

Determination of Secretory Structures and Trichome Biomineralization in *Corylus avellana* cv. 'Palaz' Husk

Yaşar Akçin¹ , Öznur Ergen Akçin² , Saim Zeki Bostan³ 

¹Nuriye Halit Çebi Vocational High School, Ordu

²Ordu University, Faculty of Science and Art, Department of Molecular Biology and Genetics, Ordu

³Ordu University, Faculty of Agriculture, Department of Horticulture, Ordu

Geliş Tarihi / Received Date: 05.05.2025

Kabul Tarihi / Accepted Date: 01.09.2025

Abstract

This study aimed to determine the glandular structures and trichome biomineralization of the husks of 'Palaz' hazelnut cultivars during the period when glandular trichomes are dense. The specimens were collected from Altınordu, Ordu, Turkey. The secretory structures in the fresh husk samples were examined both by scanning electron microscopy (SEM) and stereo microscopy. Energy-dispersive X-ray (EDX) analyses were performed using a JEOL JMS-7001F SEM equipped with secondary electron (SE) and backscattered electron (BSE) detectors. Five types of glandular structures were found on the husk surface. A total of 8 minerals including C, O, N, K, Ca, Cl, Si and Mg were determined in the glandular trichomes examined. Among these minerals, C, O, N, K, Ca minerals were determined in all trichome types with different percentages. The most abundant minerals in glandular trichomes are carbon and oxygen minerals.

Anahtar Kelimeler: biomineral, hazelnut, husk, secretory trichome

Corylus avellana cv. 'Palaz' Zurufunda bulunan Salgı Yapılarının ve Trikom Biyomineralizasyonunun Belirlenmesi

Öz

Bu çalışma, glandüler trikomların yoğun olduğu dönemde 'Palaz' fındık çeşidinin zuruflarının glandüler yapılarını ve trikom biyomineralizasyonunu belirlemeyi amaçlamıştır. Örnekler Altınordu, Ordu, Türkiye'den toplanmıştır. Taze kabuk örneklerindeki salgı yapıları hem taramalı elektron mikroskobu (SEM) hem de stereo mikroskop ile incelenmiştir. Enerji dağılımlı X-ışını (EDX) analizleri, ikincil elektron (SE) ve geri saçılan elektron (BSE) dedektörleri ile donatılmış bir JEOL JMS-7001F SEM kullanılarak gerçekleştirilmiştir. Kabuk yüzeyinde beş tip glandüler yapı bulunmuştur. İncelenen glandüler trikomlarda C, O, N, K, Ca, Cl, Si ve Mg olmak üzere toplam 8 mineral tespit edilmiştir. Bu minerallerden C, O, N, K, Ca mineralleri tüm trikom tiplerinde farklı oranlarda tespit edilmiştir. Glandüler trikomlarda en bol bulunan mineraller karbon ve oksijen mineralleridir.

Keywords: biyomineral, fındık, zuruf, salgı tüyü

Introduction

Plants have evolved a variety of adaptive mechanisms to cope with different environmental conditions. Among these mechanisms release of secretions by secretory trichomes or secretory structures, and biomineralization mechanisms play a significant role. (Bauer et al., 2011; Kaur & Kariyat, 2020). Glandular trichomes represent the primary secretory structures in plants, and their morphological characteristics vary among taxa (Huchelmann et al., 2017). Biomineralization processes enhance the structural integrity of the plant. The presence of biominerals, such as calcium phosphate, calcium carbonate, and silica, which are abundant in plants, serves to enhance the structural endurance of the plant and provides protection against environmental stress factors. Some glandular trichomes contribute to biomineralization processes and maintain the mineral balance of the plant. Recently, various studies have been conducted to determine the presence of secretory structures and secretory substances in plants and to detect the presence of biominerals. These studies are particularly focused on species of economic value (Ensikat & Weigend, 2021; He et al., 2014; Hopewell et al., 2021).

The common hazelnut (*Corylus avellana* L.) is an important and economically valuable horticultural plant grown for human consumption. There are 20 hazelnut cultivars of this species in Turkey, of which 18 are registered, and 2 are unregistered cultivars. "Palaz" is a registered cultivar. It is widely grown in the northern region of Turkey (Balık et al., 2016). As the economic benefits of hazelnut continue to increase, the area under hazelnut cultivation and the amount of hazelnut by-products are also increasing worldwide. While the hazelnut kernel is the primary product, a considerable quantity of by-products are generated throughout the pre-harvest, harvesting, and processing phases. These include shells, husks, and leaves (Allegrini et al., 2022).

It has been demonstrated that the substances secreted from the glandular trichomes provide the plant with protection against herbivores and aphids. Aphids also feed on the husk of hazelnut trees. This causes nutrient loss, reduced photosynthesis and long-term crop losses. It has been observed that when the husks begin to dry, the number of hairs on the surface of the husks begins to decrease. The identification of secretory trichome types, and biominerals in different plant parts is crucial for the utilization of plants in diverse settings. The objective of this study was to ascertain the type of glandular trichomes, and the biominerals they contain in the husks of the 'Palaz' hazelnut cultivar during the period when glandular trichomes are dense and herbivores are observed.

Material and Methods

Material

The study was conducted in a Palaz orchard situated in Ordu province (N40.975535, E37.966505) on May-July 2023. The trees in the orchard are 32 years old. Sampling was randomly selected from the orchard. The distance between the ocaks varies between 3.5-5 m. No fertilization was applied in the orchard. The whole orchard is sunny and 10 m above sea level.

Methods

The secretion structures in fresh husk samples were analysed by stereo microscope, and the secretion structures in dry husks were analysed by scanning electron microscopy (SEM) (Figure 1-2). For scanning electron microscopy, dried husks were mounted on stubs using double-sided adhesive tape. Husk samples were coated with 12.5-15.0 nm gold and electron microscopy (Hitachi-SU 1510) shots were taken with a voltage of 10-15 kilovolts (kV).

For the biomineralization process, the husk samples were sputter-coated (SC7620) with a thin layer (<30 nm) of palladium. Energy-dispersive X-ray (EDX) analyses were performed using a JEOL JMS-7001F SEM equipped with secondary electron (SE) and backscattered electron (BSE) detectors. EDX mapping was performed and color images were generated by combining SE and BSE images. Electron images, EDS images and map sum spectra of glandular trichome types are shown in Figures 3 and 4. The colors used to represent the elements are indicated below the figures. The figures provide detailed information about the identified elements of the derived EDS spectrum analysis. In this context, wt% represents the weight of an element in percent.

Results and Discussion

Glandular Structure of the Husk

It was determined that the glandular structures were in the form of glandular trichomes in the husk of the 'Palaz' cultivar. Glandular trichomes are densely present on the husks. Five types of glandular structures were found on the husk surface (Figure1-2):

Type 1: This type is the most abundant secretory structure. Glandular trichomes have a cup-shaped unicellular, red tipped secretive cell, and multicellular -uniseriate stalk. As the husk is forming, these trichomes initially have transparent, colored secretive cells. During growth, the trichomes first acquire a pinkish color. When the trichomes have completed their development, the secretory cell is completely filled with red-colored secretion. The mean trichome length is 500 μ (Figure1 A-H).

Type 2: This type of glandular trichome is characterized by bulb-shaped transparent secretory cell, a multicellular – uniseriate stalk, and a neck cell. The glandular tips of these trichomes are shiny. They can reach a size of 50-75 μ . Mucilage is secreted from these trichomes, facilitating the adhesion of insects (Figure 1 H-I, Figure 2 A-D,).

Type 3: This type of glandular trichomes have a flat or ovoid shaped head cell bulging towards the tip and 2-multi celled stalk cells. They can reach a size of 300-350 μ (Figure 2 E-H).

Type 4: This type of glandular trichome is characterized by the presence of round glandular cells and a pluriseriate stalk. They can reach a size of 200-250 μ (Figure 2 I-J).

Type 5: These are peltate trichomes with or without very short stalks. They have a light bright color. This type of trichome is less common than the other types. Glandular trichomes have globose heads. The length of these trichomes can reach up to 50 mm. (Figure 2L-M).

Secretory trichomes are structures that play a role in the production and storage of essential oils and many secondary metabolites in plants. The secretions released from the trichomes are effective in the plant's self-defence against biotic and abiotic stresses. Additionally, glandular trichomes play a role in attracting pollinators to the plant and deterring pests. (Chen et al., 2020; Glas et al., 2012; Gostin & Blidar, 2024; Zhou et al., 2021). Akçin (2019) reported that the leaves of the "Karafındık" cultivar had non-glandular and glandular trichomes. It has been reported that non-glandular trichomes are simple, short unicellular or long multicellular trichomes, and glandular trichomes are multicellular. Uzunova (1999) observed one type of glandular trichomes in *C. avellana* and two types of glandular hair in *C. colurna* L. We have demonstrated that "Palaz" cultivar husks have five types of glandular trichomes. It is also found non-glandular trichomes in the husk of the "Palaz". Aphids feed on the young stems, leaves, and husks of hazelnut trees. This causes nutrient loss. Photosynthesis may be reduced due to molds formed in the sap secretions of aphids. Decreased photosynthesis can cause significant crop losses in the long run. Large populations of aphids feeding on hazelnut plants may cause premature nut drop and reduced nut quality (Tuncer & Ecevit, 1997; Walton et al., 2009). In our study, it was observed that during this period of aphid emergence, dense glandular trichomes were formed on the leaves and husk of hazelnut. Some of these glandular trichomes were red, while others were white. The plant tries to protect itself with secretions from the glandular trichomes. Essential compounds emitted from glandular trichomes in plants are known to have allelopathic

effects against herbivores. Mucilage secreted from trichomes adheres to insects, trapping them, preventing their movement, and even causing their death (Gantner & Najda, 2013). In our study, mucilage was found to be secreted from type 2 glandular trichomes. It was observed that the secreted mucilage had such an effect on insects and aphids were captured by the secretions released from the trichomes Figure 2N-O. The more the aphids try to move, the more the mucilage sticks to them, and after a while they are unable to move. It has been observed that aphids adhering to the husk surface die after a while. With this method, the plant tries to protect itself from aphids. A correlation between trichome density and pest resistance was shown by Tian et al. (2012). Glands secreting lipophilic substances can be used in chemical protection against various herbivore and pathogen species by spraying or poisoning them.

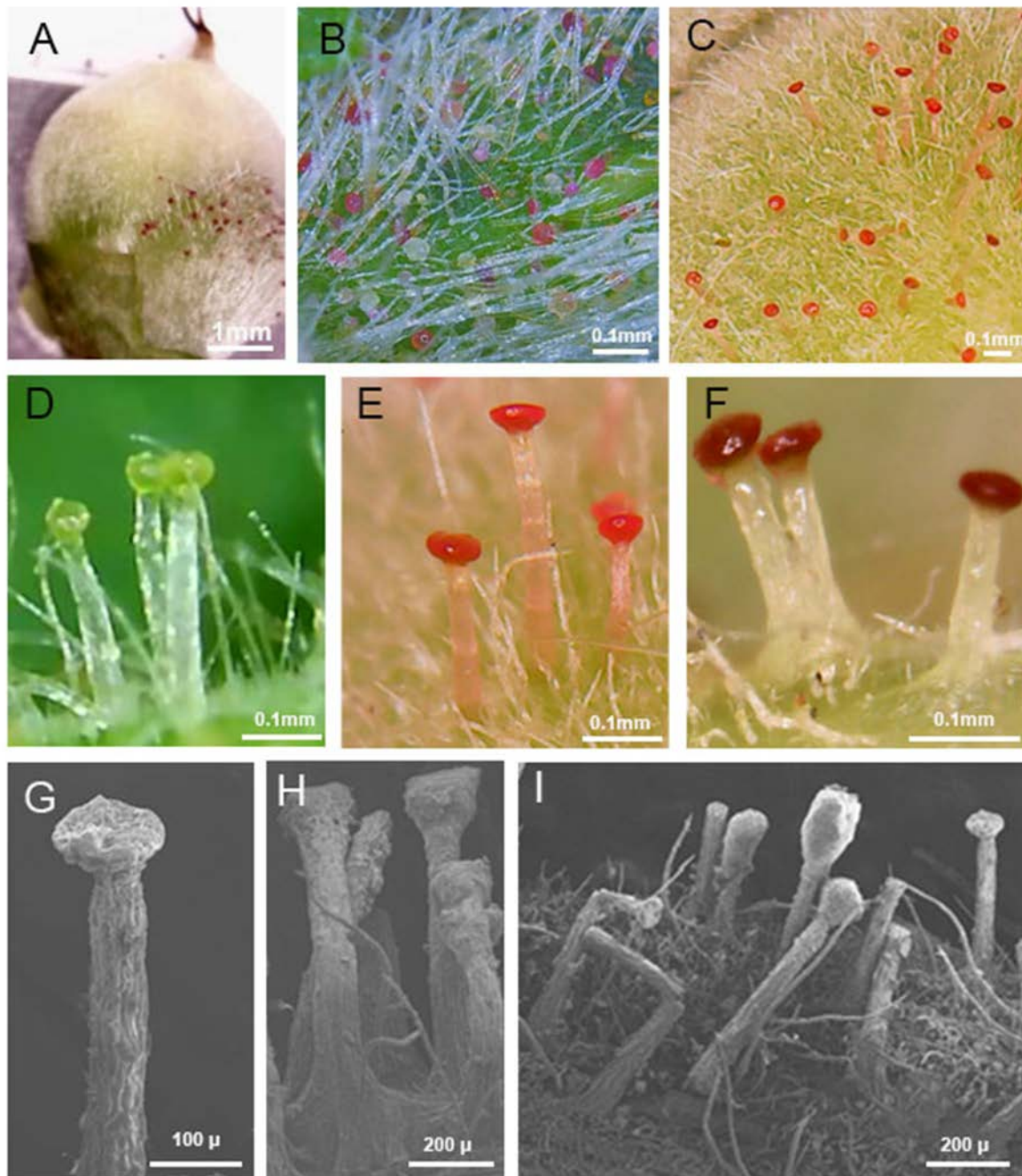


Figure 1. Stereomicroscopy and Scanning Electron Microscopy (SEM) Images of Glandular Trichomes in the Hazelnut Husk

A-C. General view of husk surface. D-F. Developmental stages of type 1 glandular trichomes. G. Type 1 glandular trichomes (SEM). H. Type 1 and type 2 glandular trichomes (SEM). I. Type 2 glandular trichomes (SEM).

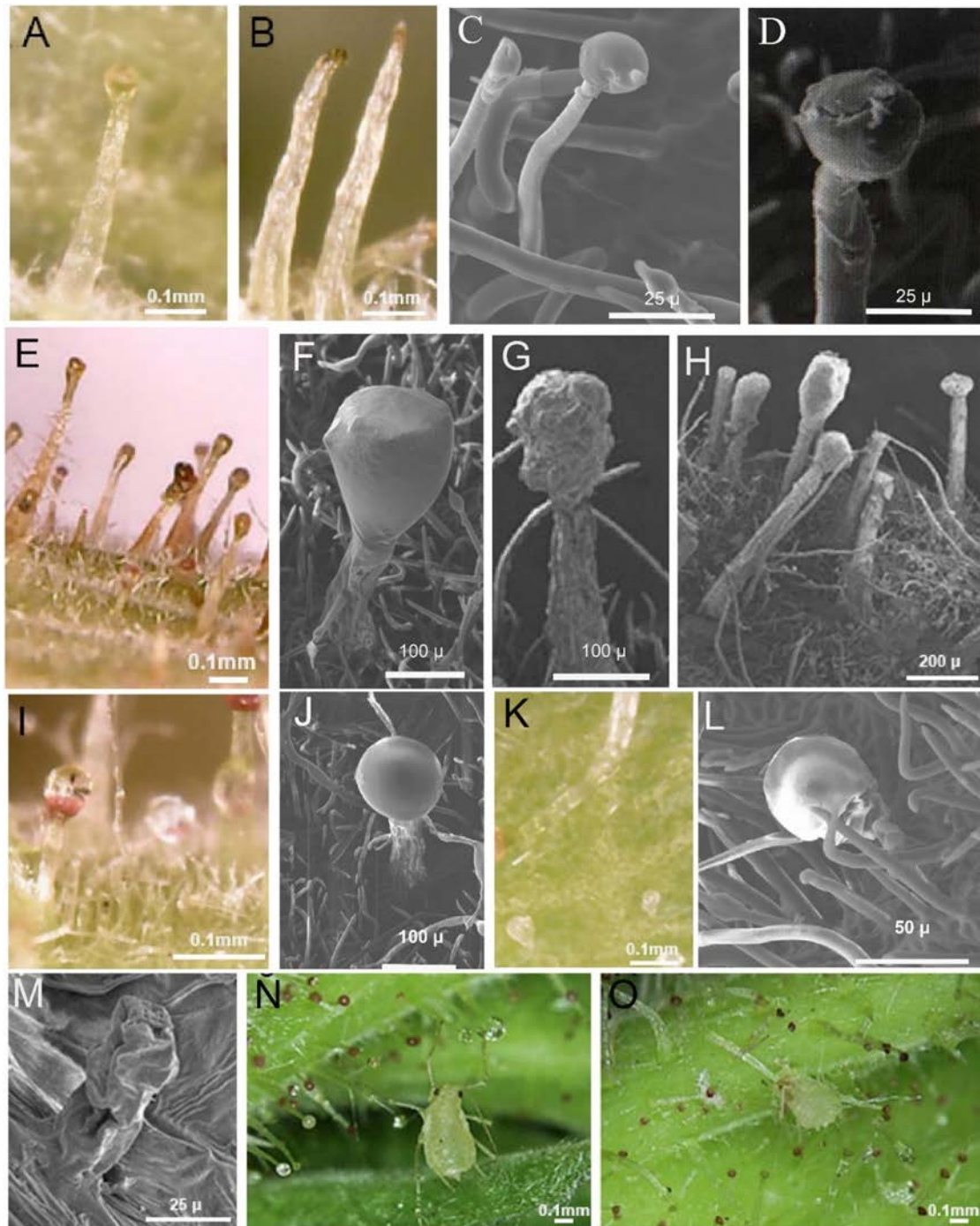


Figure 2. Stereomicroscopy and Scanning Electron Microscopy (SEM) Images of Glandular Trichomes and Aphids in the Hazelnut Husk

A. Type 2 glandular trichomes. B. Type 2 glandular trichome with a burst glandular cell. C. Type 2 glandular trichomes with uni-cellular head cells and burst head cells. D. Type 2 glandular trichomes with uni-cellular head cells. E. Stereomicroscope image of type 3 glandular trichomes. F. Type 3 glandular trichome bulging towards the tip and with a flat top head cell. G. Type 3 glandular trichomes with ovoid head. H. SEM image of type 3 and type 1 glandular trichomes. I. Stereomicroscope image of type 4 glandular trichomes with uni-cellular head. J. SEM image of type 4 glandular trichome. K. Stereomicroscope image of type 5 glandular trichome. L. SEM image of type 5 glandular trichome. M. Type 5 glandular trichomes with secretion released and shrunken head. N-O. Aphids adhering to different types of glandular hairs and secretions

Mineralization of Glandular Trichomes

Various biominerals were found in 5 types of glandular hairs identified in hazelnut husks. Figures 3 -5 illustrate the electron images, EDS images, and map sum spectra of glandular trichome types. A total of 8 minerals including C, O, N, K, Ca, Cl, Si and Mg were determined in the glandular trichomes examined. Among these minerals, C, O, N, K, Ca minerals were determined in all trichome types with different percentages. The most abundant minerals in glandular trichomes are carbon and oxygen minerals. The percentages of these minerals vary according to the trichome type, as can be seen from the data. The highest C value was found in glandular trichome type 1 with 64.4%, while the lowest value was observed in glandular trichome type 5 with 57.4%. When O values were analysed, glandular trichome type 5 showed the highest value with 36.7%, while the lowest value was observed in glandular trichome type 1 with 30.5%. Analyses showed that N and K were present at lower levels in the trichomes examined. The highest concentration of nitrogen was found in type 1 glandular trichomes (3.9%) and the highest concentration of potassium was found in type 4 glandular trichomes (1.7%). The majority of minerals were present in type 1 glandular trichomes, but four of these minerals (K, Ca, Cl and Si) were present in trace amounts. Six minerals were found in the remaining glandular trichomes. In types 3, 4 and 5, only two elements were found in trace amounts. Calcium and silicium were found in trace amounts in type 3 and 4 glandular trichomes, and magnesium and calcium were present in trace amounts in type 5 glandular trichomes.

The process of biomineralization in plants exhibits considerable structural and compositional diversity. The functions of biominerals may be contingent upon their shape, size, abundance, localisation and chemical composition (Bauer et al., 2011; He et al., 2014). The present study determined the presence of eight minerals (C, O, N, K, Ca, Cl, Si and Mg) in the glandular hairs of hazelnut husks. It was observed that the minerals C, O, N, K and Ca were present in all glandular trichomes types. However, variations were observed in the rate of their occurrence. A number of minerals, including calcium carbonate and silicium, are stored in the cell walls of trichomes (He et al., 2014; Lanning & Eleuterius 1989). Biominerals are involved in a number of physiological processes, including calcium regulation, detoxification of aluminium and heavy metals, light regulation and pollen release, germination, mechanical support and have an impact on plant ecology. Additionally, they provide protection against insect and herbivore attacks (He et al., 2014; Raven & Giordano, 2009).

In *Arabidopsis thaliana*, trichomes have been found to function as herbivore deterrents (Handley et al., 2005). The most abundant mineral in the trichome types analysed is C. All living organisms are carbon-based. It is therefore unsurprising that carbon is the most abundant element in glandular trichomes. In plants, carbon plays a role in promoting healthier and more productive growth. Nitrogen is one of the most essential mineral elements for plant growth. Potassium plays a vital role in nitrogen metabolism. Nitrogen plays a significant role in modern agriculture (Chen et al., 2018). Potassium is essential for optimal plant growth (Xu et al., 2020). Potassium is an activator of enzymes involved in numerous processes, including protein synthesis, nitrogen (N) and carbon (C) metabolism, and photosynthesis. It plays a pivotal role in the formation of yield and the enhancement of quality (Oosterhuis et al., 2014; Xu et al., 2020). Calcium is a vital phytonutrient that plays a crucial role in cellular metabolism (White & Broadley, 2003). Calcium is present in plant trichomes in the form of calcium phosphate or calcium carbonate. In mineralised plant trichomes, the trichome tips typically exhibit high concentrations of minerals, including silica, calcium and phosphate. Conversely, the bases of these structures often contain calcium carbonate and show lower mineralisation (Weigend et al., 2018). The analysis revealed the presence of calcium mineral in all glandular trichome types. The secretory parts or tips of the trichome plumage exhibited mineralization patterns consistent with those documented in the literature, although the densities observed differed. Silicium is a vital mineral for plants, enhancing their resilience to biotic and abiotic stresses. In numerous plant species, the precipitation of silicium in cell walls with aluminium and other heavy metals may be a mechanism by which the toxicity of these heavy metals is mitigated (He et al., 2014; Wang et al.,

2004). This is corroborated by the observation that plants subjected to herbivory tend to accumulate greater quantities of silicium in their leaves relative to those that have not been attacked (Gallaher et al., 2020; Nawaz et al., 2019). The presence of silicium was identified in type 1, type 3 and type 4 glandular trichomes in hazelnut husks. It is hypothesised that the plant utilises these minerals in conjunction with certain ethereal oils to safeguard itself against herbivores.

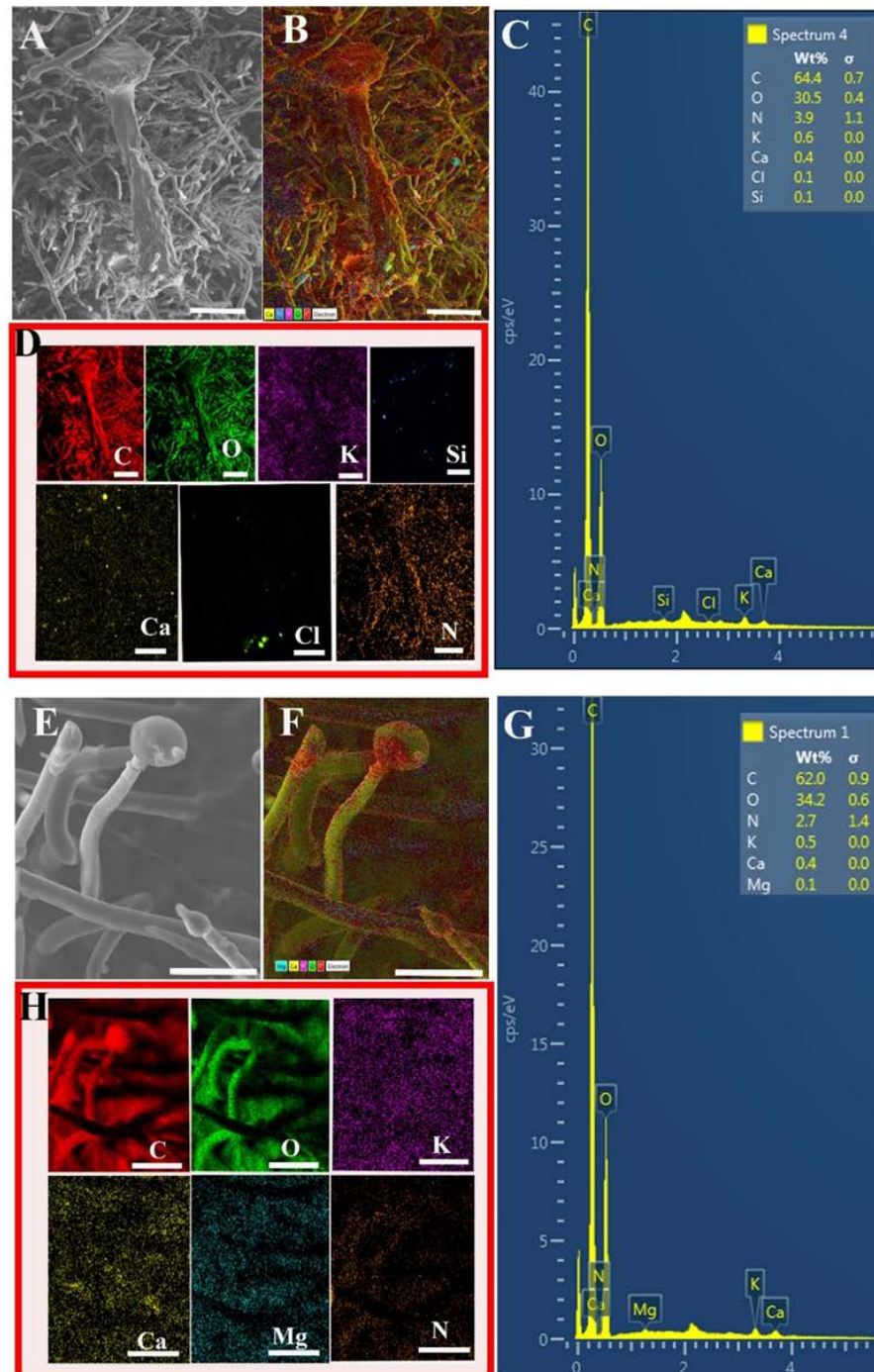


Figure 3. Scanning Electron Microscopy (SEM) Images and Energy Dispersive X-ray Microanalysis (EDX) Spectra of Biominerals of Type 1(A-D) and Type 2 (E-H) Secretory Trichomes in Husk

A. SEM image of type 1 glandular trichomes. B. Element-mapped SEM image of type 1 glandular trichomes. C. Spectra of biominerals in type 1 glandular trichomes D. Determined mineral substances E. SEM image of type 2 glandular trichomes. F. Element-mapped SEM image of type 2 glandular trichomes. In the secretory cell, C, Mg, O are more abundant at the base, while O, K, Ca, Mg are more abundant at the tip. G. Spectra of biominerals in type 2 glandular trichomes H. Determined mineral substances. Bars: (A, B, D): 100 μ , (E, F, H): 25 μ

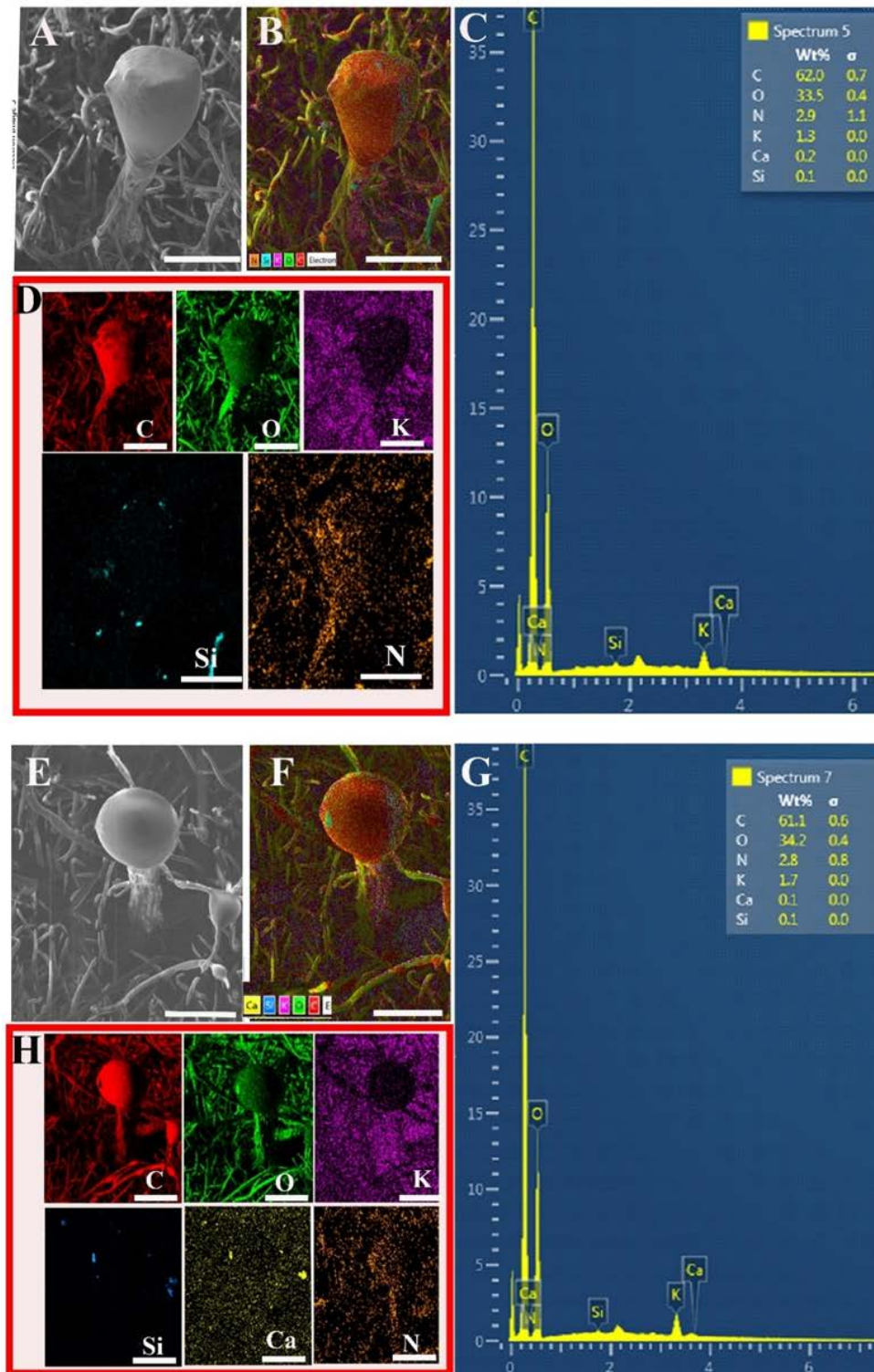


Figure 4. Scanning Electron Microscopy (SEM) Images and Energy Dispersive X-ray Microanalysis (EDX) Spectra of Biominerals of Type 3 (A-D) and Type 4 (E-H) Secretory Trichomes in Husk

A. SEM image of type 3 glandular trichomes. B. Element-mapped SEM image of type 3 glandular trichomes. C and O are present in greater concentrations within the glandular trichomes, while Ca, K, Si and N minerals are also present. C. Spectra of biominerals in type 3 glandular trichomes D. Determined mineral substances E. SEM image of type 4 glandular trichomes. F. Element-mapped SEM image of type 4 glandular trichomes. In the secretory cell, C is more abundant, while O, N, K, Si, and Ca are also present. G. Spectra of biominerals in type 4 glandular trichomes. H. Determined mineral substances. Bars:100 μ

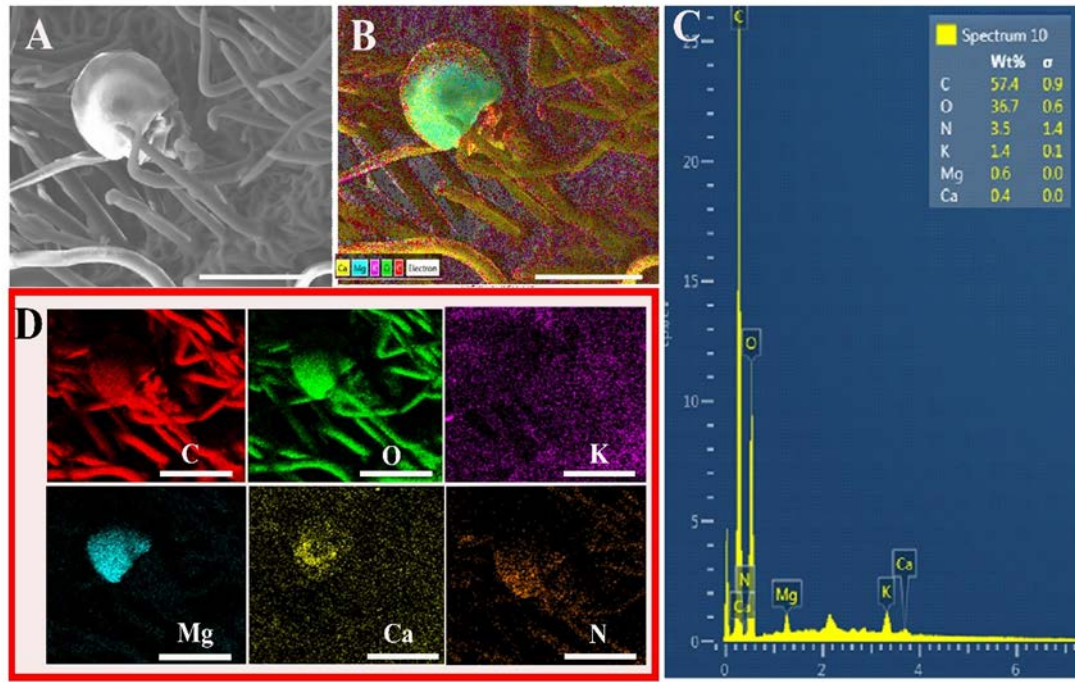


Figure 5. Scanning Electron Microscopy (SEM) Images and Energy dispersive X-ray Microanalysis EDX Spectra of Biominerals of Type 5 Secretory Trichomes in Husk

A. SEM image of type 5 glandular trichomes. B. Element-mapped SEM image of type5 glandular trichomes. C, O and N are present in greater concentrations within the glandular trichomes, while Ca, K and Mg minerals are also present. C. Spectra of biominerals in type 3 glandular trichomes D. Determined mineral substances Bars:50 μ

Conclusion

This study was carried out to determine the glandular hairs on the shell and their mineralisation in 'Palaz' hazelnut variety. A total of five different types of glandular trichomes were detected in hazelnut shells. As a result of mineralization of glandular trichomes, eight minerals were determined as C, O, N, K, Ca, Cl, Si, Mg. Although the concentrations of C, O, N, K, Ca were different, they were observed in all trichome types. The study is important in terms of investigating the combined effects of glandular trichomes and trichome mineralisation in hazelnut shells and it is the first study on this subject. It is thought to be an example for other studies to be carried out on the varieties.

Author Contributions

The authors collaborated throughout all stages of the study. All authors contributed equally to the article.

Ethics

There are no ethical issues related to the publication of this article.

Conflict of Interest

The authors declare that they have no conflict of interest.

ORCID

Yaşar Akçin  <https://orcid.org/0000-0002-6302-9754>

Öznur Ergen Akçin  <https://orcid.org/0000-0002-6875-6045>

Saim Zeki Bostan  <https://orcid.org/0000-0001-6398-1916>

References

- Akçin, Y. (2019). Some leaf properties of 'Karafındık' hazelnut cultivar (*Corylus avellana* L.). *Academic Journal of Agriculture*, 8, 141-144. <https://doi.org/10.29278/azd.647428>
- Allegrini, A., Salvaneschi, P., Schirone, B., Cianfaglione, K., & Michele, A. D. (2022). Multipurpose plant species and circular economy: *Corylus avellana* L. as a study case. *Frontiers in Bioscience*, 27(1), 1-20. <https://doi.org/10.31083/j.fbl2701011>
- Balık, H. I., Balık, S. K., Beyhan, N., & Erdoğan, V., (2016). *Hazelnut Cultivars*. Klasman Press.
- Bauer, P., Elbaum, R., & Weiss, I. M. (2011). Calcium and silicon mineralization in land plants: transport, structure and function. *Plant Science*, 180, 746-756. <https://doi.org/10.1016/j.plantsci.2011.01.019>
- Chen, H., Li, D., Zhao, J., Xiao, K., & Wang, K. (2018). Effects of nitrogen addition on activities of soil nitrogen acquisition enzymes: A meta-analysis. *Agriculture, Ecosystems & Environment*, 252, 126-131. <https://doi.org/10.3390/agronomy14071352>
- Chen, S., Zhang, L., Cai, X., Li, X., Bian, L., Luo, Z., Li, Z., Chen, Z., & Xin, Z. (2020). (E)-Nerolidol is a volatile signal that induces defenses against insects and pathogens in tea plants. *Horticulture Research* 7(1), 52. <https://doi.org/10.1038/s41438-020-0275-7>
- Ensikat, H. J., & Weigend, M. (2021). Distribution of biominerals and mineral-organic composites in plant trichomes. *Frontiers in Bioengineering and Biotechnology*, 9, 763690. <https://doi.org/10.3389/fbioe.2021.763690>
- Gallaher, J. T., Akbar, S. Z., Klahs, C. P., Marvet, C. R., Senske, A. M., Clark, L. G., & Stromberg, C. A. E. (2020). 3D shape analysis of grass silica short cell phytoliths: A new method for fossil classification and analysis of shape evolution. *New Phytologist*, 228, 376-392. <https://doi.org/10.1111/nph.16677>
- Gantner, M., & Najda, A. (2013). Essential oils from buds and leaves of two hazelnut (*Corylus* L.) cultivars with different resistance to filbert big bud mite (*Phytoptus avellanae* Nal.) and filbert aphid (*Myzocallis coryli* Goetze). *Arthropod-Plant Interactions*, 7, 659-666. <https://doi.org/10.1007/s11829-013-9281-0>
- Glas, J., Schimmel, B., Alba, J., Escobar-Bravo, R., Schuurink, R., & Kant, M. (2012). Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. *International Journal of Molecular Sciences*, 13, 17077-17103. <https://doi.org/10.3390/ijms131217077>
- Gostin, I. N., & Blidar, C. F. (2024). Glandular trichomes and essential oils variability in species of the genus *Phlomis* L.: A review. *Plants*, 13(10), 1338. <https://doi.org/10.3390/plants13101338>
- Handley, R., Ekbom, B., Agren, J. (2005). Variation in trichome density and resistance against a specialist insect herbivore in natural populations of *Arabidopsis thaliana*. *Ecological Entomology*, 30, 284-292. <https://doi.org/10.1111/j.0307-6946.2005.00699.x>
- He H., Veneklaas, E. J., Kuo, J., & Lambers, H. (2014). Physiological and ecological significance of biomineralization in plants. *Trends in Plant Science*, 9(3), 166-174. <https://doi.org/10.1016/j.tplants.2013.11.002>

- Hopewell, T., Selvi, F., Ensikat, H. J., & Weigend, M. (2021). Trichome biomineralization and soil chemistry in brassicaceae from mediterranean ultramafic and calcareous soils. *Plants*, 10, 377. <https://doi.org/10.3390/plants10020377>
- Huchelmann, A., Boutry, M., & Hachez, C. (2017). Plant Glandular Trichomes: Natural Cell Factories of High Biotechnological Interest. *Plant Physiology*, 175(1), 6–22. <https://doi.org/10.1104/pp.17.00727>
- Kaur, J., & Kariyat, R. (2020). Role of trichomes in plant stress Biology. In J. Nunez-Farfan, P. Valverde (Ed). *Evolutionary Ecology of Plant-Herbivore Interaction* (pp.15-35). Springer: Champs.
- Lanning, F. C., & Eleuterius, L. N. (1989). Silica deposition in some C3 and C4 species of grasses, sedges and composites in the USA. *Annals of Botany*, 64, 395–410. <https://doi.org/10.1093/oxfordjournals.aob.a087858>
- Nawaz, M. A., Zakharenko, A. M., Zemchenko, I. V., Haider, M. S., Ali, M. A., Imtiaz, M., Chung, G., Tsatsakis, A., Sun, S., & Golokhvast, K. S. (2019). Phytolith formation in plants: From soil to cell. *Plants*, 8, 249. <https://doi.org/10.3390/plants8080249>
- Oosterhuis, D., Loka, D., Kawakami, E., & Pettigrew, W. (2014). The physiology of potassium in crop production. *Advances in Agronomy*, 126, 203–234. <https://doi.org/10.1016/B978-0-12-800132-5.00003-1>
- Raven, J.A. & Giordano, M. (2009) Biomineralization by photosynthetic organisms: Evidence of coevolution of the organisms and their environment. *Geobiology*, 7, 140–154. <https://doi.org/10.1111/j.1472-4669.2008.00181.x>
- Tian, D., Tooker, J., Peiffer, M., Chung, S. H., & Felton, G. W. (2012). Role of trichomes in defense against herbivores: comparison of herbivore response to woolly and hairless trichome mutants in tomato (*Solanum lycopersicum*). *Planta*, 236, 1053-1066. <https://doi.org/10.1007/s00425-012-1651-9>
- Tuncer, C., & Ecevit, O. (1997). Current status of hazelnut pests in Turkey. *Acta Horticulture*, 445, 545-552. <https://doi.org/10.17660/ActaHortic.1997.445.70>
- Uzunova, K. (1999). Comparative study of leaf epidermis in European Corylaceae. *Feddes Repertorium*, 110, 209-218. <https://doi.org/10.1002/fedr.19991100307>
- Walton, V. M., Chambers U., & Olsen J. L. (2009). The current status of the newly invasive hazelnut aphid in Oregon hazelnut orchards. *Acta Horticulturae*, 845, 479- 485. <https://doi.org/10.17660/ActaHortic.2009.845.74>
- Wang, Y., Stass, A., & Hors, W. I. (2004) Apoplastic binding of aluminum is involved in silicon-induced amelioration of aluminum toxicity in maize. *Plant Physiology*, 136, 3762–3770. <https://doi.org/10.1104/pp.104.045005>
- Weigend, M., Mustafa, A., & Ensikat, H. J. (2018). Calcium phosphate in plant trichomes: The overlooked biomineral. *Planta*, 247, 277–285. <https://doi.org/10.1007/s00425-017-2826-1>
- White, P. J., & Broadley, M. R. (2003). Calcium in plants. *Annals of Botany*, 92, 487–511. <https://doi.org/10.1093/aob/mcg164>
- Xu, X., Du, X., Wang, F., Sha, J., Chen, Q., Tian, G., Zhu, Z., Ge, S., & Jiang, Y. (2020). Effects of potassium levels on plant growth, accumulation and distribution of carbon, and nitrate metabolism in apple dwarf rootstock seedlings. *Frontiers in Plant Science*, 11, 904. <https://doi.org/10.3389/fpls.2020.00904>

Zhou, S., Han, C., Zhang, C., Kuchkarova, N., Wei, C., Zhang, C., & Shao, H. (2021). Allelopathic, phytotoxic, and insecticidal effects of *Thymus proximus* serg. Essential oil and its major constituents. *Frontiers in Plant Science*, 12, 689875. <https://doi.org/10.3389/fpls.2021.689875>