



Genotypic variation in UV-B absorbing compounds of hazelnut pollen grains

Özkan KİLİN¹, Orçun TOKSÖZ², Aslihan ÇETİNBAS-GENÇ^{3*}

^{1,2,3}Marmara University, Faculty of Science, Department of Biology, Istanbul, Türkiye

*aslihan.cetinbas@marmara.edu.tr, ¹ozkankilin@gmail.com, ²toksozorcun@gmail.com

Received : 30.06.2025
Accepted : 23.09.2025
Online : 02.10.2025

Fındık polen tanelerinde UV-B absorplayıcı bileşiklerin genotipik varyasyonu

Abstract: Pollen grains, as highly sensitive reproductive units, rely on structural and biochemical mechanisms to withstand environmental stressors, particularly UV-B radiation. This study evaluated the UV-B absorbance capacity of UV-B absorbing compounds extracted from cytoplasmic, wall-bound, and sporopollenin-associated fractions of pollen grains from four *Corylus avellana* genotypes (Sarı, Palaz, Kara, Yomra). Spectral analyses revealed distinct fraction-specific absorbance patterns, showing a general decrease between 280–315 nm in the cytoplasmic and wall-bound fractions, whereas the sporopollenin fraction exhibited an increasing trend. Spectrophotometric analyses revealed that the cytoplasmic fraction exhibited the highest UV-B absorbance across all genotypes, followed by the sporopollenin and wall-bound fractions. Genotype-specific patterns were evident, with Palaz showing the highest cytoplasmic absorbance and Sarı displaying superior sporopollenin-associated absorbance, while Kara consistently recorded the lowest across all fractions. Multivariate analyses, including principal component analysis and heatmap clustering, confirmed distinct groupings among genotypes and UV-B absorbing compounds fractions. These findings suggest that inherent variability in UV-B absorbing compounds distribution contributes to differential photoprotection potential among genotypes. Identifying hazelnut genotypes with stronger inherent UV-B defense capacity may inform breeding strategies aimed at improving reproductive resilience under increasing UV-B exposure.

Key words: UV-B radiation, pollen grain, ultraviolet-absorbing compounds, sporopollenin

Özet: Polen taneleri oldukça hassas üreme yapılarıdır ve UV-B radyasyonu da dahil olmak üzere çevresel streslere karşı dayanım için yapısal ve biyokimyasal mekanizmaları kullanırlar. Bu çalışmada, dört farklı *Corylus avellana* genotipine (Sarı, Palaz, Kara, Yomra) ait polen tanelerinin sitoplazmik, hücre duvarına bağlı ve sporopolleninle ilişkili fraksiyonlardan izole edilen UV-B absorplayıcı bileşiklerin UV-B absorbsiyon kapasitesi değerlendirilmiştir. Çalışmada, spektral analizler, sitoplazmik ve duvar bağlı fraksiyonlarda 280–315 nm arasında genel bir azalma, sporopollenin fraksiyonunda ise artış eğilimi göstererek fraksiyonlara özgü farklı absorbsiyon paternlerini ortaya koymuştur. Tüm genotipler içerisinde en yüksek UV-B absorbsiyonunun sitoplazmik fraksiyonda gerçekleştiği, bunu sırasıyla sporopollenin ve duvar bağlı fraksiyonların izlediği belirlenmiştir. Genotipe özgü örüntüler belirgin olup, Palaz genotipi sitoplazmik absorbsiyonda en yüksek değeri gösterirken, Sarı genotipi sporopolleninle ilişkili absorbsiyonda öne çıkmış, Kara ise tüm fraksiyonlarda en düşük değerlere sahip olmuştur. Temel bileşenler ve ısı haritası kümeleme dahil çok değişkenli analizler, genotipler ve UV-B absorplayıcı bileşik fraksiyonları arasında belirgin ayrışmaları doğrulamıştır. Bu bulgular, UV-B absorplayıcı bileşiklerin dağılımındaki kalıtsal farklılıkların genotipler arası fotokoruyucu potansiyel farklılıklarına katkıda bulunduğunu göstermektedir. UV-B'ye karşı doğal savunma kapasitesi yüksek olan fındık genotiplerinin belirlenmesi, artan UV-B maruziyeti altında üreme dayanıklılığını artırmaya yönelik ıslah stratejilerine yol gösterebilir.

Anahtar Kelimeler: UV-B radyasyonu, polen tanesi, ultraviyole absorplayıcı bileşikler, sporopollenin

Citation: Kilin Ö, Toksöz O, Çetinbaş-Genç A (2025). Assessment of the UV-B absorbing compounds' absorbance levels in pollen grains of hazelnut genotypes. *Anatolian Journal of Botany* 9(2): 176-181.

1. Introduction

The reliance of plants on sunlight for photosynthesis, combined with their constant exposure to open environments, makes UV-B radiation an unavoidable stressor (Llorens et al., 2015). It is well documented that UV-B radiation can directly or indirectly impair plant growth and development by inducing various detrimental effects (Yadav et al., 2020). However, the majority of previous research have concentrated on vegetative organs of plants, while relatively few researches have addressed the effects of UV-B radiation on reproductive structures and the protective mechanisms these structures may develop (Llorens et al., 2015). Yet, reproductive structures are often more susceptible to UV-B radiation than vegetative tissues (Llorens et al., 2015). UV-B-induced

alterations in reproductive processes can also lead to considerable financial losses by reducing crop yield and quality (Llorens et al., 2015). Pollen grains are among the least protected components of plant reproductive structures, making them more exposed and significantly more sensitive to UV-B radiation (Feng et al., 2000).

Pollen grains possess inherent structural features that provide a certain level of protection against environmental stressors, including a robust exine layer and a lipid- and pigment-rich outer coating known as pollenkitt (Blackmore, 2007). In addition to these physical barriers, biochemical defense against UV-B radiation is partially supported by the presence of UV-B absorbing compounds (UACs) (Sugioka et al., 2018; Seddon et al., 2019). These compounds have the ability to selectively absorb UV-B

wavelengths and reduce the oxidative stress associated with UV exposure (Fraser et al., 2014). Within pollen grains, UACs are distributed across three major fractions: a soluble cytoplasmic fraction, an insoluble wall-bound fraction, and an insoluble fraction associated with sporopollenin (Rozema et al., 2001). The exine, serving as the external wall of the pollen grain, is primarily composed of sporopollenin—an extremely durable and chemically inert biopolymer known for its exceptional stability against physical, chemical, and enzymatic degradation (Hegedüs et al., 2021). This sporopollenin-based structure not only ensures mechanical protection but also contributes to UV shielding by retaining UACs within its matrix (Fraser et al., 2012). Sporopollenin-associated UACs, located at the most exposed interface, provide long-lasting and passive photoprotection. Cytoplasmic UACs help neutralize reactive oxygen species (ROS) generated within the cell, while wall-bound UACs may act as a barrier limiting UV-B transmission into the cytoplasm. This compartmentalized distribution of UACs, together with the sporopollenin-rich exine architecture, forms a multilayered defense strategy that enhances the resilience of pollen grains to UV-B radiation at both structural and biochemical levels (Rozema et al., 2001). However, this multilayered defense system may not function uniformly across all genotypes, as UV-B tolerance varies not only between species but also among genotypes, presumably caused by variations in composition and distribution of UACs (Rozema et al., 2001).

UAC levels may vary in response to UV-B exposure, evaluating their initial abundance allows for a comparative analysis of the inherent structural photoprotective potential among genotypes (Rozema et al., 2001). Given that hazelnut pollen remains viable for an extended period before fertilization and is exposed to various environmental stressors during this time (Paradinas et al., 2022), identifying genotypes with naturally higher UAC content is important for selecting more resilient pollinator candidates. For this reason, in this study, the UV-B absorbance capacities of UACs, isolated under natural conditions from pollen grains of different hazelnut genotypes prior to any UV-B exposure, were evaluated. UACs were extracted from three main fractions—cytoplasmic, wall-bound, and sporopollenin-associated—and their distribution within the pollen structure as well as their potential protective roles were comprehensively assessed.

2. Materials and Method

2.1. Material

The study material was sourced from Akçakoca/Düzce (Türkiye) in February 2024. Pollen grains were collected from mature male catkins and cleaned by tapping over parchment paper and sieving through a 100 µm mesh. Following overnight desiccation in silica gel, pollen grains were stored at -20 °C until the use.

2.2. Extraction of UACs

The UACs potentials of pollen samples belonging to the Sarı, Kara, Palaz and Yomra genotypes were determined between genotypes and in cytoplasmic, wall-bound and sporopollenin fraction extracts. Spectral absorbance measurements for all three extracts were performed using a Beckman Coulter DU 730 UV/Vis spectrophotometer equipped with cuvettes with a path length of 1 cm, taking measurements at 5 nm intervals in the 280–315 nm

absorbance range. For statistical comparisons, absorbance values were evaluated at 300 nm. This wavelength was chosen because it lies within the biologically relevant UV-B range and has been widely used in previous studies as a standard reference point for assessing UV-B absorbance in pollen fractions (Rozema et al., 2001). Using 300 nm therefore allows both meaningful comparisons among genotypes and consistency with existing literature (Demchik and Day, 1996; Ruhland et al., 2000).

2.3. Cytoplasmic fraction

For cytoplasmic UAC extraction, 10 ml of methanol-water-hydrochloric acid solution (79:20:1, v/v) was added to 0.05 mg of pollen grains and incubated in a 90 °C water bath for 2 hours. The pollen-containing solvent solution was then centrifuged at 3500 rpm for 15 minutes. After centrifugation, the supernatant representing the soluble cytoplasmic fraction was carefully collected, while the pellet was used to obtain the wall-bound fraction and the sporopollenin-associated fraction. To determine the UACs activity of the cytoplasmic fraction, a blank methanol-water-hydrochloric acid solution (79:20:1, v/v) was used as a blank and the supernatant was used for spectral measurements.

2.3. Wall-bound fraction

Following the cytoplasmic fraction extraction process, the remaining pellet was air-dried and then subjected to alkaline hydrolysis by adding 10 ml of 2 M NaOH. After 5 minutes of sonication, the mixture was shaken at room temperature for 1 hour. After centrifugation at 3500 rpm, 15 minutes, the supernatant was acidified with concentrated HCl (220 µl) to adjust the pH to 1.0, and then used for spectral measurements. 2 M NaOH was used as a blank.

2.4. Sporopollenin-associated fraction

Following the wall bound fraction extraction process, the remaining pellet was reacted with a mixture of 95% H₂SO₄ and acetic anhydride (1:9, v/v) and incubated in a boiling water bath at 90 °C for 1 hour with continuous shaking. After cooling and centrifugation (3500 rpm, 15 minutes), the pellet was rinsed twice with acetic acid and three times with distilled water. The resulting brown residue was dissolved in 1 ml glycerol, and then used for spectral measurements (Ruhland et al., 2000; Rozema et al., 2001). Glycerol was used as a blank.

2.5. Statistical analysis

Statistical evaluation was carried out using both SPSS 16.0 and the R programming environment. Differences among the groups were statistically assessed via one-way ANOVA, with statistical significance set at $p < 0.05$. For data visualization and multivariate analysis, R packages were utilized. Prior to the generation of heatmaps, the data were normalized to enable direct comparisons across variables. To identify similarities among genotypes and fractions, hierarchical clustering was performed using the *heatmap* package, with Euclidean distance as the dissimilarity metric and complete linkage as the clustering method. This approach revealed similarity patterns among genotypes as well as relationships between fractions. Principal component analysis (PCA) was performed using the *FactoMineR* package, and the results were visualized with *factoextra*. This multivariate approach enabled dimensionality reduction and helped identify the main

sources of variation in UV-B absorbance. Experimental groups were color-coded on the resulting biplots to illustrate group separation.

3. Results

To assess the distribution of UACs among pollen fractions, spectral analyses were first conducted. The UV-B absorption spectra of different pollen fractions from genotypes revealed distinct variations. In the cytoplasmic fraction, the highest absorbance values were recorded in Palaz and Sari, respectively; Yomra showed intermediate levels and Kara exhibited the lowest absorbance. A slight decreasing trend was observed across all genotypes between 280 and 315 nm (Fig 1a). In the wall-bound fraction, Sari and Palaz displayed the highest absorbance, respectively; Yomra showed intermediate values, and Kara had the lowest, with a clear decreasing trend across all genotypes (Fig 1b). In the sporopollenin fraction, Sari exhibited by far the highest absorbance values. Yomra and Kara showed moderate levels but no absorbance was detected in the 280–285 nm range. Palaz displayed the lowest overall absorbance, with no measurable values between 280 and 290 nm. Interestingly, in all genotypes, the sporopollenin fraction showed a distinct increasing trend in absorbance with increasing wavelength (Fig 1c).

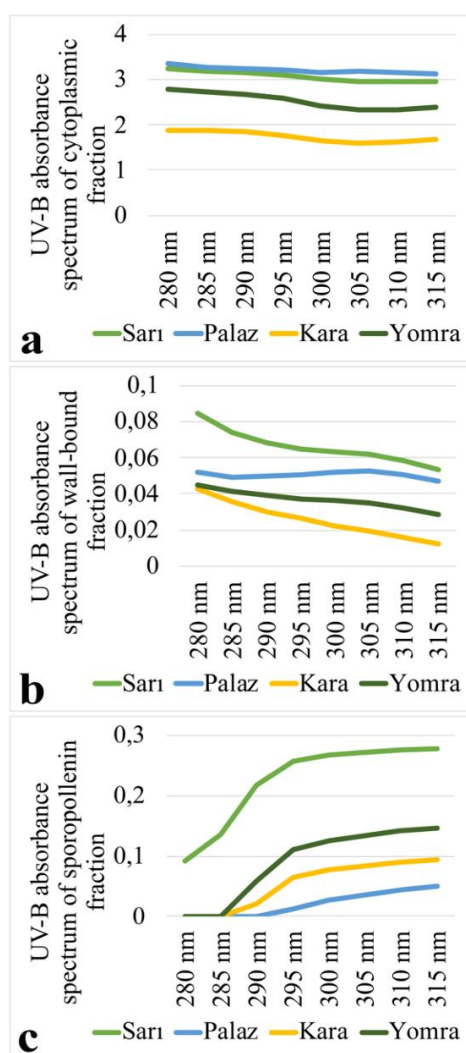


Figure 1. UV-B absorbance spectra of different pollen fractions. **a.** Cytoplasmic fraction, **b.** Wall-bound fraction, **c.** Sporopollenin fraction.

Following the spectral profiling, UV-B absorbance levels at 300 nm were statistically compared across the different fractions within each genotype. Among all genotypes, the cytoplasmic fraction exhibited the highest overall UV-B absorbance. The wall-bound fraction exhibited the lowest values in the Sari, Kara, and Yomra genotypes, whereas in the Palaz genotype, the sporopollenin fraction showed the lowest value (Fig 2a).

In the next step, UV-B absorbance values at 300 nm were examined in different fractions of the genotypes. In the cytoplasmic fraction, the highest absorbance was recorded in Palaz, followed by Sari and Yomra, while Kara showed the lowest value (Fig 2b). For the wall-bound fraction, Sari displayed the highest absorbance, Kara the lowest, with Yomra showing lower absorbance than Palaz (Fig 2c). In the sporopollenin-associated fraction, Sari exhibited the highest absorbance, while Palaz showed the lowest, and Kara had lower values than Yomra (Fig 2d). Statistically significant differences were observed among all fractions within each genotype.

The relationships among cytoplasmic, wall-bound, and sporopollenin fractions, as well as the similarities between genotypes, were evaluated using heatmap and PCA analyses (Fig 3). According to the heatmap generated based on the UV-B absorbance values of UAC fractions, Kara and Yomra clustered together in the same subgroup, while Sari and Palaz formed a separate subgroup (Fig 3a). The cytoplasmic and wall-bound fractions were grouped within the same cluster, which in turn was joined by the sporopollenin fraction at a higher hierarchical level. When all fractions were evaluated collectively, the overall UV-B absorbance—based on column totals of the heatmap—ranked the genotypes from highest to lowest as follows: Sari, Palaz, Yomra, and Kara (Fig 3a).

In the PCA analysis, the Kara genotype was positioned in the positive direction of Dim1, far from all three fractions, suggesting that its biochemical profile differs substantially from the fraction-specific patterns observed in other genotypes. Sari appeared in the upper-left quadrant, close to the sporopollenin fraction, indicating that its composition is more similar to this fraction compared with others. Palaz was located in the negative directions of both Dim1 and Dim2, making it the closest genotype to the cytoplasmic fraction, implying a higher relative contribution of cytoplasmic components. Yomra was near the origin of the plot, reflecting an intermediate profile without a strong association to any single fraction (Fig 3b).

4. Discussions

Spectral analyses revealed marked fraction-dependent differences among hazelnut genotypes. In the cytoplasmic fraction, the highest absorbance was recorded in Palaz and Sari, whereas Kara exhibited the lowest values; in the wall-bound fraction, Sari and Palaz again showed the highest absorbance, while Kara displayed the lowest; and in the sporopollenin fraction, Sari exhibited the highest absorbance, while Palaz showed the lowest. These findings indicate that genotypes have developed distinct fraction-specific defense strategies against UV-B radiation (Rozema et al., 2001; Llorens et al., 2015).

The sequential extraction of UACs from distinct structural components of pollen revealed a consistent absorption pattern across all hazelnut genotypes: the cytoplasmic

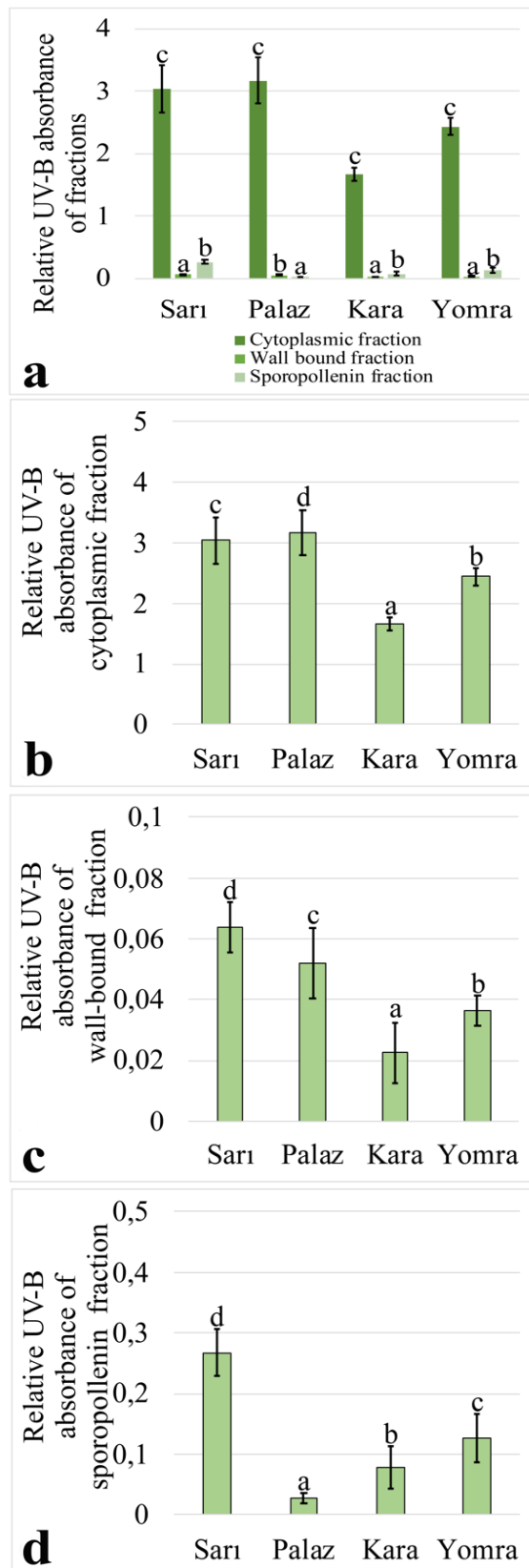


Figure 2. UV-B absorbing compounds' absorbance in pollen grains of four hazelnut genotypes. **a.** Comparison of fractions showing overall differences in UV-B absorbance, **b.** Relative UV-B absorbance of cytoplasmic fraction, **c.** Relative UV-B absorbance of wall-bound fraction, **d.** Relative UV-B absorbance of sporopollenin fraction. Different letters above bars indicate statistically significant differences between groups according to one-way ANOVA ($p < 0.05$).

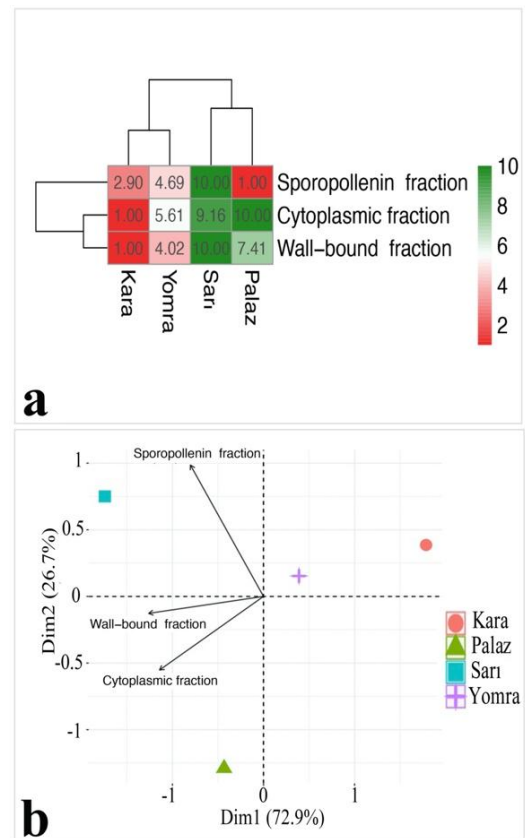


Figure 3. Comparative analysis of UV-B absorbing compound fractions in hazelnut genotypes. **a.** Heat-map showing clustering of genotypes and fractions based on UV-B absorbance values, **b.** PCA biplot illustrating the relationships among genotypes and fractions, with explained variance of Dim1 = 72.9% and PC2 = 26.7%

fraction exhibited the highest UV-B absorbance across all genotypes. The wall-bound fraction generally showed the lowest absorbance, with the exception of Sarı, which displayed higher values than the other genotypes in this fraction. This pattern indicates that the majority of UV-B absorbing metabolites are synthesized and stored in the cytoplasm, where they can actively neutralize ROS generated by UV-B exposure (Musil and Wand, 1994; Fraser et al., 2014). The intermediate absorbance of the sporopollenin fraction suggests a primarily passive but highly durable barrier function, while the low absorbance of the wall-bound fraction implies a limited role in UV attenuation, likely due to lower phenolic content compared to other fractions (Rozema et al., 2001).

Despite the general trend, significant genotype-dependent differences were observed in absorbance levels. For instance, the Palaz genotype showed the greatest absorbance in the cytoplasmic fraction, whereas Sarı stood out with the greatest absorbance in the sporopollenin fraction. In contrast, Kara displayed the lowest absorbance in the cytoplasmic and wall-bound fractions, while Yomra exhibited a more balanced and intermediate absorbance profile across all three fractions. The high cytoplasmic absorbance in Palaz could be explained by higher metabolic activity or upregulation of phenolic biosynthetic pathways in the cytosol (Musil and Wand, 1994; Yadav et al., 2020), enhancing its ability to counteract UV-induced oxidative stress—especially considering that up to 20% of incident UV-B can penetrate the exine and reach the generative cell

(Demchik and Day, 1996). In Sari, the elevated sporopollenin absorbance may reflect a genotype-specific allocation of photoprotective compounds to the outer exine layer, enhancing long-term passive defense during extended pollen exposure (Fraser et al., 2012; Hegedüs et al., 2021). The consistently low absorbance of cytoplasmic and wall-bound fractions in Kara suggests reduced investment in biochemical UV-B defenses, potentially increasing its vulnerability under enhanced UV-B exposure (Llorens et al., 2015). Yomra's intermediate profile may indicate a generalized defense strategy without strong specialization in either active (cytoplasmic) or passive (sporopollenin) mechanisms.

Similar fraction-based absorbance patterns have been reported in other species. Rozema et al. (2001) showed that the wall-bound fraction had the lowest UV-B absorbance in *Helleborus foetidus*, likely due to its relatively low compound content compared to the cytoplasm and sporopollenin. However, the same study also reported that the sporopollenin fraction had the greatest absorbance, while the cytoplasmic fraction was average. This divergence from our findings could be ascribed to species-specific discrepancies in the composition (quantity and kinds of phenolic and related compounds) of sporopollenin (Muthreich et al., 2020). Interestingly, Rozema et al. (2001) later found that in *Betula pendula*—a species from the same family as hazelnut—the cytoplasmic fraction exhibited the highest absorbance, which aligns with our results. This may reflect a shared UV defense strategy within the Betulaceae family. This may point to a family-level evolutionary tendency to prioritize cytoplasmic accumulation of UACs as a primary UV-B defense mechanism.

Sporopollenin, a highly resistant biopolymer located in the outermost layer of the pollen grain, can absorb up to 80% of incident UV-B radiation (Demchik and Day, 1996), making it a key structural component in UV defense. In our study, the sporopollenin fraction consistently exhibited intermediate absorbance levels across genotypes; however, the Sari genotype showed notably high absorbance in this fraction, suggesting genotype-specific variation in the UV-shielding role of sporopollenin. This could be due to higher sporopollenin density or specific compositional traits that favor the retention of UV-absorbing phenolics (Muthreich

et al., 2020). Meanwhile, UAC biosynthesis is known to occur primarily in the cytoplasm (Musil and Wand, 1997), which aligns with our finding that the cytoplasmic fraction displayed the highest UV-B absorbance in all genotypes, particularly in Palaz. This strong absorbance likely reflects both the abundance and activity of UV-absorbing compounds within the cytosol. Such cytoplasmic accumulation is particularly vital, given that up to 20% of UV-B radiation can bypass the outer wall and reach the inner structures of the pollen grain, including the generative cell (Demchik and Day, 1996). Thus, elevated cytoplasmic UAC levels, as observed in certain genotypes, may serve a critical role in safeguarding reproductive viability under UV stress. Such cytoplasmic enrichment is critical because UV-B radiation that bypasses the outer wall can damage the generative cell, directly impairing fertilization success.

Our findings demonstrate that hazelnut genotypes differ significantly in their inherent pollen-based UV-B defense mechanisms. From a breeding perspective, genotypes like Palaz and Sari—with elevated cytoplasmic and sporopollenin absorbance, respectively—may be more resilient in high UV-B environments. Conversely, genotypes like Kara may require protective agronomic measures when cultivated under intense UV conditions. Importantly, this study assessed UAC levels under natural, non-induced conditions, avoiding potential confounding effects of UV-B-induced upregulation and allowing for a clearer comparison of baseline photoprotective capacity across genotypes. By highlighting these inherent differences, our work provides a foundational framework for future studies aiming to identify UV-B-resistant pollen sources, both within hazelnut breeding programs and more broadly across plant species affected by ozone depletion. This approach provides a reliable foundation for selecting UV-B-resistant pollinator sources both in hazelnut breeding programs and in broader plant species affected by ozone depletion.

Conflict of Interest

The authors declare that they have no conflict of interest.

Authors' Contribution

The authors contributed equally.

References

- Blackmore S (2007). Pollen and spores: Microscopic keys to understanding the earth's biodiversity. *Plant Systematics and Evolution* 263:3-12. DOI: <https://doi.org/10.1007/s00606-006-0464-3>
- Demchik SM, Day TA (1996). Effect of enhanced UV-B radiation on pollen quantity, quality, and seed yield in *Brassica rapa* (Brassicaceae). *American Journal of Botany* 83(5):573-579. DOI: <https://doi.org/10.1002/j.1537-2197.1996.tb12741.x>
- Feng H, An L, Tan L, Hou Z, Wang X (2000). Effect of enhanced ultraviolet-B radiation on pollen germination and tube growth of 19 taxa in vitro. *Environmental and Experimental Botany*. 43:45–53. DOI: [https://doi.org/10.1016/S0098-8472\(99\)00042-8](https://doi.org/10.1016/S0098-8472(99)00042-8)
- Fraser WT, Lomax BH, Jardine PE, Gosling WD, Sephton MA (2014) Pollen and spores as a passive monitor of ultraviolet radiation. *Frontiers in Ecology and Evolution*. 2:12. DOI: <https://doi.org/10.3389/fevo.2014.00012>
- Fraser WT, Scott AC, Forbs AES, Glasspool IJ, Plotnick RE, Kenig F, Lomax BH (2012). Evolutionary stasis of sporopollenin biochemistry revealed by unaltered Pennsylvanian spores. *New Phytologist* 196:397–401. <https://doi.org/10.1111/j.1469-8137.2012.04301.x>
- Hegedüs K, Fehér C, Jalsovszky I, Kristóf Z, Rohonczy J, Vass E, Farkas A, Csizmadia T, Friedbacher G, Hantz P (2021). Facile isolation and analysis of sporopollenin exine from bee pollen. *Scientific Reports* 11(1): 1-16. DOI: <https://doi.org/10.1038/s41598-021-87619-8>
- Llorens L, Badenes-Pérez FR, Julkunen-Tiitto R, Zidorn C, Fereres A, Jansen MA (2015) The role of UV-B radiation in plant sexual reproduction. *Perspectives in Plant Ecology, Evolution and Systematics* 17:243–254. DOI: <https://doi.org/10.1016/j.ppees.2015.03.001>

- Musil CF, Wand SJE (1994) Differential stimulation of an arid-environment winter ephemeral *Dimorphotheca pluvialis* (L.) Moench by ultraviolet-B radiation under nutrient limitation. *Plant Cell Environment* 17:245–255. DOI: <https://doi.org/10.1111/j.1365-3040.1994.tb00290.x>
- Muthreich F, Zimmermann B, Birks HJB, Vila-Viçosa CM, Seddon AW (2020) Chemical variations in *Quercus* pollen as a tool for taxonomic identification: Implications for long-term ecological and biogeographical research. *Journal of Biogeography* 47:1298–1309. DOI: <https://doi.org/10.1111/jbi.13817>
- Paradinas A, Ramade L, Mulot-Greffeuille C, Hamidi R, Thomas M, Toillon J (2022). Phenological growth stages of ‘Barcelona’ hazelnut (*Corylus avellana* L.) described using an extended BBCH scale. *Scientia Horticulturae*, 296:110902. DOI: <https://doi.org/10.1016/j.scienta.2022.110902>
- Rozema J, Noordijk AJ, Broekman RA, Van Beem A, Meijkamp BM, De Bakker NVJ, van de Staaij JWM, Stroetenga M, Bohncke SJP, Konert M, Kars S, Peat H, Smith RIL, Convey P (2001). (Poly) phenolic compounds in pollen and spores of Antarctic plants as indicators of solar UV-B—A new proxy for the reconstruction of past solar UV-B?. *Plant Ecology* 154(1):9–26. DOI: https://doi.org/10.1007/978-94-017-2892-8_2
- Ruhland CT, Day TA (2000). Effects of ultraviolet-B radiation on leaf elongation, production and phenylpropanoid concentrations of *Deschampsia antarctica* and *Colobanthus quitensis* in Antarctica. *Physiologia Plantarum* 109:244–251. DOI: <https://doi.org/10.1034/j.1399-3054.2000.100304.x>
- Seddon AW, Festi D, Robson TM, Zimmermann B (2019). Fossil pollen and spores as a tool for reconstructing ancient solar-ultraviolet irradiance received by plants: An assessment of prospects and challenges using proxy-system modelling. *Photochemical & Photobiological Sciences* 18:275–294. DOI: <https://doi.org/10.1039/C8PP00490K>
- Sugioka N, Kawakami M, Hirai N, Osakabe M (2018). A pollen diet confers ultraviolet-B resistance in phytoseiid mites by providing antioxidants. *Frontiers in Ecology and Evolution* 6:133. DOI: <https://doi.org/10.3389/fevo.2018.00133>
- Yadav A, Singh D, Lingwan M, Yadukrishnan P, Masakapalli SK, Datta S (2020). Light signaling and UV-B-mediated plant growth regulation. *Journal of Integrative Plant Biology* 62(9):1270–1292. DOI: <https://doi.org/10.1111/jipb.12932>