

Article

The Effect of Alternative Nutrient Supplements on Histological Traits and Postharvest Water Loss in Pepper Fruit

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Abstract

Postharvest water loss critically determines the shelf life and quality of pepper fruits. This study investigated how three alternative soil amendments—rhyolite tuff (RT), composted and pelletized poultry litter (CPPL), and clarifying agent (CA)—affect water loss, structural traits, and their interrelationships across three ripening stages (immature, mature, and overripe) in the Hungarian wax pepper cultivar ‘Tizenegyes’. A completely randomized design (CRD) was applied in a small-plot field experiment. Macro- and micromorphometrical analyses included pericarp, cuticle, epidermis, collenchyma, hypodermis, parenchyma, and endocarp thickness; fruit fresh weight; surface area; and the surface area-to-weight ratio (SA/W). Daily weight measurements were used to quantify water loss, while cuticle function was assessed by comparing wax-removed and intact fruits. The water loss rate (WLR) was strongly influenced by pericarp tissue structure—particularly cuticle thickness, hypodermal cell layer number and thickness, and collenchyma cell wall thickness—as well as fruit size at ripening stage. Among treatments, RT was the most effective in reducing postharvest water loss and extending fruit shelf life. Fruits from the control plots lost 26% more water than RT samples, 12.8% more than CPPL, and 14.2% more than CA. Although RT-treated fruits were smaller, they had thicker pericarp and hypodermis layers, more collenchymatous cell rows, and thicker cell walls, all of which contributed to lower water loss and prolonged freshness. These findings highlight RT as a promising alternative nutrient source for sustainable pepper production, with significant potential to improve postharvest quality.

Keywords: alternative soil amendments; *Capsicum annuum*; cuticle thickness; pericarp micromorphometry; postharvest water loss; rhyolite tuff; shelf life



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1. Introduction

The genus *Capsicum* includes 37 species, of which five (*C. baccatum* L., *C. frutescens* L., *C. pubescens*, *C. chinense* Jacq., and *C. annuum* L.) are domesticated and widely cultivated, with an annual global consumption of about 36 million tons [1,2]. These species are economically and nutritionally important, showing broad variation in fruit traits such as size, weight, shape, color, pericarp thickness, flavor, and pungency.

Pepper fruits (*Capsicum* spp.) are covered by a thick cuticle that limits water loss, regulates gas and water exchange, and protects against pathogens, thereby influencing postharvest shelf life [3–6]. Cuticle properties and dynamics are economically significant, as

water loss and decay during harvest, storage, retail display, or in the consumer's household cause substantial fruit losses [4].

Cuticle thickness, composition, and wax content vary considerably among cultivars [7–12]. The main wax components are fatty acids, primary alcohols, n-alkanes, triterpenoids, and sterols [12], with water loss reduction depending more on very-long-chain fatty acid derivatives rather than total wax content [12–14]. Genetic and developmental factors regulate cuticle structure, which in turn affects water loss and shelf life [6,15–17].

Water loss is a major postharvest problem in peppers, strongly influenced by storage conditions, including relative humidity, ventilation, packaging, storage duration, and temperature. O'Donoghue et al. [18] highlighted fruit size, hollow structure, and pericarp water content as key drivers of susceptibility. Even small water losses rapidly reduce pericarp turgor, leading to softening, quality deterioration, and reduced shelf life. Typically, peppers lose approximately 5% their fresh mass within 6–9 days of storage [17,19].

There are numerous solutions to minimizing water loss in peppers after harvest and extending their storage life. Several of these focus on preventing excessive water loss by optimizing storage conditions: maintaining high relative humidity and low storage temperature reduces fruit transpiration [17,18]; plastic packaging provides an effective physical barrier against water loss [18]; and hot water treatment combined with scrubbing smooths out irregularities in the fruit cuticle, thereby reducing evaporation through microcracks [20]. The application of shrink-wrap technology in combination with corrugated fiberboard boxes also helps maintain optimal relative humidity inside the packaging, delaying fruit senescence and minimizing water loss [21]. Edible coatings such as chitosan, gelatin, and layer-by-layer (LbL) chitosan–gelatin composites can also be effective in reducing water loss in pepper fruits [22]. These coatings improve the physical appearance of freshly harvested fruits and create a protective barrier against respiration and water loss. Moreover, the deterioration of pepper fruit quality after harvest can be mitigated by the combined application of salicylic acid (SA) spraying and caraway (*Carum carvi*) oil coating [23].

Given that fruit water loss is a major concern for the postharvest shelf life of peppers intended for the fresh market, studies aimed at developing cultivars with reduced water loss have gained increasing importance [24]. Breeding programs focus on identifying lines and hybrids with genetically thicker cuticles to enhance shelf life through greater genetic variability. These programs also aim to create new segregating populations from crosses between low-water-loss lines [25].

Although the cuticle is the primary barrier to water loss [15,17,26], cultivar differences are also linked to fruit shape, surface area, pericarp thickness, cuticle thickness, and the presence of microcracks [27–30]. Water loss may occur through stomata on the calyx and pedicel [15,17,29,31]. The stage of maturity further influences dehydration: overripe fruits generally lose water faster due to weakened cell wall adhesion, while immature fruits may also lose water rapidly because of their higher pericarp water content [17,28,29,31,32].

Nutrient supply significantly affects pericarp anatomy, fruit size, and weight, thereby altering postharvest water loss [33–37]. Calcium, for example, enhances firmness, reduces respiration, and delays senescence [38,39], while nutrient deficiencies increase storage weight loss [40].

Current agricultural systems remain yield-oriented, but organic farming is gaining importance due to consumer demand for healthy food [41]. Since synthetic fertilizers are prohibited, alternative nutrient sources are needed to ensure high-quality fruits with extended shelf life [42–45]. Naturally derived amendments and food industry by-products offer sustainable options, improving soil fertility, structure, and water management while reducing chemical inputs [46].

Among these, rhyolite tuff (RT), composted and pelletized poultry litter (CPPL), and clarifying agent (CA) have shown positive effects on soil and crop performance. Rhyolite tuff improves soil fertility, aeration, water management, and fruit quality [47–54]. Composted and pelletized poultry litter enhances soil properties and crop yield, with a reported yield increase of 5–20% depending on dosage [55–59]. Food industry by-product, such as bentonite-based clarifying agents, also improve soil nutrient status, water retention, microbial activity, and drought tolerance, while enhancing fruit quality traits [60–70].

Based on this background, the objectives of this experiment were to: (i) analyze, through histological measures—CPPL, CA, and RT—the thickness of the pepper pericarp, cuticle, and hypodermal layer; (ii) determine how these amendments influence fruit tissue structure at different ripening stages, thereby affecting water loss and shelf life; and (iii) identify the most suitable alternative nutrient source for organic farming that improves soil condition and nutrient availability without causing environmental pollution, while exerting the greatest positive effect on the aesthetic quality, storability, and market shelf life of peppers.

2. Materials and Methods

2.1. Experiment Site Description

A one-year open-field small-plot experiment was conducted in 2023 with the Hungarian sweet wax pepper cultivar ‘Tizenegyes’. The research site was located in the Demonstration Garden of the University of Nyíregyháza (47.9737° N, 21.7089° E), Nyíregyháza, Szabolcs-Szatmár-Bereg County, Hungary. The site is located in the Loess-Nyírség microregion, which forms part of the Nyírség mesoregion, the Great Hungarian Plain (Alföld) macroregion, and the Danube–Tisza Basin as a major landscape unit. The area is characterized as a slightly undulating loess alluvial fan plain. Climatically, it belongs to the moderately warm and dry zone of Hungary [71]. The mean annual temperature ranges between 9 and 11 °C, while the mean annual precipitation ranges from 500 to 700 mm [72]. Meteorological data (average temperature in °C and monthly total precipitation in mm) are shown in Table 1. In 2023, the experimental year, the average temperature during the growing season was higher, while the monthly total precipitation was lower than the long-term average for the May–October period.

Table 1. Meteorological data (average temperature in °C and monthly total precipitation in mm) for 2023 and multi-year average (Nyíregyháza, Hungary).

Year	Data	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
MYA	Temperature	−2.4	−0.1	4.6	10.7	15.9	19.0	20.6	19.8	15.5	9.9	4.2	−0.4	9.77
2023	(°C)	4.4	2.6	7	9.8	16.5	19.7	22.4	22.8	19.5	13.7	5.8	2.6	12.23
MYA	Precipitation	29.5	30	30	39.5	54	76	66.5	65	43	44	46.5	40.5	564.5
2023	(mm)	65.9	8.5	48.7	46.4	47.8	99.4	53.6	59.1	37.5	61.3	122.5	65.1	715.8

Meteorological data for 2023 were obtained from the Research Institute of Nyíregyháza (Institutes for Agricultural Research and Educational Farm of the University of Debrecen). The multi-year average data (MYA: 1870–2002) were collected by Kormány [73].

During the growing season (May–October), the average temperature was 19.1 °C, exceeding the long-term average by 2.32 °C. As pepper is a heat-demanding crop, its optimal daily cultivation temperature ranges between 18 and 32 °C [74]. Therefore, the rising average monthly temperatures during the growing season—currently characteristic of Hungary’s climate—do not adversely affect its cultivation potential in the country. The total precipitation recorded during the May–October period of the study year was 358.7 mm. However, rainfall distribution was uneven: while June was particularly wet (99.4 mm), the period from July to September was characterized by moderate rainfall (37.5 to 59.1 mm).

Given that the water requirement of pepper is approximately 500–600 mm [74], the remaining 150–200 mm was supplemented during dry periods using a drip irrigation system.

The predominant soil types in the Nyírség area are acidic sandy soils, sandy loam texture, and genetically brown forest soils. In April 2023, before the soil treatments, the basic characteristics of the experimental area's soil at a depth of 0–30 cm were as follows: sandy loam texture; pH-KCl: 7.09; total salt ($\text{m m}^{-1}\%$): <0.02 ; CaCO_3 ($\text{m m}^{-1}\%$): <0.1 ; humus ($\text{m m}^{-1}\%$): 2.85%; $\text{NO}_2\text{-N-NO}_3\text{-N}$: 15.29; SO_4^{2-} : 603.4; P_2O_5 : 603.4, K_2O : 365.65, Na: 28.02; Mg: 147.7; Cu: 2.02, Mn: 43.25, and Zn: 6.34 mg kg^{-1} . Analyses were performed in accordance with Hungarian Standard MSZ-08-0210:1977, MSZ-08-0206-2:1978, MSZ-08-0458:1980, and Standard MSZ 20135:1999 [75–78].

2.2. Plant Material

For the experimental setup, the white-fleshed Hungarian wax pepper cultivar 'Tizenegyes' was used. The seeds were supplied by Rédei Kertmag Seed Trading Co. (H-2886 Réde, Lesalja major, Hungary).

This cultivar is characterized by determinate growth, rapid development, and high yield potential. Plants reach an average height of approximately 25–30 cm. It is suitable for cultivation both under protected conditions (greenhouse forcing) and in open fields, including direct sowing. The berry fruits have an average mass of 60–80 g. The 'Tizenegyes' cultivar is prone to over-setting, which may result in reduced fruit size; no fruit thinning was carried out during the experiment. The fruits have a pendant orientation, a conical shape, and white, sweet flesh. The cultivar exhibits good tolerance to low-light conditions and is notable for its dark green foliage. It shows tolerance to *Xanthomonas* spp. and resistance to common strains of tobacco mosaic virus (TMV) [79]. 'Tizenegyes' was officially registered as a recognized cultivar on 10 May 1986, and its variety maintenance is carried out by the ZKI Vegetable Crops Research Institute Co. (H-6000 Kecskemét, Mészöly Str. 6., Hungary).

In the 'Tizenegyes' cultivar, approximately 76 days elapse from sowing to fruit set of about 2 cm in size, followed by an additional 25 days to reach commercial maturity. According to Zatykó [74], a further 25 days are required from commercial maturity to reach physiological maturity.

Immature fruits—characterized by soft flesh consistency and a dull skin color—are not considered marketable, although they may appear on the market as lower-priced produce. In this stage, the pepper fruit is green, with a thin pericarp, and the berries are small and less firm. The rate of postharvest water loss is high. From a marketability perspective, correct harvest timing is crucial. Hungarian wax pepper cultivars intended for stuffing ('TV' types) are harvested at the commercial maturity stage (mature), which best meets market expectations. At this stage, the fruit reaches the typical varietal size; has firm flesh, a glossy surface, and a creamy-yellow color; and can be easily detached from the pedicel. The pericarp is thick, water loss is moderate, and the shelf life is relatively long.

Overripe fruits are orange or reddish, corresponding to the physiological maturity stage. The fruit begins to wrinkle slightly, the flesh softens, and storability decreases, accompanied by accelerated postharvest moisture loss.

2.3. Experimental Design

Vegetable pepper seedlings were sown on 24 March 2023 in the double-walled, heated Rishel greenhouse of the University of Nyíregyháza. The seedlings were transplanted on 26 May 2023 to the Experimental and Research Farm of University of Nyíregyháza. Prior to transplanting, on 4 May 2023, three different soil conditioners were applied to three plots each (excluding the three control plots): rhyolite tuff (RT), composted and pelletized poultry litter (CPPL), and clarifying agent (CA).

The one-factor open-field small-plot experiment was set up in a completely randomized design (CRD) with control (C) and three treatments (RT, CPPL, and CA) in three replications, totaling 12 small plots. Each plot measured 1 m × 10 m and was separated by 0.9 m between replications. Pepper seedlings were transplanted at an in-row spacing of 30 cm, with 30 plants each (Figure 1).

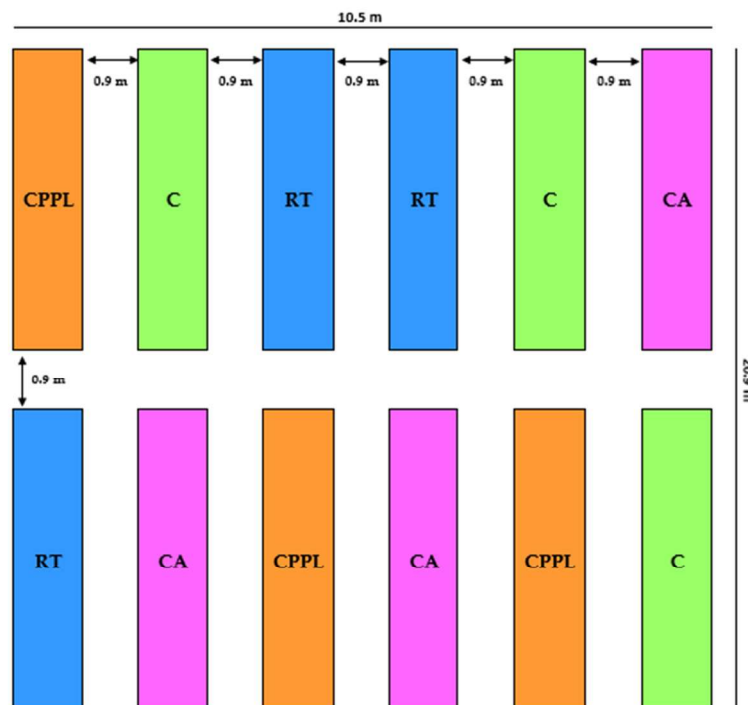


Figure 1. Scheme of completely randomized design (CRD) experiment with the Hungarian wax pepper cultivar ‘Tizenegyes’ and soil treatments in 2023 (Nyíregyháza, Hungary). C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent.

The RT was produced by Colas-Északkő Bányászati Ltd. (Tarcál, Hungary) and applied to the topsoil at a rate of 20 t ha⁻¹. Rhyolite tuff is classified as a volcanic tuff and is mined at several locations across Hungary. Previous experiments [50,80] have demonstrated its beneficial effects of improving the physical and chemical properties of soil, as well as its positive impact on crop yield and quality. Rhyolite tuff is rich in macronutrients such as potassium, calcium, and magnesium, and also contains essential micronutrients including zinc and iron, while being free of toxic elements [50,80]. The basic physical and chemical characteristics of the applied RT were as follows: pH-H₂O: 6.91; pH-KCl: 6.07; electrical conductivity: 306 (μS cm⁻¹); organic matter (m m⁻¹): 0.53%; NO₂-N–NO₃-N: 22.8; SO₄²⁻: 71.2; P₂O₅: 12.8, K₂O: 139, Na: 68.9; Mg: 149; Cu: <0.5, Mn: 16.1, Ca: 1138; Fe: 16.2, and Zn: 0.48 mg kg⁻¹. Analyses were performed in accordance with Hungarian Standard MSZ-08-0210:1977, MSZ-08-0206-2:1978, MSZ-08-0458:1980, and Standard MSZ 20135:1999 [75–78].

The CPPL, marketed under the name *BioFer Natur*, was produced and distributed by Baromfi-Coop Ltd. (a Hungarian poultry farming company; Nyírájkó, Hungary). The CPPL used in this study was composted in a Hosoya composting system facility, using 53% deep litter from broiler and laying hen farms (consisting of heat-treated and ground straw bedding with low moisture content due to the high absorption capacity of straw pellets), 27% manure from broiler and laying hen farms, and 20% filtered wastewater sludge from slaughterhouses and hatcheries (chicken meal: meat and bone meal) [46]. The topsoil was treated with composted and pelletized poultry litter at a rate of 2 t ha⁻¹. Among the

numerous advantages of CPPL, it is worth highlighting that the nitrogen forms it contains are readily available to plants, and neither its production nor its use contribute to air or environmental pollution [81]. Another advantage is that CPPL, as an alternative fertilizer, provides organic components, has a high microelement content, improves soil fertility, structure, and organic matter content, and positively affects soil and water management properties [46]. Chemical analysis confirmed that this soil conditioner is rich in calcium (Ca; 59,295 mg kg⁻¹ d.m.), phosphorus (P₂O₅; 12,605 mg kg⁻¹ d.m.), potassium (K₂O; 26,221 mg kg⁻¹ d.m.), and magnesium (Mg; 2741 mg kg⁻¹ d.m.). Basic characteristics of the CPPL were the followings: pH-H₂O: 6.82; pH-KCl: 6.75; electrical conductivity: 12.3 (μS cm⁻¹); organic matter (m m⁻¹%): 72%; NO₂-N–NO₃-N: 11.8; SO₄²⁻: 16,468; Na: 3445; Cu: 43.3, Mn: 276, Fe: 265, and Zn: 323 mg kg⁻¹.

The CA was a saturated by-product with a high organic matter content, originating from the production of clear apple juice and containing bentonite and activated carbon. This material was provided by an apple juice manufacturing company operating in Szabolcs-Szatmár-Bereg County, Hungary, which requested anonymity. The applied amount of CA was 20 t ha⁻¹. The basic characteristics of the applied CA were as follows: pH-H₂O: 6.14; pH-KCl: 4.55; electrical conductivity: 381 (μS cm⁻¹); organic matter (m m⁻¹%): 89.7%; NO₂-N–NO₃-N: 2.69; SO₄²⁻: 307; P₂O₅: 497, K₂O: 673, Na: 235; Mg: 80.9; Cu: 3.9, Mn: <1, Ca:413; Fe:20.9, and Zn: <0.4 mg kg⁻¹.

The incorporated soil conditioners were worked into the top 30–40 cm of soil using an “Oleo Mac” petrol-powered rotary tiller.

Plants were irrigated using Aqua-Traxx soft-walled drip tape with a 30 cm emitter spacing, providing a discharge rate of 1.14 L h⁻¹ per emitter [82]. From early June to the end of September, irrigation was carried out once a week. The irrigation dose (amount of water applied per event) was approximately 13–17 mm, achieved through 3–4 h of irrigation per session. The total irrigation volume over the entire growing season amounted to approximately 200–280 mm.

No plant protection treatments were applied, either during the seedling phase or after transplanting to the open field.

2.4. Soil Sampling and Analysis

Initial soil sampling of the experimental plots was conducted on 2 May 2023. Three samples per plot were taken from a depth of 30 cm using a standard gouge auger (Royal Eikelkamp, Giesbeek, The Netherlands). Approximately 1.2–1.5 kg of mixed composite soil per plot was collected. All soil sampling was done in three replicates per treatment. After sampling, all soil samples were homogenized and spread in a thin layer. Following 21 days of drying at room temperature, the air-dried samples were passed through a 2 mm sieve.

Soil elemental content was determined according to Hungarian Standards MSZ-08-0210:1977, MSZ-08-0206-2:1978, MSZ-08-0458:1980, and Standard MSZ 20135:1999 [75–78]. For macro- and micronutrient analysis, 2 g of soil was weighed on an analytical balance (Ohaus® Pioneer® analytical balance, Model PX124M, Ohaus Corporation, Parsippany, NJ, USA), and 5 mL of concentrated hydrochloric acid, along with 2 mL of 30% hydrogen peroxide were added. Digestion was performed at 130 °C for 1.5 h using a Kjeldatherm Digester (C. Gerhardt GmbH & Co. KG, Königswinter, Germany). After cooling, the digested samples were filtered through Whatman no. 42 filter paper (Cytiva bioscience holding limited, Little Chalfont, Buckinghamshire, UK) and diluted to a final volume of 50 mL. Elemental analysis of soil and plant samples was conducted using a Perkin Elmer Optima PinAAcle 500 Atomic Absorption Spectrometer (PerkinElmer Company, Waltham, MA, USA) for Mg (KCl-soluble), K₂O (AL-soluble), Na (AL-soluble), Zn (EDTA-soluble), Cu (EDTA-soluble), and Mn (EDTA-soluble). PG Instruments T600 Spectrophotometer (PG

Instruments Ltd., Lutterworth, UK) was used for humus content and SO_4^{2-} (KCl-soluble), and MLE FIA Compact Analyzer (Medizin- und Labortechnik Engineering GmbH Dresden, Radebeul, Germany) for $\text{NO}_2\text{-N}$ and $\text{NO}_3\text{-N}$ (KCl-soluble), and P_2O_5 (AL-soluble). All measurements were performed in triplicate.

2.5. Samplings for Macromorphological and Micromorphometric Analyses of Fruits

Fruits for macromorphological and micromorphometric analyses were collected on 4 September 2023. Fruit fresh mass (hereafter referred to as fruit weight) was measured using an Ohaus[®] Pioneer[®] analytical balance (Model PX124M, Ohaus Corporation, Parsippany, NJ, USA), and fruit length, fruit diameter, and pericarp thickness were measured with a Scienceware[®] Digi-Max[™] slide caliper (SP Bel-Art, Wayne, NJ, USA).

For micromorphometric analysis, fruits were sampled from all treatments (C, RT, CPPL, and CA), three replications, and three ripening stages (unripe, ripe, and overripe), with two fruits per plant. Transverse hand sections were prepared from the basal, central, and apical thirds using razor blades. Measured parameters included: exocarp (cuticle, epidermis) thickness; hypoderma thickness (epidermis, lamellar collenchyma, and angular collenchyma layers); collenchyma cell walls thickness; number of cell rows in the hypoderma; mesocarp/parenchyma thickness; and endocarp (giant cells, inner epidermis) thickness. Measurements (10 per cross-section per sample) were taken without staining using an Olympus BX51-type light microscope (Olympus BioSystems, Munich, Germany) at 10×10 , 10×20 , and 10×40 magnifications. Images were captured with a VSI RZ302 3M CMOS camera (Beijing BestScope Technology Co., Beijing, China) and analyzed using VSI RZ302 software. In total, 1080 measurements were recorded for cuticle thickness and 360 for each of the other parameters, and mean values were used for statistical analyses.

2.6. Measurement of Water Loss Rate of Fruit

Fruits were collected from each treated plot at three ripening stages: immature (13 July 2023), commercially mature (20 July 2023), and physiologically mature (15 August 2023). After harvest, fruits were stored under laboratory conditions ($\sim 22^\circ\text{C}$, 65–70% RH) for 14 days. Fruit weight was recorded daily using an Ohaus[®] Pioneer[®] analytical balance (Model PX124M, Ohaus Corporation, Parsippany, NJ, USA). To minimize water loss through the pedicel and calyx, both structures were coated with petroleum jelly [29].

The pepper fruit was modeled as a cone. Knowing the fruit length and the diameter of its basal end, the surface area was calculated using the formula for the surface area of the cone (cm^2):

$$A = \pi \times r \times s,$$

where r is the radius of the base and s is the slant height.

From the day of harvest, the mass of individual fruits from each treatment (three per treatment per replicate) was measured daily for 14 days. All values were expressed relative to the mass on day 0. The percentage of water loss (WL) on each day was calculated as:

$$\text{WL} = W_n / W_0 \times 100$$

where n is the measurement day ($n = 14$).

Daily water loss percentages (WLR) were calculated as the difference in WL between consecutive days, according to the method of Díaz-Pérez et al. [17] and Albert et al. [29]. The total WLR was obtained as the cumulative sum of daily WLR values:

$$\text{WLR} = \sum_{n=0}^n \text{WLR}_n$$

Cuticle function was assessed using a modified method of Albert [83], substituting hexane for chloroform. Fruits from all treatments (C, RT, CPPL, and CA) and maturity stage of the “Tizenegyes” variety were weighed; half ($n = 6$) were immersed in 99% hexane for 60 s to remove the cuticular wax layer (treated fruits), while the remainder were left intact (untreated fruits). Pedicels and calyces were coated with petroleum jelly to prevent water loss through these structures. In treated fruits, this occurred only through the cuticle-free wall; in untreated fruits, it occurred through the intact cuticle.

Fruit mass was recorded daily for 14 days using an Ohaus[®] Pioneer[®] analytical balance (Model PX124M, Ohaus Corporation, Parsippany, NJ, USA).

Water loss (%) was calculated relative to initial mass (day 0) for each treatment and maturity stage.

2.7. Statistical Analysis

Normality of the data was tested using the Shapiro–Wilk test (IBM SPSS Statistics 26.0 software, IBM Corp., Armonk, NY, USA). The data on soil nutrient concentrations and the macro- and micromorphometric parameters of the pepper pericarp were normally distributed. Pearson’s correlation coefficients (r) were calculated to assess the relationships between the different soil conditioner treatments, maturity stage, and macro- and micromorphometric parameters, and the water loss rate (WLR) in pepper fruits, using IBM SPSS Statistics 26.0. Further analyses of the experimental data were conducted using analysis of variance (ANOVA), followed by post hoc comparisons with Tukey’s *b*-test (IBM SPSS Statistics 26.0), with a significance level of $p < 0.05$. Lowercase letters (a, b, c, and d) in the manuscript indicate statistically significant differences.

3. Results

3.1. Microanatomical Structure of the Fruit Pericarp in the Hungarian Wax Pepper Cultivar ‘Tizenegyes’

A general anatomical examination of the pericarp of the Hungarian wax pepper cultivar ‘Tizenegyes’ revealed the following structural features. The exocarp consists of two distinct layers: an outer cuticular layer, and a single-cell-thick epidermis located beneath it (Figure 2). The outer tangential cell walls of the epidermal cells are noticeably thicker than the other walls.

The mesocarp is composed of a 5-to-7-cell-layer-thick collenchyma zone located directly below the epidermis. The outer portion of this zone is formed by lamellar collenchyma, while the inner portion consists of angular collenchyma. Together, the epidermis and the collenchyma layers form the hypoderma. Beneath this zone lies parenchymatous tissue composed of thin-walled, large-lumen cells containing large nuclei. In overripe fruits, both collenchyma and parenchyma cells typically contain numerous chromoplasts of various colors (orange and red) within their protoplasts. Vascular bundles are embedded within the parenchymatous layers and contain tracheary elements with annular and spiral secondary wall thickenings. The parenchyma cells are loosely arranged and generally uniform in size.

The endocarp consists of two distinct layers. The layer adjacent to the mesocarp is composed of significantly enlarged cells, appearing as giant cells. The inner layer of the endocarp (inner epidermis), which covers the seed cavity of fruit, is a single cell layer with heavily thickened cell walls, substantially thicker than those of the epidermal layer covering the outer fruit surface.

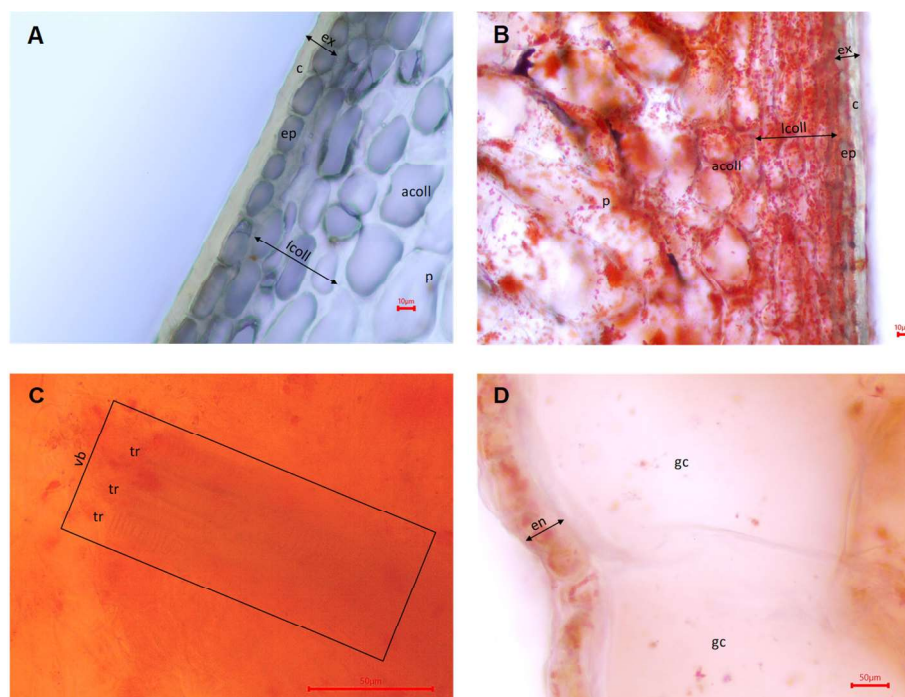


Figure 2. Transverse section of fruit pericarp anatomy in Hungarian wax pepper cultivar ‘Tizenegyes’. (A,B) Pericarp transverse sections showing the hypodermis (exocarp (cuticle and epidermis) and collenchyma) (20×, 10×)—ripe fruit/overripe fruit, (C) parenchyma and vascular bundle (40×)—overripe fruit, (D) giant cells and single-layer endocarp (20×)—overripe fruit. ex: exocarp, c: cuticle, ep: epidermis, lcoll: lamellar collenchyma, acoll: angular collenchyma, p: parenchyma, vb: vascular bundle, tr: tracheid, gc: giant cell, en: endocarp. Scale bars: (A) 10 μm, (B) 10 μm, (C) 50 μm, (D) 50 μm.

3.2. Ripening Stage and Treatment-Dependent Changes in the Fruit Pericarp Microanatomy of the ‘Tizenegyes’ Pepper Cultivar

3.2.1. Effects of Ripening Stage on the Characteristics of the Fruit Pericarp

The main structural characteristics of the fruit pericarp differed both among the ripening stages and between fruits from different treatments. In samples from the control plot, the exocarp was significantly thickest in fruits at the mature stage ($28.97 \pm 0.67 \mu\text{m}$), 9.2% thicker compared to immature fruits ($26.52 \pm 0.64 \mu\text{m}$) and 1.2% thicker than in overripe fruits ($28.6 \pm 1.3 \mu\text{m}$). The most pronounced significant difference was observed in the epidermal layer: immature fruits had a significantly thinner epidermis, whereas the epidermis of mature and overripe fruits was significantly thicker (11% thicker in mature fruits and 6% thicker in overripe fruits compared to immature ones). The thickest epidermal layer occurred in fruits at the mature stage. No statistically significant differences were found in cuticle thickness among ripening stages, although the cuticle was 6.2% thicker in mature fruits and 10.2% thicker in overripe fruits than in immature ones (Table 2).

Regarding mesocarp thickness, fruits at the mature stage had a significantly thicker mesocarp ($4568.45 \pm 391.3 \mu\text{m}$), 8.7% thicker than in immature fruits ($4202.36 \pm 411.3 \mu\text{m}$) and 27.2% thicker than in overripe fruits ($3592.15 \pm 352 \mu\text{m}$). The mesocarp of immature fruits was 16.9% thicker than that of overripe fruits. The collenchyma layer, which forms part of the mesocarp, was also significantly thickest in mature fruits ($58.23 \pm 6.18 \mu\text{m}$), while its thickness in immature fruits ($51.98 \pm 5.05 \mu\text{m}$) was significantly greater than in overripe ones ($41.87 \pm 5.54 \mu\text{m}$). The collenchyma cell walls were likewise significantly thickest in mature fruits.

Table 2. Microanatomical characteristics of the fruit pericarp of the Hungarian wax pepper cultivar ‘Tizenegyés’ at different ripening stages.

		C		
		Immature Fruit	Mature Fruit	Overripe Fruit
exocarp	Cuticle (μm)	11.51 \pm 1.09a	12.32 \pm 1.01a	12.68 \pm 2.33a
	Epidermis (μm)	15.01 \pm 0.2a	16.65 \pm 0.28c	15.92 \pm 0.14b
mesocarp	Collenchyma thickness (μm)	51.98 \pm 5.05b	58.23 \pm 6.18c	41.87 \pm 5.54a
	Collenchyma cell walls (μm)	4.19 \pm 1.02a	5.18 \pm 1.14b	4.09 \pm 1.02a
endocarp	Parenchyma (μm)	4150.38 \pm 420.5b	4510.22 \pm 400.26c	3550.28 \pm 370.21a
	Giant cells (μm)	343.28 \pm 69.18a	408.09 \pm 65.95b	352.56 \pm 59.87a
	Inner epidermis (μm)	36.77 \pm 4.92a	50.04 \pm 5.12b	38.02 \pm 4.32a
		RT		
		Immature fruit	Mature fruit	Overripe fruit
exocarp	Cuticle (μm)	10.67 \pm 1.15a	10.61 \pm 1.27a	12.18 \pm 1.59b
	Epidermis (μm)	13.87 \pm 2.04a	14.38 \pm 1.75a	16.08 \pm 1.82b
mesocarp	Collenchyma thickness (μm)	72.38 \pm 2.09c	63.62 \pm 1.71b	26.44 \pm 4.55a
	Collenchyma cell walls (μm)	6.47 \pm 1.08c	5.27 \pm 1.02b	3.89 \pm 0.98a
endocarp	Parenchyma (μm)	5040 \pm 730ab	5300 \pm 730b	4500 \pm 190a
	Giant cells (μm)	367.87 \pm 37.86a	459.87 \pm 67.98b	382.12 \pm 58.99a
	Inner epidermis (μm)	40.67 \pm 5.02a	54.98 \pm 4.67b	42.12 \pm 3.98a
		CPPL		
		Immature fruit	Mature fruit	Overripe fruit
exocarp	Cuticle (μm)	11.34 \pm 1.89a	12.52 \pm 1.08b	10.39 \pm 1.15a
	Epidermis (μm)	9.58 \pm 1.98b	8.46 \pm 0.97a	8.79 \pm 0.76ab
mesocarp	Collenchyma thickness (μm)	68.51 \pm 3.89c	45.59 \pm 6.48b	35.21 \pm 5.32a
	Collenchyma cell walls (μm)	5.18 \pm 1.12b	4.23 \pm 0.98a	3.99 \pm 0.87a
endocarp	Parenchyma (μm)	4000 \pm 770a	4840 \pm 480b	3970 \pm 141a
	Giant cells (μm)	332.17 \pm 24.13a	354.18 \pm 42.68a	312.98 \pm 22.89a
	Inner epidermis (μm)	42.12 \pm 3.89a	54.68 \pm 4.36b	46.89 \pm 4.42a
		CA		
		Immature fruit	Mature fruit	Overripe fruit
exocarp	Cuticle (μm)	11.46 \pm 1.23ab	12.20 \pm 1.95b	11.05 \pm 0.81a
	Epidermis (μm)	11.34 \pm 1.02b	12.12 \pm 1.12b	10.02 \pm 0.78a
mesocarp	Collenchyma thickness (μm)	71.4 \pm 6.72c	37.75 \pm 3.83b	29.67 \pm 3.59a
	Collenchyma cell walls (μm)	4.89 \pm 0.97b	3.89 \pm 0.56a	3.04 \pm 0.71a
endocarp	Parenchyma (μm)	4220 \pm 950b	4390 \pm 70b	3380 \pm 440a
	Giant cells (μm)	372.01 \pm 12.54b	381.11 \pm 42.32b	314.67 \pm 23.11a
	Inner epidermis (μm)	33.56 \pm 3.23b	36.98 \pm 3.36b	30.06 \pm 2.24a

C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. Data are means of three replications. ANOVA followed by Tukey's b-test. Means within a row followed by the same lowercase letters are not statistically different at $p < 0.05$.

The thickness of the endocarp, especially the inner epidermis and the giant cell layers, showed a similar pattern. In mature fruits, both the inner epidermis (408.09 \pm 65.95 μm) and the giant cell layers (50.04 \pm 5.12 μm) were significantly thicker than in immature fruits (343.28 \pm 69.18 μm and 36.77 \pm 4.92 μm , respectively) and overripe fruits (352.56 \pm 59.87 μm and 38.02 \pm 4.32 μm , respectively). In mature fruits, this endocarp region was 20.5% thicker (458.13 \pm 62.32 μm) than in immature fruits (380.05 \pm 62.18 μm) and 17.3% thicker than in overripe fruits (390.58 \pm 57.18 μm). During over-ripening, endocarp thickness decreased, approaching the values observed in immature fruits; in fact, overripe fruits had an endocarp only 2.8% thicker than that of immature fruits.

3.2.2. Effects of Treatments on the Characteristics of the Fruit Pericarp

The soil conditioners applied during the experiment affected the structural parameters of the pericarp layers in different ways. In fruits from the plot treated with rhyolite tuff (RT), the exocarp thickness in overripe fruits ($28.26 \pm 1.21 \mu\text{m}$) was significantly greater than in both immature ($24.54 \pm 1.18 \mu\text{m}$) and mature fruits ($24.99 \pm 1.08 \mu\text{m}$). Specifically, the exocarp in overripe fruits was 13% thicker than in mature fruits and 15% thicker than in immature fruits. Overripe fruits also had significantly thicker cuticle and epidermis layers than both immature and mature fruits. However, no statistically significant differences in these parameters were observed between immature and mature fruits (Table 2).

Regarding the development of mesocarp tissue thickness, immature fruits had a significantly thicker collenchyma layer ($72.38 \pm 2.09 \mu\text{m}$) than fruits at other ripening stages—13.8% thicker than in mature fruits ($63.62 \pm 1.71 \mu\text{m}$) and 173% thicker than in overripe fruits ($26.44 \pm 4.55 \mu\text{m}$). Mature fruits, in turn, had a collenchyma layer that was 140% thicker than that of overripe fruits. The thickest collenchyma cell walls were also observed in immature fruits.

The extent of the parenchymatous tissue in the pericarp was significantly greater in mature fruits ($5300 \pm 730 \mu\text{m}$) than in overripe fruits ($4500 \pm 190 \mu\text{m}$). The endocarp thickness in mature fruits was also significantly and markedly greater than in both immature (by 26%) and overripe fruits (by 20%).

Among all treatments, the thickest endocarp layer was recorded in fruits from the RT treatment, primarily due to the exceptionally thick giant cell layer. The thickness of the giant cell layer in RT-treated fruits exceeded that of the control (C) by an average of 9.6%, that of the CPPL treatment by 21%, and that of the CA treatment by 13% (Table 2).

In fruits harvested from plots treated with CPPL, the cuticle layer of the exocarp in mature fruits was significantly the thickest ($12.52 \pm 1.08 \mu\text{m}$), exceeding that of immature fruits by 10% ($11.34 \pm 1.89 \mu\text{m}$) and that of overripe fruits by 20.5% ($10.39 \pm 1.15 \mu\text{m}$). The epidermis layer was significantly the thickest in immature fruits, with thickness gradually decreasing as ripening progressed.

While the collenchymatous tissue of the mesocarp was most extensive in immature fruits ($71.4 \pm 6.72 \mu\text{m}$), the parenchymatous tissue reached its maximum thickness ($4840 \pm 480 \mu\text{m}$) in mature fruits. The extent of both tissue types within the mesocarp decreased during ripening. The collenchyma layer in immature fruits was 50.2% thicker than in mature fruits and 94.6% thicker than in overripe fruits. The extent of parenchymatous tissue in overripe fruits was 21% lower than in mature fruits, and a similar 21% reduction was observed in immature fruits.

No significant differences were detected in the extent of the giant cells forming the endocarp among fruits at different ripening stages. However, analysis of the inner epidermis revealed that mature fruits had a significantly thicker inner epidermis layer ($54.68 \pm 4.36 \mu\text{m}$), which was 16.4% thicker than that of overripe fruits (the second thickest), and 29.8% thicker than that of immature fruits.

In samples from plots treated with CA, mature fruits exhibited the significantly thickest exocarp ($24.32 \pm 1.18 \mu\text{m}$). The exocarp thickness in mature fruits exceeded that of immature fruits by 6.6% ($22.8 \pm 1.18 \mu\text{m}$) and that of overripe fruits by 15.4% ($21.07 \pm 0.68 \mu\text{m}$). The thickness of the exocarp components—the cuticle and epidermis—decreased substantially in the overripe stage compared to the mature stage, by 10.4% and 20.9%, respectively.

The total mesocarp thickness was significantly greatest in immature fruits, decreasing markedly by 25.9% as ripening progressed. The collenchyma layer was also significantly thickest in immature fruits ($71.4 \pm 6.72 \mu\text{m}$) but was reduced by 47.1% in mature fruits ($37.75 \pm 3.83 \mu\text{m}$) and by 58.4% in overripe fruits ($29.67 \pm 3.59 \mu\text{m}$).

No significant differences were found in the thickness of the endocarp between immature and mature fruits, either in the giant cell layer or in the inner epidermis. However, in overripe fruits, both parameters were significantly reduced compared to those in immature and mature fruits.

By comparing the histological parameters of fruits from the different treatments, the following trends were observed: the cuticle thickness increased in the order $C < CA < CPPL < RT$; the epidermis thickness increased in the order $C < RT < CA < CPPL$; the thickness of the collenchyma layer increased in the order $RT < C < CPPL < CA$; the extent of the parenchymatic tissue within the mesocarp also followed the trend $RT < C < CPPL < CA$; the thickness of the giant cell layer increased in the order $RT < C < CA < CPPL$; while the inner epidermis thickness decreased in the order $CPPL < RT < C < CA$.

3.3. Effect of Soil Conditioner Treatments and Ripening Stage on Daily Water Loss Rates

Overall, when examining the daily water loss (%) of fruits at different ripening stages throughout the entire period, statistically significant differences between the control and other treatments were only detected during the first three days and on the 10th day of maturation. On day 7, water loss in fruits from the C plots (11.44 ± 1.58) was, on average, 26.1% higher than in fruits from the RT plots (8.44 ± 0.74), 31.3% higher than from CPPL plots (8.71 ± 2.84), and 16.7% higher than from CA-treated plots (9.80 ± 0.74). By day 14, water loss in fruits from the C plots (19.47 ± 3.73) exceeded that of the RT samples (15.05 ± 3.98) by 29.4%, CPPL (15.25 ± 4.36) by 27.7%, and CA (16.72 ± 1.72) by 16.4%. Among immature fruits, those from the RT-treated plots had the lowest water loss rates, while CPPL- and CA-treated fruits showed similar levels and patterns of water loss during the 14-day storage period (Figure 3).

Regarding the water loss of mature (commercially mature) fruits, a pattern similar to that observed for immature fruits was evident across treatments: throughout the 14-day observation period, fruits from the control (C) plots exhibited the highest water loss. On days 1, 2, and 14, water loss in control samples was significantly higher than in fruits from all other treatments. Fruits from CPPL-treated plots had the second-highest water loss, followed by those from CA-treated plots. Throughout the storage period, the lowest daily water loss rates were recorded in samples from the RT plots, which were 15.2% more than those of CPPL samples (15.36 ± 0.17), and 19.7% more than those of CA samples (14.78 ± 0.54).

In the case of overripe (physiologically mature) fruits, samples from CA-treated plots showed the highest daily postharvest water loss starting from day 1. In contrast, fruits from the control (C) plots consistently showed lower water loss compared with CA. On day 7, the water loss of overripe fruits from CA plots (12.36 ± 0.15) was 37.8% higher than that of RT fruits (8.97 ± 0.71), 36.1% higher than that of fruits from CPPL plots (9.08 ± 0.35), and 24.1% higher than that of C fruits (9.96 ± 0.09). By day 14, these differences persisted: CA fruits (20.64 ± 1.61) showed 29.4% higher water loss than RT fruits (15.94 ± 1.59), 36.8% higher than CPPL fruits (15.08 ± 0.44), and 20.9% higher than C fruits (17.06 ± 1.1). On day 14, the water loss of CA fruits was significantly greater than that of fruits from all other treatments.

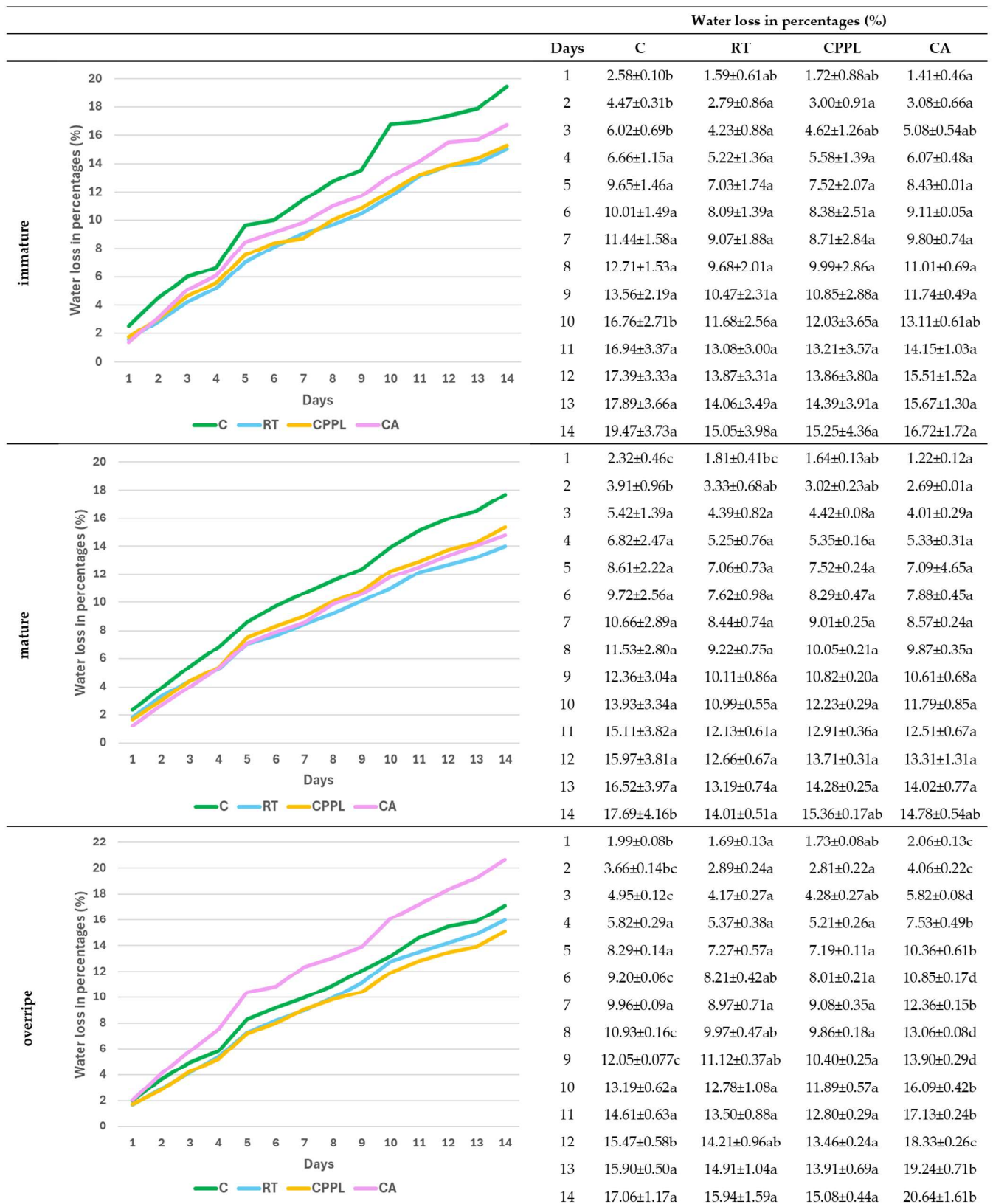


Figure 3. Average daily water loss rates (WLRs) of fruits, by ripening stage and soil conditioner treatment. Stages of fruit ripening: immature, mature, overripe. C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. Data are means of three replications. ANOVA followed by Tukey’s b-test. Means within a row followed by the same lowercase letter are not statistically different at $p < 0.05$.

3.4. Ripening Stage and Treatment-Dependent Changes in Water Loss Rate and Micromorphometric Parameters of Fruits of the 'Tizenegyes' Pepper Cultivar

To assess postharvest water loss in pepper fruits, we measured water loss (%) over a 14-day period in both cuticle-intact (untreated) and cuticle-removed (treated, hexane-washed) fruits. The following findings were obtained for samples from different treatments and ripening stages.

For fruits from the control plots, total water loss (measured on day 14) was not significantly influenced by the ripening stage in cuticle-intact fruits. Across all three stages, fruits showed relatively high water loss compared to the other treatments, averaging between 16% and 21% of their initial weight. Removal of the cuticle increased water loss in all ripening stages: by 22.57% in immature fruits (untreated: 20.73 ± 6.51 , treated: 25.41 ± 8.15), 23.74% in mature fruits (untreated: 18.59 ± 3.27 , treated: 23.01 ± 9.17), and 40.89% in overripe fruits compared with cuticle-intact fruits (untreated: 16.31 ± 4.15 , treated: 22.98 ± 15.41) (Figure 4). These results indicate that, in control-plot samples, the cuticle contributed to postharvest water retention to a similar extent across all ripening stages. This was observed despite a measurable increase in cuticle thickness during ripening: compared with immature fruits ($11.51 \pm 1.09 \mu\text{m}$), cuticle thickness increased by 7% in mature ($12.32 \pm 1.01 \mu\text{m}$) and by 10.2% in overripe fruits ($12.68 \pm 2.33 \mu\text{m}$). At all ripening stages, fruits from the control plots had a significantly thicker cuticle than those from any other treatments (Table 3, Figure 5).

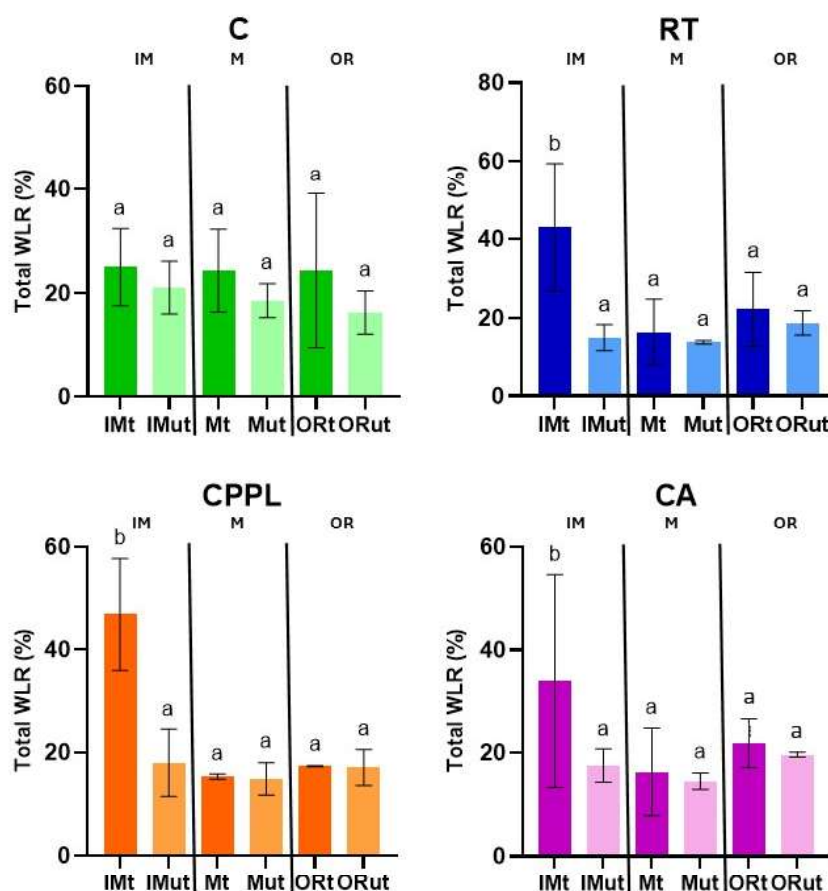


Figure 4. Total water loss (%) of fruits in different ripening stages (immature (IM), mature (M), overripe (OR), calculated as the sum of daily WLRs over 14 days for cuticle-intact (untreated) and cuticle-removed (treated, hexane-washed) samples). C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. IMt: immature, treated, IMut: immature, untreated,

Mt: mature, treated, Mut: mature, untreated, ORt: overripe, treated, ORut: overripe, untreated. Different letters on the same bars in every ripening stage (immature, mature, overripe) indicate significant differences within a given ripening group according to Tukey’s test ($p \leq 0.05$). Data are presented as means \pm SD, $n = 6$.

Table 3. Ripening-stage- and treatment-dependent changes in water loss rate and fruit micromorphic and morphometric characteristics.

Ripening Stages	Soil Treatments	Water Loss (WLR) 7th day	Water Loss (WLR) 14th day	Cuticle Thickness	Hypoderm Thickness	Pericarp Thickness	Fruit Diameter	Fruit Length	Fruit Surface Area	Fruit Weight	Surface Area/Fruit Weight
		%	%	μm	μm	mm	mm	mm	mm ²	g	
immature	C	10.61 \pm 3.51a	20.73 \pm 6.51b	11.51 \pm 1.09b	70.88 \pm 6.18a	4.15 \pm 0.42ab	32.65 \pm 2.55a	76.12 \pm 9.15a	3903.14 \pm 23.46c	26.43 \pm 4.75a	155.94 \pm 30.05a
	RT	9.07 \pm 1.54a	15.05 \pm 3.25a	10.67 \pm 1.15a	86.19 \pm 2.09c	5.04 \pm 0.73bc	36.87 \pm 6.67a	75.24 \pm 9.6a	4354.15 \pm 98.96d	25.25 \pm 5.28a	177.94 \pm 35.92a
	CPPL	9.56 \pm 3.32a	17.97 \pm 6.52a	11.34 \pm 1.89ab	78.09 \pm 3.89b	4.00 \pm 0.77a	32.43 \pm 4.19a	67.87 \pm 17.60a	3454.54 \pm 112.05b	23.79 \pm 5.76a	175.55 \pm 32.47a
	CA	10.13 \pm 1.59a	17.53 \pm 3.22a	11.46 \pm 1.23b	82.74 \pm 6.72bc	4.22 \pm 0.95ab	31.92 \pm 4.12a	61.36 \pm 15.69a	3075.02 \pm 100.84a	30.64 \pm 3.48a	115.19 \pm 19.52a
mature	C	10.72 \pm 3.13a	18.59 \pm 3.27b	12.32 \pm 1.01b	62.99 \pm 5.05b	4.51 \pm 0.40ab	40.40 \pm 5.63a	81.10 \pm 2.41a	5144.01 \pm 41.16a	42.18 \pm 9.16a	107.53 \pm 10.55ab
	RT	8.15 \pm 0.69a	13.81 \pm 0.48a	10.61 \pm 1.27a	78.00 \pm 1.71c	5.30 \pm 0.73b	39.97 \pm 4.20a	82.13 \pm 4.29ab	5152.61 \pm 24.63a	38.38 \pm 7.03a	150.3 \pm 12.69c
	CPPL	9.19 \pm 1.68a	15.79 \pm 3.13ab	12.52 \pm 1.08b	54.05 \pm 6.48a	4.84 \pm 0.48ab	40.66 \pm 5.01a	81.30 \pm 4.74a	5189.88 \pm 37.82a	46.06 \pm 8.91a	97.96 \pm 6.52a
	CA	8.69 \pm 0.98a	14.49 \pm 1.57ab	12.20 \pm 1.95b	49.87 \pm 3.83a	4.39 \pm 0.07a	40.09 \pm 8.59a	85.61 \pm 6.20b	5530.03 \pm 87.69b	41.34 \pm 12.43a	152.55 \pm 16.87c
overripe	C	9.78 \pm 1.79a	16.31 \pm 4.15a	12.68 \pm 2.33c	53.80 \pm 5.55b	3.55 \pm 0.37a	36.20 \pm 3.49ab	85.30 \pm 4.49a	4847.94 \pm 25.87a	31.78 \pm 6.92a	168.08 \pm 29.84b
	RT	8.76 \pm 0.81a	18.72 \pm 3.78a	12.18 \pm 1.59bc	42.52 \pm 4.55a	4.50 \pm 1.9a	39.00 \pm 6.39b	87.64 \pm 13.81a	5366.2 \pm 136.42c	34.16 \pm 4.55a	151.52 \pm 18.32ab
	CPPL	12.54 \pm 5.01a	19.35 \pm 5.35a	10.39 \pm 1.15a	44.00 \pm 5.32a	3.97 \pm 1.41a	32.40 \pm 3.92a	90.62 \pm 10.92a	4609.66 \pm 65.89a	41.80 \pm 7.43a	134.76 \pm 20.01a
	CA	12.84 \pm 2.3a	21.81 \pm 4.69a	11.05 \pm 0.81b	39.69 \pm 3.59a	3.38 \pm 0.44a	37.30 \pm 5.89ab	88.43 \pm 11.22a	5178.54 \pm 102.12b	41.66 \pm 6.65a	113.16 \pm 17.76a

C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. Data are means of 6 replications. ANOVA Tukey’s b-test. Means within the rows followed by the same lowercase letter are not statistically different at $p < 0.05$.

With respect to additional histological and morphological parameters that may influence postharvest water loss, the following trends were observed: hypodermal thickness decreased by 11.1% in mature fruits ($62.99 \pm 5.05 \mu\text{m}$) and by 24.1% in overripe fruits ($53.80 \pm 5.55 \mu\text{m}$) compared to immature ones ($70.88 \pm 6.18 \mu\text{m}$). Nevertheless, in the control samples, hypodermal thickness in mature and overripe fruits remained the second largest and the largest, respectively, among all treatments (Table 3, Figure 6).

Pericarp thickness increased by 8.7% in mature fruits ($4.51 \pm 0.40 \text{ mm}$) compared to immature ones ($4.15 \pm 0.42 \text{ mm}$) but decreased by 14.5% in overripe fruits ($3.55 \pm 0.37 \text{ mm}$) relative to immature fruits and by 21.3% compared to mature fruits. At the overripe stage, fruits from control plots exhibited a significantly thinner pericarp than those from the other treatments (Table 3).

A similar trend was observed for surface area, which increased by 31.8% from the immature ($3903.14 \pm 23.46 \text{ mm}^2$) to the mature stage ($5144.01 \pm 41.16 \text{ mm}^2$) but then decreased by 5.8% in overripe fruits ($4847.94 \pm 25.87 \text{ mm}^2$) compared to mature fruits. At both the mature and overripe stages, control fruits had among the smallest surface areas, significantly lower than those of fruits from the RT, CPPL, and CA treatments.

In immature fruits from the control plots, the SA/FW ratio did not differ significantly from that of fruits from other treatments. In ripe fruits, however, the SA/FW ratio of control fruits was significantly lower than that of ripe fruits from the RT- and CA-treated plots. In overripe fruits, by contrast, control samples exhibited the highest SA/FW values, which likely contributed to their greater postharvest water loss (Table 3).

In RT-treated plots, both immature and mature fruits exhibited nearly identical and consistently low postharvest water loss values, remaining below those of all other treatments (C, CPPL, and CA). This effect was observed despite the significantly thinner cuticle in RT-treated fruits at these ripening stages compared to other treatments (Table 3, Figure 5).

The water loss of cuticle-removed fruits exceeded that of cuticle-intact fruits by 176.94% in the immature stage (untreated: 15.05 ± 3.25 , treated: 41.68 ± 18.15), 15.74% in the mature stage (untreated: 13.81 ± 0.48 , treated: 15.98 ± 9.59), and 15.59% in the overripe stage (untreated: 18.72 ± 3.78 , treated: 21.64 ± 9.15). This occurred despite the fact that, in fruits from RT-treated plots, cuticle thickness increased by 12.49% in overripe fruits ($12.18 \pm 1.59 \mu\text{m}$) compared to both immature ($10.67 \pm 1.15 \mu\text{m}$) and mature ones

($10.61 \pm 1.27 \mu\text{m}$). In contrast, no significant difference in cuticle thickness was observed between immature and mature fruits (Figure 5). Based on these findings, it can also be concluded that, in samples from RT-treated plots, the cuticle plays a significant role in reducing postharvest water loss at the immature ripening stage.

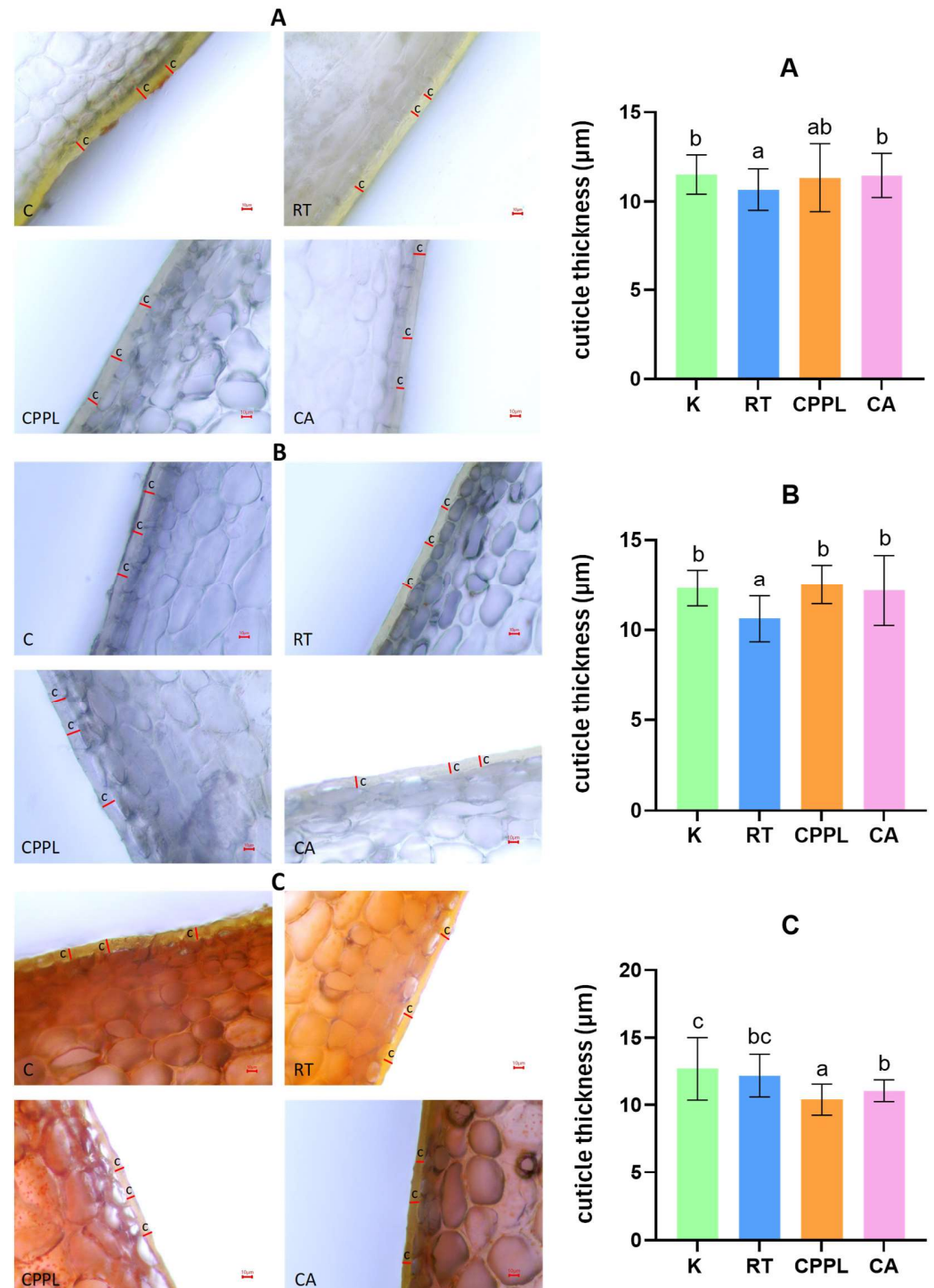


Figure 5. Effects of soil treatments on the microanatomical characteristics of fruits of the Hungarian wax pepper cultivar 'Tizenegyes' at different stages of fruit ripening, grown in an open-field experiment (Nyíregyháza, Hungary). Cuticle thickness (μm) ($10\times$). Stages of fruit ripening: (A) immature fruit, (B) mature fruit, (C) overripe fruit. C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. c: cuticle. Different lowercase letters on the same bars indicate significant differences according to Tukey's test ($p \leq 0.05$). Data are means \pm SD, $n = 60$.

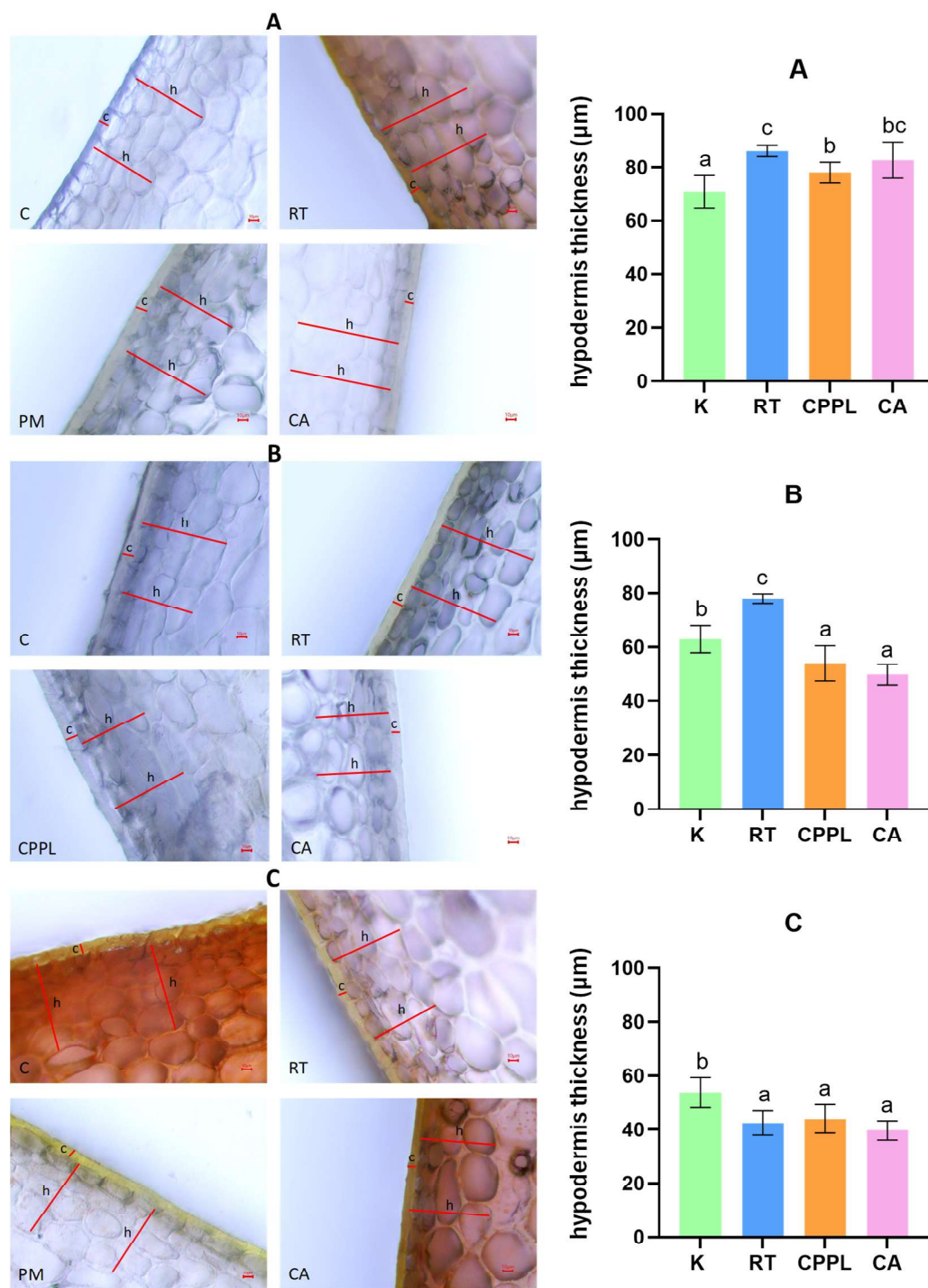


Figure 6. Effects of soil treatments on the microanatomical characteristics of fruits of the Hungarian wax pepper cultivar ‘Tizenegyes’ at different stages of fruit ripening, grown in an open-field experiment (Nyíregyháza, Hungary). Hypodermis thickness (μm) ($10\times$). Stages of fruit ripening: (A) immature fruit, (B) mature fruit, (C) overripe fruit. C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. c: cuticle, h: hypodermis. Different letters on the same bars indicate significant differences according to Tukey’s test ($p \leq 0.05$). Data are means \pm SD, $n = 60$.

Fruits from the RT-treated plots had significantly thicker hypodermal layers in both the immature and mature ripening stages compared to all other treatments (Table 3, Figure 6), despite a decrease in thickness as ripening progressed: the hypodermal layer was 10.5% thinner in mature fruits ($78.00 \pm 1.71 \mu\text{m}$) than in immature ones ($86.19 \pm 2.09 \mu\text{m}$), and

50.7% thinner in overripe fruits ($42.52 \pm 4.55 \mu\text{m}$). Notably, fruits from RT-treated plots also had the thickest collenchyma cell walls among all treatments (Table 3).

In mature fruits, pericarp thickness ($5.30 \pm 0.73 \text{ mm}$) increased by 5.16% compared to immature fruits ($5.04 \pm 0.73 \text{ mm}$). However, in overripe fruits, pericarp thickness decreased by 15.1% relative to mature fruits ($4.50 \pm 1.9 \text{ mm}$). In both the immature and mature stages, fruits from RT-treated plots had significantly thicker pericarp layers than those from the other treatments.

Fruit surface area increased consistently during ripening: it was 18.3% higher in mature fruits ($5152.61 \pm 24.63 \text{ mm}^2$) and 23.2% higher in overripe fruits ($5366.2 \pm 136.42 \text{ mm}^2$) compared to the average surface area of immature fruits ($4354.15 \pm 98.96 \text{ mm}^2$). In both the immature and overripe stages, fruits from RT-treated plots had significantly larger surface areas than those from the other treatments (C, CPPL, and CA) (Table 3).

In immature fruits from the RT-treated plots, no significant differences in the SA/FW ratio were observed compared with samples from the other treatments. In ripe fruits, however, the SA/FW ratio of RT fruits was significantly the highest among all treatments, while in overripe fruits, the SA/FW values of RT samples ranked second highest. Nevertheless, across all ripening stages, fruits from the RT-treated plots had the thickest pericarp and hypodermis layers, as well as the thickest collenchyma cell walls, compared with fruits from the other treatments. Consequently, despite their higher SA/FW values, these samples did not exhibit the highest WLR values. Statistical analysis confirmed that mature fruits from RT-treated plots had significantly the lowest postharvest water loss after 14 days of storage (Table 3). A similar trend was observed in immature fruits, although the difference was not statistically significant. For overripe fruits, water loss was the second lowest, but again, the difference was not statistically significant.

In samples from CPPL-treated plots, total water loss (%) on day 14 was not strongly affected by the ripening stage. Compared to immature fruits (17.97 ± 6.52), mature fruits exhibited a slightly lower water loss (12.1% lower) (15.79 ± 3.13), whereas overripe fruits (19.35 ± 5.35) showed an increase of 8.8% compared to immature and 22.5% compared to mature fruits (Table 3). The water loss of hexane-treated (cuticle-removed) fruits was substantially higher in the immature stage (160.8% higher; untreated: 17.97 ± 6.52 , treated: 46.86 ± 11.45), slightly higher in the mature stage (3.0% higher; untreated: 15.79 ± 3.13 , treated: 16.26 ± 0.75), and only marginally higher in the overripe stage (1.4% higher; untreated: 19.35 ± 5.35 , treated: 19.62 ± 0.12) compared with cuticle-intact fruits (Figure 4). These results indicate that, among the micromorphometric parameters examined, the cuticle likely plays a key role in regulating postharvest water loss in immature fruits from CPPL-treated plots.

As a result of CPPL soil treatment, the cuticle thickness of mature fruits ($12.52 \pm 1.08 \mu\text{m}$) increased by 10.4% compared to immature fruits ($11.34 \pm 1.89 \mu\text{m}$). However, in overripe fruits, cuticle thickness ($10.39 \pm 1.15 \mu\text{m}$) decreased by 8.4% and 17% compared to immature and mature fruits, respectively. In the immature stage, fruits from CPPL-treated plots had the third thickest cuticle among all treatments. In the mature stage, the cuticle thickness was significantly greater than that of the RT samples, while in the overripe stage, they exhibited the thinnest cuticle layer overall, with statistically significant differences (Table 3; Figure 5).

The hypodermis layer, which also influences water loss, was relatively thick in the immature stage. In this phase, CPPL-treated fruits showed the third thickest hypodermis ($78.09 \pm 3.89 \mu\text{m}$) among all treatments. However, in both the mature and overripe stages, CPPL fruits had the thinnest hypodermis layer ($54.05 \pm 6.48 \mu\text{m}$ and $44.00 \pm 5.32 \mu\text{m}$, respectively) compared to all other treatments. Hypodermis thickness decreased progressively during ripening—by 30.8% in the mature and by 43.7% in the overripe stage compared to immature fruits (Figure 6).

Pericarp thickness followed a similar trend to that observed for the hypodermis. Compared to immature fruits (4.00 ± 0.77 mm), pericarp thickness increased by 21.0% in the mature stage (4.84 ± 0.48 mm) but decreased by 0.8% in the overripe stage (3.97 ± 1.41 mm) relative to immature fruits and by 17.9% relative to mature fruits. Among the different treatments, CPPL fruits had significantly the lowest pericarp thickness in both immature and overripe stages (Table 3).

The surface area of the fruits increased during ripening, being 50.2% larger in mature fruits (5189.88 ± 37.82 mm²) compared to immature ones (3454.54 ± 112.05 mm²). However, in the overripe stage, surface area decreased by an average of 11.2% compared to mature fruits (4609.66 ± 65.89 mm²). In the CPPL treatment, fruits in the mature and overripe stages had significantly smaller surface areas than those from the other treatments, whereas in the immature stage, they exhibited the third largest surface area, with statistically significant differences.

In immature fruits from the CPPL-treated plots, no significant differences in the SA/FW ratio were detected compared with immature fruits from the other treatments. In ripe fruits, however, the SA/FW ratio of CPPL samples was significantly the lowest among all treatments, which positively affected their WLR values. In overripe fruits, the SA/FW values of CPPL samples were the third highest.

In fruits from CA-treated plots, the lowest water loss (%) on day 14 was observed in the mature ripening stage. In contrast, immature fruits exhibited the highest postharvest water loss (17.53 ± 3.22), exceeding that of mature fruits by 21% (14.49 ± 1.57). In the overripe stage, water loss increased again (21.81 ± 4.69)—by 55.8% compared to mature fruits and by 24.5% compared to immature fruits. In hexane-treated, cuticle-removed fruits, water loss in the immature stage (untreated: 17.53 ± 3.22 , treated: 33.93 ± 11.45) was substantially higher (93.61%), while in the mature (untreated: 14.49 ± 1.57 , treated: 16.28 ± 11.45) and overripe stages (untreated: 21.81 ± 4.69 , treated: 25.08 ± 11.45), water loss was only slightly higher compared to intact/untreated fruits (12.4% and 15%, respectively) (Figure 4). These findings suggest that, among the examined micromorphometric features, the cuticle likely plays a key regulatory role in postharvest water loss in immature fruits from CA-treated plots.

As a result of CA soil treatment, cuticle thickness in mature fruits (12.20 ± 1.95 μm) increased by 6.5% compared to immature fruits (11.46 ± 1.23 μm). However, in the overripe stage, cuticle thickness decreased by 3.7% (11.05 ± 0.81 μm) compared to immature and 9.4% compared to mature fruits (Figure 5). In both the immature and mature stages, CA-treated fruits had a significantly thicker cuticle than fruits from RT-treated plots, while in the overripe stage, cuticle thickness was similar to that of RT samples but still significantly greater than in CPPL-treated fruits (Table 3, Figure 5).

The hypodermis thickness in immature fruits from CA-treated plots was the greatest among all treatments (82.74 ± 6.72 μm). However, in the mature and overripe stages, a marked reduction in hypodermis thickness was observed—39.7% lower in mature fruits (49.87 ± 3.83 μm) and 52.0% lower in overripe fruits (39.69 ± 3.59 μm) compared to immature fruits. In both stages, CA-treated fruits had the thinnest hypodermis layer compared to the other treatments (C, RT) (Figure 6).

Among all treatments, CA-treated fruits had the thinnest pericarp in both immature and mature stages, with statistically significant differences. Pericarp thickness increased by 4% from the immature (4.22 ± 0.95 mm) to the mature stage (4.39 ± 0.07 mm), but in the overripe stage (3.38 ± 0.44 mm), it was 19.9% thinner than in immature fruits and 23% thinner than in mature fruits (Table 3).

Fruit surface area increased significantly during ripening: in mature fruits (5530.03 ± 87.69 mm²), it was 79.8% larger than in immature fruits (3075.02 ± 100.84 mm²).

In the overripe stage ($5178.54 \pm 102.12 \text{ mm}^2$), a slight decrease in surface area was recorded, with values 6.4% smaller than in mature fruits. Among all treatments, CA-treated fruits had the largest surface area in the mature stage and the second largest in the overripe stage, with statistically significant differences (Table 3).

In immature fruits from the CA-treated plots, no significant differences in the SA/FW ratio were detected compared to samples from the other treatments. In ripe fruits, however, CA samples had the significantly highest SA/FW values, whereas in overripe fruits, CA samples had the significantly the lowest SA/FW values (Table 3).

Pearson's correlation analysis revealed that in immature fruits from the control plots, day 7 WLR showed negative correlation with pericarp thickness ($r_7 = -0.735$) and cuticle thickness ($r_7 = -0.647$). Day 14 WLR was moderately reduced by both parameters ($r_{14} = -0.610$ and $r_{14} = -0.652$). In other treatments, WLR was strongly influenced by surface area, fruit weight, and SA/W ratio, whereas in controls, these correlations were weak. In RT fruits, day 7 and day 14 WLR correlated very strongly negatively with surface area ($r = -0.995$). In CPPL fruits, WLR also correlated very strongly negatively with hypoderm thickness ($r_7 = -0.964$; $r_{14} = -0.966$) and surface area ($r_7 = -0.995$; $r_{14} = -0.992$), and strongly with SA/W ratio ($r_7 = -0.874$; $r_{14} = -0.865$). In CA fruits, SA/W ratio was the main determinant ($r_7 = -0.975$; $r_{14} = -0.916$) (Figure 7).

In mature fruits, increases in fruit size (fruit weight, surface area, and pericarp thickness) were associated with decrease in WLR. As fruit weight increased, the SA/W ratio decreased compared to immature fruits, contributing substantially to the reduction in WLR across all treatments. In control samples, fruit weight showed a strong positive correlation with both day 7 and day 14 WLR ($r_7 = 0.799$; $r_{14} = 0.715$), while the SA/W ratio displayed a strong negative correlation ($r_7 = -0.853$; $r_{14} = -0.788$).

In RT-treated fruits, the reduction in WLR was largely associated with increased pericarp thickness ($r_7 = -0.628$; $r_{14} = -0.701$), fruit weight ($r_7 = 0.978$; $r_{14} = 0.909$), and SA/W ratio ($r_7 = -0.972$; $r_{14} = -0.889$). In CPPL-treated fruits, the SA/W ratio also played a significant role, showing a strong negative correlation with WLRA ($r_7 = -0.782$; $r_{14} = -0.869$). In CA-treated ripe fruits, the SA/W ratio—similar to the above treatments—was the dominant factor, with a very strong (day 7, $r_7 = -0.994$) and strong (day 14, $r_{14} = -0.777$) negative correlation. In addition, WLR in CA-treated ripe fruits showed a very strong negative correlation with hypodermis thickness ($r_7 = -0.798$; $r_{14} = -0.997$), and a strong positive correlation with fruit weight ($r_7 = 0.963$; $r_{14} = 0.724$) (Figure 7). Overall, in ripe fruits from all treatments, the decrease in WLR with increasing fruit size was largely explained by the reduction in the SA/W ratio.

In overripe fruits, WLR values on both day 7 and day 14 were generally higher than in ripe fruits. This increase in WLR was accompanied by decrease in pericarp thickness, fruit weight, and surface area, alongside a renewed increase in SA/W ratio. While cuticle thickness did not significantly influence WLR in immature or ripe fruits, in overripe fruits from all treatment—except CPPL—a strong negative correlation was found between cuticle thickness and water loss on day 14: $r_{14} = -0.720$ for control samples, $r_{14} = -0.795$ for RT-treated samples, and $r_{14} = -0.737$ for CA-treated samples. In RT-treated overripe fruits, day 14 WLR was also strongly and negatively correlated with hypodermis thickness ($r_{14} = -0.652$) and cuticle thickness ($r_{14} = -0.795$), whereas in CA-treated fruits, day 14 water loss was significantly reduced by increase in both pericarp thickness ($r_{14} = -0.871$) and cuticle thickness ($r_{14} = -0.737$) (Figure 7).

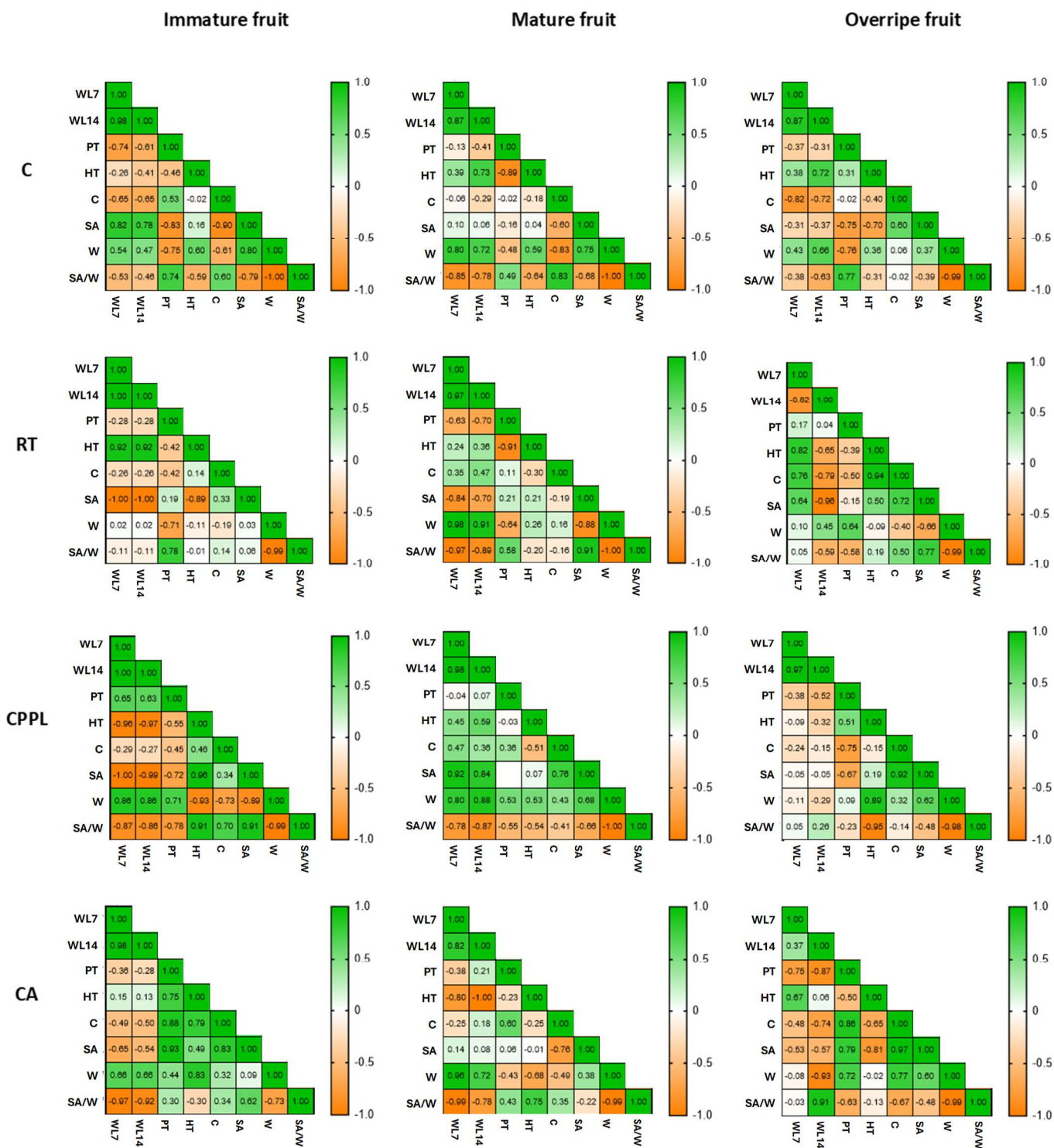


Figure 7. Relationship between fruit water loss rate (WLR) and treatment, maturity stage, and fruit macro- and micromorphometric parameters. WL7: water loss 7th day, WL14: water loss 14th day, PT: pericarp thickness, HT: hypoderm thickness, CT: cuticle thickness, SA: fruit surface area, W: fruit weight, SA/W: surface area/fruit weight ratio. C: control, RT: rhyolite tuff, CPPL: composted and pelletized poultry litter, CA: clarifying agent. Pearson correlation, $p \leq 0.05$.

4. Discussion

4.1. Micromorphometrical Changes During Ripening

Pepper fruit ripening involved distinct dimensional and tissue-level changes in the pericarp, typically following a sigmoid growth pattern: a slow initial phase; a rapid phase

marked by substantial increases in volume, weight, and accumulation of water and soluble solids; and a final phase with minimal further growth [84–87]. Ripening is accompanied by cell wall depolymerization and alterations in cuticle composition, which intensify after harvest, resulting in pericarp softening and loosening and increased water loss [85].

We can conclude that similar micromorphometric changes of pepper pericarp can be observed across all treatments. The cuticle, which is crucial for fruit development, ripening, and postharvest shelf life, thickened progressively during ripening, consistent with previous reports [4,88,89].

Pericarp thickness increased from the immature to mature stage, then decreased in overripe fruits, in line with earlier findings that fruit size in *C. annuum* depends first on cell division and later on cell expansion [85,90].

In our study, across all treatments, ripening was marked by reduced hypodermal thickness [32,91] and thinner collenchyma cell walls. Similar to some earlier statements [92–94], we concluded that in all treatments, the parenchymatous tissue in the pericarp increased from the immature to the mature stage but declined in overripe fruits. Previous findings [28,32,87,91–94] suggest that these are likely due to structural loosening of pericarp (thinner hypodermis, reduced mesocarp and endocarp), which has been associated with enhanced polygalacturonase activity that depolymerizes pectic polysaccharides and hemicelluloses, thereby weakening the pericarp and promoting water loss. However, the thickness of the cell wall, particularly in collenchyma, is influenced by nutrition and calcium availability [94]. These processes are hormonally regulated, with auxin promoting greater thickness and water content, and auxin-induced gibberellin biosynthesis contributing to pericarp cell enlargement [84,95].

4.2. Role of the Cuticle in Water Loss of Pepper Fruit

The role of the cuticle was assessed by comparing intact and hexane-washed fruits. In all treatments, cuticle removal increased water loss, but the amount of water loss varied by treatment and ripening stage. The greatest differences between intact and cuticle-removed fruits were observed in the control, particularly at the mature and overripe phases of ripening, where the cuticle was thickest. This conclusion is similar to previous findings [83,96,97] and confirms the cuticle's role as a barrier to water loss, although cuticle thickness alone did not always explain the differences observed. In the RT, CPPL, and CA treatments, the thinnest cuticle was observed in the case of immature fruits, which confirms those previous findings that immature peppers do not have a fully developed cuticle layer, which can increase the water loss of pepper fruit [96]. Our results are consistent with reports that cuticle thickness is not directly correlated with water retention capacity, and that other histological factors, such as hypodermis and collenchyma thickness, contribute substantially to storability [83,97–99]. The cuticle's role in water loss is determined not only by thickness but also by fatty acid composition, which is strongly influenced by the cultivation environment [98]. These results agree with Colombari et al. [99], who linked greater postharvest water loss in overripe peppers to stress-related enzyme activity, cell wall loosening, and pectin loss. Moderate water loss, however, can limit oxidative stress and delay quality deterioration.

4.3. Effects of the Nutrient Supply on the Micromorphometric Parameters of Pericarp

Calcium supply has a strong influence on pericarp rigidity. Cell wall thickness, particularly in collenchyma, is influenced by nutrition and calcium availability, as calcium pectate in the middle lamella is critical for rigidity and pathogen resistance [92]. In this study, CPPL contained 52 times more calcium than RT and 144 times more than CA, and CPPL-treated fruits had the second-highest collenchyma cell wall thickness among all

treatments. Nevertheless, CPPL fruits did not always exhibit lower water loss, indicating that cuticle composition, rather than thickness, may be decisive. As Parsons et al. [31] noted, water loss correlates positively with cuticular triterpenoid and sterol content, and negatively with alkane content and the triterpenoid-to-sterol ratio. They stated that the impermeability of cuticle depends on the amount of straight-chain aliphatic components. Nutrient supply can cause changes in enzyme activity, which also affects postharvest water balance. Russo and Biles [98] showed that nutrient supply modifies β -galactosidase and peroxidase activity, which accelerates cell wall loosening and water loss during ripening.

4.4. Surface-Area-to-Weight Ratio and Pepper Fruit Water Loss

When calculating the surface-area-to-weight (SA/W) ratio for all treatments and ripening stages, and assessing its role in water loss, we observed differences compared to Diaz et al. [17]. While, in immature fruits, the largest SA/W ratio occurred in the RT treatment—and Diaz et al. [17] suggested that a higher SA/W ratio corresponds to greater fruit water loss—these fruits, in our study, had the lowest WLR values. Among mature fruits, the highest SA/W ratio was found in the CA treatment, and the lowest in CPPL. In overripe fruits, the control had the highest SA/W ratio and the lowest water loss, while CA fruits had the lowest SA/W ratio but the highest WLR.

In all treatments, water loss was greatest in immature fruits and generally decreased with fruit size, except in control plots, where WLR did not decline during ripening. In overripe fruits, a decrease in pericarp thickness—except in the control—was accompanied by an increase in WLR.

Based on our results, our findings are also consistent with Tsegay et al. [100], who observed higher water loss in overripe than mature fruits, and with previous reports [100–103]. Other studies connect overripe water loss to lipid-peroxidation-induced cell wall loosening, noting that *C. annuum* is non-climacteric and not ethylene-driven [104,105]. Kosma et al. [106], however, argued that in overripe fruits, cuticle properties dominate over cell wall changes in determining water loss.

Consistent with the findings of Lownds et al. [107] and Maalekuu et al. [108], we also reported a negative correlation between water loss in pepper fruits and both the thickness and total amount of the cuticular wax layer. Maalekuu et al. [108] further found a negative correlation between water loss and fruit fresh weight, surface area, and initial water content, but no correlation between water loss and pericarp thickness. Studying postharvest water loss in pepper fruits, Konishi et al. [8] also reported a negative correlation between postharvest water loss and fruit fresh weight. In agreement with our results, they found that smaller fruits tended to have thicker cuticle layers than larger fruits.

Similar to their results, we can also conclude that peppers with thin pericarps tended to have thick cuticles, as the thicker cuticle provides mechanical support to the thinner pericarp. However, pepper fruits with a thick cuticle but thin pericarp were more prone to higher water loss than those with a thin cuticle, but a thicker pericarp can also be observed.

4.5. Effect of Rhyolite Tuff as an Alternative Nutrient Supplement on Water Loss in Pepper Fruit

We can conclude that among the histological parameters examined, cuticle thickness, pericarp thickness, hypodermis thickness, and the SA/W ratio are the key determinants of water loss in pepper fruits. Among the alternative nutrient supplements used, the rhyolite tuff (RT) has a large effect on the reducing of pepper fruit water loss and can help to prolong the pepper fruit quality. At the mature stage, the RT-treated pepper fruits have smaller size and weight, but they have thicker pericarp and hypodermis layers, a higher number of collenchymatous cell layers, and thicker cell walls in collenchymatous tissues compared to other treatments. These histological features can reduce the water loss of fruits, thereby

preserving the freshness and crispness of them. However, in case of the RT treatment, the cuticle thickness is decreased thanks to the positive effect of RT on soil water management. The structure and composition of rhyolite tuff improve the soil's water retention capacity by 20–25%, thus optimizing water management even during dry periods. It also promotes better nutrient uptake, which directly affects the quality, histological structure, and taste of the fruit of cultivated plants. The stable microclimate provided by rhyolite tuff and the modification of the soil pH value towards neutral further strengthen the stress tolerance and growth potential of cultivated plants. Due to its adsorption capacity, RT reduces soil toxicity and protects plants from harmful fungi and bacteria. In addition, RT has a favorable heat storage capacity, which can help to re-radiate heat accumulated during the day at night, thereby reducing frost risk and creating a more stable microclimate [50,80].

5. Conclusions

This study combined macro- and micromorphometric analyses with postharvest water loss measurements to identify key structural determinants of pepper fruit water loss. Cuticle, pericarp, and hypodermis thickness, together with the SA/W ratio, were the most influential traits.

Among the alternative nutrient sources tested, rhyolite tuff (RT) was the most effective in reducing postharvest water loss, slowing shrinkage, prolonging crispness, and extending shelf life. Although RT fruits were smaller, they developed thicker pericarp and hypodermis layers, more collenchymatous cell layers, and thicker cell walls, which together helped maintain water content and crispness. Reduced cuticle thickness in RT fruits did not negatively affect water loss rates due to these structural advantages.

The findings, obtained from a one-year study on a single Hungarian wax pepper cultivar (Tizenegyes), highlight the potential of RT as a sustainable alternative nutrient source. Future research should extend to additional pepper varieties (e.g., Kapia types), longer experimental periods, and field conditions to confirm broader applicability.

For organic farmers, RT offers a promising approach to producing residue-free peppers with improved postharvest quality, though possible reductions in fruit size should be considered.

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