-linking reactions between epoxidized linseed oil and suberin (Menager *et al.*, 2021).

The formation of covalent bonds between suberin molecules can increase the mechanical strength and durability of the polymer and improve its resistance to degradation (Fernandes *et al.*, 2014). Cross-linking can also alter the porosity and permeability of suberin, affecting its barrier properties and ability to transport molecules (De Simone *et al.*, 2003). Cross-linking of suberin can be used to modify the



physical and chemical properties of the polymer for various applications. For example, cross-linked suberin can be used as a coating material for packaging to improve the barrier properties and shelf-life of food and pharmaceutical products (Heinämäki *et al.*, 2015; Kunam *et al.*, 2022). Cross-linked suberin can also be used as a material for drug delivery systems due to its biocompatibility and ability to encapsulate hydrophobic drugs (Baranwal *et al.*, 2022).

## 6. Suberin applications

Suberin's unique set of properties, such as hydrophobicity, barrier functionality, mechanical resilience, etc., make it an ideal material or precursor for various industrial applications. One such application is in the development of biocomposites and biopolymers. Suberin's barrier properties and mechanical performance as a biopolymer provide the industry with an alternative for petroleum-based materials in the production of bio-based and biodegradable plastics and composites. Studies show that the incorporation of suberin-derived monomers—such as suberin fatty acids (SFAs)—into polymer matrices can yield materials with improved interfacial adhesion, thermal stability, and hydrophobicity (Fernandes *et al.*, 2014). In addition, suberin's  $\omega$ -hydroxy fatty acids and  $\alpha,\omega$ -diacids have been observed, in biocomposites, to contribute to both material integrity and performance under various environmental conditions. The use of these suberin-based monomers as bio-based polyesters not only shows promise in replacing petrochemical components but also provides the additional benefit of biodegradability, especially when combined with renewable materials like cellulose nanocrystals (Ankita & Rashmi, 2022.; Bruvere *et al.*, 2024).

Animals produce biopolymeric proteins like collagen and modified sugars such as chitin for their growth and development. There is no known evidence of interactions between suberin and these biopolymers. Still, the similarities in their roles as structural or protective polymers suggest a potential for the fabrication of hybrid biomaterials with suberin. The lamellar structures and self-assembly properties of suberin could complement the bioactivity of collagen and chitin, such as the primary component of bone extracellular matrix (ECM), forming composite scaffolds with enhanced mechanical properties and osteogenic potential, mimicking the ECM of teeth and used as scaffolds for periodontal regeneration (Aguilar *et al.*, 2019; Chacon *et al.*, 2022), antibacterial agents, and implant coatings to minimize or prevent infection, and biodegradable barriers for tissue engineering (Kligman *et al.*, 2022; Serra & Geldner, 2022).

Another area of application of suberin is in the production of lightweight materials such as syntactic foams used in insulation and protective packaging. One of the key advantages of suberin is its low permeability to liquids and gases as a result of its closed cellular structure. This characteristic makes it lightweight and contributes to its thermal insulation properties (Prasetia *et al.*, 2023). Recent studies have shown that syntactic foams derived from suberin show potential for good mechanical performance. For instance, a study by Cho *et al.* demonstrated that these foams can be engineered to improve mechanical performance by adjusting cell size and porosity thereby making them suitable for structural components and protective packaging (Cho *et al.*, 2022). The functionality of these suberin-derived foams can be further improved by leveraging the flame-retardant properties of suberin to make them applicable in various industries, including construction and transportation, where fire safety is required (Trovagunta & Hubbe, 2023).

Another industrial application of suberin is in the manufacture of protective covering and barrier films which are useful in food and pharmaceutical packaging. The hydrophobic nature of suberin allows it to form a barrier that protects sensitive products from environmental factors that could lead to spoilage or degradation. In addition to its moisture barrier capabilities, suberin is a useful substance

for use in packaging because of its aromatic moieties, which help to prevent the growth of bacteria and fungi, thereby directly improving product shelf life and maintaining the freshness and efficacy of products (Qasim *et al.*, 2024). This is particularly impactful for the pharmaceutical industry where the integrity of active ingredients is important, and contamination could compromise the therapeutic effects of products (Yang *et al.*, 2019).

Suberin has also shown promise in the agricultural sector through its applications in biodegradable mulch films and soil remediation. Suberin-based biodegradable mulch films can serve as an alternative to conventional plastic mulch films for improved soil moisture retention. A recent study showed that biodegradable mulch films can increase water use efficiency (WUE) by 64.5% to 73.1% compared to control soil samples (Deng *et al.*, 2019). In addition to soil moisture retention, biodegradable suberin-based mulch films can be used as a measure for weed control. Studies have indicated that the weed-control effect of biodegradable mulch films is comparable to that of traditional herbicide-containing films, which makes them a viable option for integrated weed management strategies. Researchers observed that biodegradable mulch showed superior performance than traditional plastic mulch in terms of water retention, soil health, nutrient availability and even microbial activity (Soylu & Kızıldeniz, 2024; Wang *et al.*, 2021).

## Conclusion

Suberin is an important biopolymer with characteristic biosynthesis and reactions that help protect plants from external biotic and abiotic stresses. The biosynthesis of suberin is composed of numerous pathways leading to the formation of two domains: the poly(aliphatic) domain which imparts hydrophobicity and the poly(aromatic) domain making linkages with the primary cell wall possible. Suberin is commonly found in plant roots, endodermis, exodermis, wound tissues, and abscission zones, locations where it is needed most in terms of protection and insulation.

Suberin is a complex, heteropolymeric polymer that is susceptible to a range of different reactions. Hydrolysis, oxidation, and cross-linking are all reactions that can occur with suberin. These reactions can alter the properties of suberin, making it more resistant to physical, chemical, and biological degradation. Its ability to act as a waterproofing, physical, and chemical barrier against external stresses, as well as its role in the plant-microbe symbiosis and signal transduction, make it a critical component of the plant's protective barrier.

The hydrolysis of suberin can release degradation products, alter the soil chemistry and microbiome, and affect the porosity and permeability of the plant cell wall. The hydrolysis of suberin is affected by a range of factors, including pH, temperature, and the chemical composition of the polymer. Suberin oxidation is an important aspect of plant-microbe interactions. Cross-linking reactions of suberin can improve the resistance of suberin to biotic and abiotic stresses and enhance its barrier function by modifying the physical and chemical properties of the polymer. Cross-linking can increase the mechanical strength and durability of suberin and improve its resistance to degradation. Suberin has been extensively studied over the years, and its various functions have been the subject of numerous investigations. Further research on suberin is needed to fully understand its functions.

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## References

- Aguilar, A., Zein, N., Harmouch, E., Hafdi, B., Bornert, F., Offner, D., Clauss, F., Fioretti, F., Huck, O., Benkirane-Jessel, N., & Hua, G. (2019). Application of Chitosan in Bone and Dental Engineering. *Molecules*, *24*(16), 3009.
- Andersen, T. G., Molina, D., Kilian, J., Franke, R. B., Ragni, L., & Geldner, N. (2021). Tissue-Autonomous Phenylpropanoid Production Is Essential for Establishment of Root Barriers. *Current Biology*, *31*(5), 965-977.e5.
- Ankita, N., & Rashmi, K. (March 2022) Res. In *Research Journal of Biotechnology* (Vol. 17, Issue 3).
- Baranwal, J., Barse, B., Fais, A., Delogu, G. L., & Kumar, A. (2022). Biopolymer: A Sustainable Material for Food and Medical Applications. *Polymers*, *14*(5).
- Barberon M. (2017). The endodermis as a checkpoint for nutrients. *New Phytologist*, *213*(4), 1604-1610
- Beaulieu, C., Sidibé, A., Jabloun, R., Simao-Beaunoir, A. M., Lerat, S., Monga, E., & Bernards, M. A. (2016). Physical, Chemical and Proteomic Evidence of Potato Suberin Degradation by the Plant Pathogenic Bacterium *Streptomyces scabiei*. *Microbes and Environments*, *31*(4), 427.
- Beisson, F., Li-Beisson, Y., & Pollard, M. (2012). Solving the puzzles of cutin and suberin polymer biosynthesis. *Current Opinion in Plant Biology*, *15*(3), 329–337.
- Bento, A., Moreira, C. J. S., Correia, V. G., Escórcio, R., Rodrigues, R., Tomé, A. S., Geneix, N., Petit, J., Bakan, B., Rothan, C., Mykhaylyk, O. O., & Silva Pereira, C. (2021). Quantification of Structure-Property Relationships for Plant Polyesters Reveals Suberin and Cutin Idiosyncrasies. *ACS Sustainable Chemistry and Engineering*, *9*(47), 15780–15792.
- Berrios, L., & Rentsch, J. D. (2022). Linking Reactive Oxygen Species (ROS) to Abiotic and Biotic Feedbacks in Plant Microbiomes: The Dose Makes the Poison. *International Journal of Molecular Sciences*, *23*(8).
- Boddy, L. (2016). Pathogens of Autotrophs. *The Fungi: Third Edition*, 245–292.
- Bruvere, B. B., Gromova, A., Jurinovs, M., Platnieks, O., Rizikovs, J., Paze, A., Godiņa, D., Mieriņa, I., Heinmaa, I., Smits, K., Rjabovs, V., & Gaidukovs, S. (2024). Valorizing Biopolyester Suberin: Modification of Cellulose Nanocrystals and Performance Assessment in 3D-Printed Biobased Acrylates. *ACS Omega*.
- Campilho, A., Nieminen, K., & Ragni, L. (2020). The development of the periderm: the final frontier between a plant and its environment. *Current Opinion in Plant Biology*, *53*, 10–14.
- Chacon, E. L., Bertolo, M. R. V., de Guzzi Plepis, A. M., da Conceição Amaro Martins, V., dos Santos, G. R., Pinto, C. A. L., Pelegrine, A.A., Teixeira, M.L., Buchaim, D.V., Nazari, F.M., Buchaim, R. L., Sugano, G.T., da Cunha, M.R. (2023). Collagen-chitosan-hydroxyapatite composite scaffolds for bone repair in ovariectomized rats. *Scientific Reports*, *13*(1), 1–12.
- Cho, S. H., Yoon, B., Lee, S. K., Nam, J. Do, & Suhr, J. (2022). Natural Cork Suberin-Originated Ecofriendly Biopolyester Syntactic Foam. *ACS Sustainable Chemistry and Engineering*, *10*(23), 7508–7514.
- Compagnon, V., Diehl, P., Benveniste, I., Meyer, D., Schaller, H., Schreiber, L., Franke, R., & Pinot, F. (2009). CYP86B1 Is Required for Very Long Chain  $\omega$ -Hydroxyacid and  $\alpha,\omega$ -Dicarboxylic Acid Synthesis in Root and Seed Suberin Polyester. *Plant Physiology*, *150*(4), 1831–1843.

- Correia, V. G., Bento, A., Pais, J., Rodrigues, R., Haliński, P., Frydrych, M., Greenhalgh, A., Stepnowski, P., Vollrath, F., King, A. W. T., & Pereira, C. S. (2020). The molecular structure and multifunctionality of the cryptic plant polymer suberin. *Materials Today Bio*, 5.
- Cottle, W., & Kolattukudy, P. E. (1982). Biosynthesis, Deposition, and Partial Characterization of Potato Suberin Phenolics. *Plant Physiology*, 69(2), 393–399.
- de Morais, M. C., Perez-Castillo, Y., Silva, V. R., de Souza Santos, L., Soares, M. B. P., Bezerra, D. P., de Castro, R. D., & de Sousa, D. P. (2021). Cytotoxic and Antifungal Amides Derived from Ferulic Acid: Molecular Docking and Mechanism of Action. *BioMed Research International*, 2021.
- De Simone, O., Haase, K., Müller, E., Junk, W. J., Hartmann, K., Schreiber, L., & Schmidt, W. (2003). Apoplasmic Barriers and Oxygen Transport Properties of Hypodermal Cell Walls in Roots from Four Amazonian Tree Species. *Plant Physiology*, 132(1), 206.
- Denaxa, N. K., Tsafouros, A., & Roussos, P. A. (2022). Role of phenolic compounds in adventitious root formation. *Environmental, Physiological and Chemical Controls of Adventitious Rooting in Cuttings*, 251–288.
- Deng, L., Yu, R., & Wang, Q. (2019). The effects of biodegradable mulch film on the growth, yield, and water use efficiency of cotton and maize in an arid region. *BioRxiv*, 703264.
- Domergue, F., & Kosma, D. K. (2017). Occurrence and Biosynthesis of Alkyl Hydroxycinnamates in Plant Lipid Barriers. *Plants*, 6(3), 468–476.
- Domergue, F., Vishwanath, S. J., Joubès, J., Ono, J., Lee, J. A., Bourdon, M., Alhattab, R., Lowe, C., Pascal, S., Lessire, R., & Rowland, O. (2010). Three Arabidopsis Fatty Acyl-Coenzyme A Reductases, FAR1, FAR4, and FAR5, Generate Primary Fatty Alcohols Associated with Suberin Deposition. *Plant Physiology*, 153(4), 1539–1554.
- Fernandes, E. M., Aroso, I. M., Mano, J. F., Covas, J. A., & Reis, R. L. (2014). Functionalized cork-polymer composites (CPC) by reactive extrusion using suberin and lignin from cork as coupling agents. *Composites Part B: Engineering*, 67, 371–380.
- Figueiredo, R., Cesarino, I., & Mazzafera, P. (2016). Suberin as an Extra Barrier to Grass Digestibility: a Closer Look to Sugarcane Forage. *Tropical Plant Biology*, 9(2), 96–108.
- Fones, H., & Preston, G. M. (2012). Reactive oxygen and oxidative stress tolerance in plant pathogenic *Pseudomonas*. *FEMS Microbiology Letters*, 327(1), 1–8.
- Forrester, S. J., Kikuchi, D. S., Hernandez, M. S., Xu, Q., & Griendling, K. K. (2018). Reactive Oxygen Species in Metabolic and Inflammatory Signaling. *Circulation Research*, 122(6), 877.
- Garcia, H., Ferreira, R., Martins, C., Sousa, A. F., Freire, C. S. R., Silvestre, A. J. D., Kunz, W., Rebelo, L. P. N., & Silva Pereira, C. (2014a). Ex situ reconstitution of the plant biopolyester suberin as a film. *Biomacromolecules*, 15(5), 1806–1813.
- Garcia, H., Ferreira, R., Martins, C., Sousa, A. F., Freire, C. S. R., Silvestre, A. J. D., Kunz, W., Rebelo, L. P. N., & Silva Pereira, C. (2014b). Ex situ reconstitution of the plant biopolyester suberin as a film. *Biomacromolecules*, 15(5), 1806–1813.
- Gou, J. Y., Yu, X. H., & Liu, C. J. (2009). A hydroxycinnamoyltransferase responsible for synthesizing suberin aromatics in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America*, 106(44), 18855–18860.
- Graça J. (2015). Suberin: The biopolyester at the frontier of plants. *Frontiers in Chemistry*, 3(OCT), 62
- Graça, J., Pereira, H. (1997). Cork suberin: A glyceryl based polyester. *Holzforschung*, 51(3), 225–234
- Harman-Ware, A. E., Sparks, S., Addison, B., & Kalluri, U. C. (2021). Importance of suberin biopolymer in plant function, contributions to soil organic carbon and in the production of bio-derived energy and materials. *Biotechnology for Biofuels* 2021 14:1, 14(1), 1–21.
- Heinämäki, J., Halenius, A., Paavo, M., Alakurtti, S., Pitkänen, P., Pirttimaa, M., Paaver, U., Kirsimäe, K., Kogermann, K., & Yliruusi, J. (2015). Suberin fatty acids isolated from outer birch bark



- improve moisture barrier properties of cellulose ether films intended for tablet coatings. *International Journal of Pharmaceutics*, 489(1–2), 91–99.
- Höfer, R., Briesen, I., Beck, M., Pinot, F., Schreiber, L., & Franke, R. (2008). The Arabidopsis cytochrome P450 CYP86A1 encodes a fatty acid  $\omega$ -hydroxylase involved in suberin monomer biosynthesis. *Journal of Experimental Botany*, 59(9), 2347–2360.
- Holbein, J., Shen, D., & Andersen, T. G. (2021). The endodermal passage cell – just another brick in the wall? *New Phytologist*, 230(4), 1321–1328.
- Jan R., Asaf S., Numan M., Lubna Kim K.M. (2021). Plant secondary metabolite biosynthesis and transcriptional regulation in response to biotic and abiotic stress conditions. *Agronomy*, 11(5), 968
- Kligman, A., Dastmalchi, K., Smith, S., John, G., & Stark, R. E. (2022). Building Blocks of the Protective Suberin Plant Polymer Self-Assemble into Lamellar Structures with Antibacterial Potential. *ACS Omega*, 7(5), 3978–3989.
- Kolattukudy, P. E. (1980). Biopolyester Membranes of Plants: Cutin and Suberin. *Science*, 208(4447), 990–1000.
- Kolattukudy, P. T. (1981). Structure, biosynthesis, and biodegradation of cutin and suberin. *Annual Review of Plant Physiology*, 32(1), 539–567.
- Kosma, D. K., Murmu, J., Razeq, F. M., Santos, P., Bourgault, R., Molina, I., & Rowland, O. (2014). AtMYB41 activates ectopic suberin synthesis and assembly in multiple plant species and cell types. *The Plant Journal*, 80(2), 216–229.
- Kunam, P. K., Ramakanth, D., Akhila, K., & Gaikwad, K. K. (2022). Bio-based materials for barrier coatings on paper packaging. *Biomass Conversion and Biorefinery*, 1, 1.
- Li-Beisson, Y., Shorrosh, B., Beisson, F., Andersson, M. X., Arondel, V., Bates, P. D., Baud, S., Bird, D., DeBono, A., Durrett, T. P., Franke, R. B., Graham, I. A., Katayama, K., Kelly, A. A., Larson, T., Markham, J. E., Miquel, M., Molina, I., Nishida, I., ... Ohlrogge, J. (2013). Acyl-Lipid Metabolism. *The Arabidopsis Book / American Society of Plant Biologists*, 11, e0161.
- Mattinen, M. L., Filpponen, I., Järvinen, R., Li, B., Kallio, H., Lektinen, P., & Argyropoulos, D. (2009). Structure of the polyphenolic component of suberin isolated from potato (*Solanum tuberosum* var. Nikola). *Journal of Agricultural and Food Chemistry*, 57(20), 9747–9753.
- Menager, C., Guigo, N., Vincent, L., & Sbirrazzuoli, N. (2021). Suberin from Cork as a Tough Cross-Linker in Bioepoxy Resins. *ACS Applied Polymer Materials*, 3(12), 6090–6101.
- Mission, E. G., & Cocero, M. J. (2022). Accessing suberin from cork via ultrafast supercritical hydrolysis. *Green Chemistry*, 24(21), 8393–8405.
- Molina, I., Li-Beisson, Y., Beisson, F., Ohlrogge, J. B., & Pollard, M. (2009). Identification of an Arabidopsis Feruloyl-Coenzyme A Transferase Required for Suberin Synthesis. *Plant Physiology*, 151(3), 1317–1328.
- Panti, A. B., Aguda, R. M., Razal, R. A., Belina-aldemita, M. D., & Tongco, J. V. (2014). Proximate analysis, phytochemical screening and total phenolic and flavonoid content of the ethanolic extract of molave *Vitex parviflora* Juss. Leaves. *Journal of Chemical and Pharmaceutical Research*, 6(3), 1538–1542.
- Philippe, G., De Bellis, D., Rose, J. K. C., & Nawrath, C. (2022). Trafficking Processes and Secretion Pathways Underlying the Formation of Plant Cuticles. *Frontiers in Plant Science*, 12, 786874.
- Prasetia, D., Purusatama, B. D., Kim, J. H., Jang, J. H., Park, S. Y., & Kim, N. H. (2023). Qualitative Anatomical Characteristics of the Virgin Cork in *Quercus variabilis* Grown in Korea. *BioResources*, 18(1), 884–898.
- Qasim, U., Sirviö, J. A., Suopajarvi, T., Hu, L., et al. (2024). A multifunctional biogenic films and coatings from synergistic aqueous dispersion of wood-derived suberin and cellulose nanofibers. *Carbohydrate Polymers*, 338, 122218.

- Ragasa, C.Y., Torres, O. B., Tongco, J. V., Razal, R. A., Shen, C.C. (2013). Resorcinols from *Myristica philippensis* Lam. *Journal of Chemical and Pharmaceutical Research*, 5(11), 614–616.
- Rasse, D. P., Rumpel, C., & Dignac, M. F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269(1–2), 341–356.
- Serra, O., & Geldner, N. (2022). The making of suberin. *New Phytologist*, 235(3), 848–866.
- Serra, O., Mähönen, A. P., Hetherington, A. J., & Ragni, L. (2022). The Making of Plant Armor: The Periderm. <https://doi.org/10.1146/annurev-arplant-102720-031405>, 73, 405–432.
- Serra, O., Soler, M., Hohn, C., Sauveplane, V., Pinot, F., Franke, R., Schreiber, L., Prat, S., Molinas, M., & Figueras, M. (2009). CYP86A33-Targeted Gene Silencing in Potato Tuber Alters Suberin Composition, Distorts Suberin Lamellae, and Impairs the Periderm's Water Barrier Function. *Plant Physiology*, 149(2), 1050–1060.
- Shabala, S., & Mackay, A. (2011). Ion Transport in Halophytes. *Advances in Botanical Research*, 57, 151–199.
- Soylu, E., & Kızıldeniz, T. (2024). Innovative approach of biodegradable mulches in sustainable agriculture for crop production and environmental conservation. *BIO Web of Conferences*, 85, 01060.
- Tongco, J. V., Villaber, R. A. P., Aguda, R. M., & Razal, R. A. (2014). Nutritional and phytochemical screening, and total phenolic and flavonoid content of *Diplazium esculentum* (Retz.) Sw. from Philippines. *Journal of Chemical and Pharmaceutical Research*, 6(8), 238–242.
- Tongco, J. V., Rodriguez, E. B., Abasolo, W. P., Mun, S. P., & Razal, R. A. (2016). Mineral, nutritional, and phytochemical profile, total phenolic content, and radical scavenging activity of Philippine bamboo “Bolo” *Gigantochloa levis* (Blanco) Merr. leaves. *Natural Product Sciences*, 22(1), 60–63.
- Trovagunta, R., & Hubbe, M. A. (2023). Suberin as a Bio-based Flame-Retardant? *BioResources*, 18(3), 4388–4391.
- Vishwanath S.J., Delude, C., Domergue, F., Rowland O. (2015). Suberin: biosynthesis, regulation, and polymer assembly of a protective extracellular barrier. *Plant Cell Reports*, 34(4), 573–586.
- Wang, K., Sun, X., Long, B., Li, F., Yang, C., Chen, J., Ma, C., Xie, D., & Wei, Y. (2021). Green Production of Biodegradable Mulch Films for Effective Weed Control. *ACS Omega*, 6(47), 32327–32333.
- Woolfson, K. N. (2018). *Suberin Biosynthesis and Deposition in the Wound-Healing Potato Suberin Biosynthesis and Deposition in the Wound-Healing Potato (Solanum tuberosum L.) Tuber Model (Solanum tuberosum L.) Tuber Model*. <https://ir.lib.uwo.ca/> & <https://ir.lib.uwo.ca/etd/5935>
- Woolfson, K. N., Esfandiari, M., & Bernards, M. A. (2022). Suberin Biosynthesis, Assembly, and Regulation. *Plants*, 11(4), 555.
- Woolfson, K.N., Haggitt, M.L., Zhang Y., Kachura A., Bjelica, A., Rey Rincon, M.A., et al. (2018). Differential induction of polar and non-polar metabolism during wound-induced suberization in potato (*Solanum tuberosum* L.) tubers. *The Plant Journal*, 93(5), 931–942
- Yang, Q., Yuan, F., Xu, L., Yan, Q., Yang, Y., Wu, D., Guo, F., & Yang, G. (2019). An Update of Moisture Barrier Coating for Drug Delivery. *Pharmaceutics*, 11(9), 436.
- Yang, W. L., & Bernards, M. A. (2007). Metabolite profiling of potato (*Solanum tuberosum* L.) tubers during wound-induced suberization. *Metabolomics*, 3(2), 147–159.

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