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Exploring the Impact of Citric Acid on Mitigating Sweet Potato Soft Rot and Enhancing Postharvest Quality

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Abstract: Citric acid (CAC) is a ubiquitous, odorless, and non-toxic food additive. Soft rot, caused by the pathogen *Rhizopus stolonifer*, is a major postharvest disease affecting sweet potato (*Ipomoea batatas* (L.) Lam). The main theme of this study is to determine the CAC inhibitory mechanism against *Rhizopus stolonifer*, the causative agent of sweet potato soft rot. To ascertain the practical applicability of CAC, both in vitro and in vivo methodologies were employed. The aim of the in vitro experiments in this study was to delineate the effects of a 0.5% (*w*/*v*) CAC solution on the growth inhibition of *Rhizopus stolonifer*, encompassing mycelial morphology and colony expansion. In vivo experiments were carried out using "Xinxiang" sweet potato varieties and the application of a 0.5% (*w*/*v*) CAC solution as a pretreatment. Specifically, the tissue treated with 0.5% CAC maintained better appearance quality and texture characteristics; peroxidase, β-1,3-glucanase, chitinase, and phenylalanine ammonia-lyase activities were enhanced. Conversely, the same treatment resulted in a downregulation of polyphenol oxidase, catalase, ascorbate peroxidase, cellulase, and polygalactosidase activities. Moreover, CAC treatment was found to maintain elevated levels of total phenolics and flavonoids within the sweet potato tissues. In summary, the study demonstrates that 0.5% CAC fortifies the resistance of sweet potato to soft rot by activating defense-related enzymes, suppressing the activity of cell wall-degrading enzymes, and promoting the accumulation of antimicrobial compounds. These results advocate for the utilization of CAC as a postharvest treatment to mitigate the incidence of sweet potato soft rot.

Keywords: *Ipomoea batatas*; microbe control; defense enzyme; mechanism; principal component analysis

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1. Introduction

Sweet potato is an important food crop and cash crop, and the roots are rich in vitamins, starch, soluble sugars, proteins, and polyphenols [1,2]. However, improper handling can cause mechanical damage to sweet potato during harvesting, transportation, and storage, thereby increasing the risk of fungal infections. Soft rot, caused by the pathogen *Rhizopus stolonifer*, is a major postharvest disease affecting sweet potato (*Ipomoea batatas* (L.) Lam), resulting in significant losses in yield and quality [3]. Upon infection by soft rot, the

pathogen activates cell wall-degrading enzymes, leading to cell wall degradation and subsequent softening and rotting of the tubers. Furthermore, infection with *Rhizopus stolonifer* can result in the loss of certain nutrients from the sweet potato. Although chemical controls are effective in disease prevention and management, they bring environmental risks and concerns regarding chemical residue [4]. Consequently, there is an imperative need to identify natural, non-toxic, and residueless treatment methods to prevent and control soft rot during storage and to keep the nutritional quality of sweet potato.

Citric acid (CAC) is a naturally occurring plant organic acid known for its antimicrobial and antioxidant properties [5]. As a safe food additive, CAC has been shown to delay ripening, browning, and disease development in a variety of fruits and vegetables, thereby extending their shelf life. For example, soaking pear fruits in a CAC (2%, w/v) solution for 15 min has been shown to effectively reduce the damage of penicillium on 'Yali' pears and maintain their quality [6]. Dai et al. [7] found that immersion in CAC solution could effectively inhibit the callus browning, with a 2×10^{-3} g L^{-1} CAC solution showing superior inhibitory effects. The browning rate of perennial ryegrass callus was 15% after two weeks of subculture. Tapia-Rodriguez et al. [8] discovered that the combination of CAC and $CaCl_2$ can extend the shelf life, maintain antioxidant capacity, and improve the sensory attributes of fresh-cut kiwifruit.

The preliminary experimental results showed that 0.5% CAC, 1% CAC, and 2% CAC could all reduce the loss caused by *Rhizopus stolonifer* infestation, but the sweet potato treated with 0.5% CAC could maintain better quality. For the economic and environmental protection concept in production practice, 0.5% CAC was selected as the optimal concentration for the CAC-induced sweet potato soft rot resistance test. Examining the CAC treatment methods on the incidence of soft rot disease and the storage quality of sweet potato holds substantial practical importance. This study investigated the influence of a CAC (0.5%, w/v) treatment on the incidence of soft rot disease and storage quality of sweet potato. In this study, we report for the first time in the literature the differential susceptibility of various sweet potato tuber sections to soft rot disease. We also explore the mechanisms underlying the inhibitory effects of CAC (0.5% w/v) on *Rhizopus stolonifer* and its impact on enhancing sweet potato disease resistance. The outcomes are anticipated to contribute to the development of effective strategies for the prevention and control of soft rot during sweet potato storage.

2. Materials and Methods

2.1. Experimental Materials and Treatments

Sweet potato (cultivar 'Xinxiang') were harvested by hand 120 day after planting in the agricultural field area of Zhejiang A & F University in June 2021. *Rhizopus stolonifer* was provided by the Xuzhou Institute of Agricultural Sciences, Jiangsu Province, China. Citric acid (CAC) was acquired from Shanghai Yuanye Bio-Technology Co., Ltd. For the experiment, sweet potato of uniform size, free of mechanical damage, diseases, pests, and sprouting, were carefully selected. First, the tubers were washed with deionized water, followed by disinfection in a 1% v/v sodium hypochlorite solution for 10 min, then rinsed thoroughly with deionized water to remove residual chlorine. Second, the samples were dried with sterile paper towels and stored under sterile conditions. The sweet potato were randomly assigned into two groups, each consisting of three replicates. The experimental group was immersed in a 0.5% w/v CAC solution for 5 min, followed by air drying, while the control group was treated with sterile deionized water. Subsequently, 5 mm puncture wounds were inflicted at both ends and the middle of each sweet potato using a sterile 5 mm perforator, and each wound was inoculated with a *Rhizopus stolonifer* spore suspension at a concentration of 1×10^6 CFU mL^{-1}.

Fresh root samples were collected from the healthy tissue located within 2 cm of the regions adjacent to the diseased pulp [9]. These samples were finely chopped using a sterile dicer, rapid frozen in liquid nitrogen, and stored at −80 °C for subsequent analysis.

Root powder was prepared as follows: Sweet potato roots were sliced into thin 5 mm slices by a slicer (HM 355S, Thermo Fisher Instrument Co., Ltd., Shanghai, China), frozen in liquid nitrogen, and lyophilized at −80 °C to remove moisture in a freeze-dryer (GAMMA1-16LSC, Marin Christ Co., Ltd., Osterode, Germany). The dehydrated root sections were then ground into a fine powder using a hammer cyclone mill (JXFM110, Daji Electric Instrument Co., Ltd., Hangzhou, China). The resulting powder was sieved through a 100-mesh sieve to ensure uniformity and stored in a dark, dry, low-temperature environment to preserve its quality. For each treatment group, three randomly selected, uniform-sized sweet potato roots were washed, dried, and processed as described above.

2.2. In Vitro Antifungal Activity of CAC Against Rhizopus stolonifer

2.2.1. Preparation of Spore Suspensions and Culture Media

The preparation of the culture medium adheres to the methodologies described by Arrebola et al. [10] and Li et al. [11] The preparation includes the following specifications:

Control Group (CK): The Potato Dextrose Agar (PDA) medium was prepared utilizing sterile deionized water.

Treatment Group (0.5% w/v CAC): The PDA medium was prepared using a CAC (0.5% v/v) solution.

Rhizopus stolonifer was cultivated on PDA plates for 7 day at a temperature of 28 °C and a relative humidity of 85%. Spores were collected by gently washing the mycelium with sterile deionized water and subsequently filtering the resulting suspension liquid through sterile gauze. The concentration of the spore suspension was calibrated to 1×10^6 CFU mL^{-1}, employing a hemocytometer for accurate determination.

2.2.2. Measurement Indicators

Colony Diameter Assessment of *Rhizopus stolonifer*: Seven days after inoculation, cultures of *Rhizopus stolonifer* were centrally inoculated onto PDA plates for each treatment group and then measured according to Chai et al. [12]. The plates were incubated in an inverted position at a temperature of 28 °C and a relative humidity of 85%. Colony diameters were measured at 12, 24, 48, 72, 96, and 120 h post-inoculation, employing the criss-cross method for accuracy.

Mycelial Growth Morphology of *Rhizopus stolonifer*: A 20 µL aliquot of the spore suspension was uniformly distributed onto a PDA medium supplemented with 0.5% w/v CAC. Once the medium had completely absorbed the suspension, the plates were incubated at 28 °C and 85% relative humidity within an artificial climate incubator (SAFE, Saifu Experimental Instrument Co., Ltd., Ningbo, China). After five days of incubation, small samples of *Rhizopus stolonifer* hyphae were collected for microscopic examination to assess mycelial morphology. Subsequently, images were captured and preserved for subsequent analysis.

2.3. Antifungal Activity on Rhizopus stolonifer In Vivo

2.3.1. Identifying Soft Rot Resistance in Different Sweet Potato Tuber Sections

The resistance of sweet potato tubers to soft rot was evaluated using a modified experimental protocol as described by Yang et al. [13]. Sweet potato tubers were inoculated with a *Rhizopus stolonifer* spore suspension at a standardized concentration and applied at specific sites. The extent of soft rot was quantified by assessing the phenotypic expression of the disease in both longitudinal and transverse sections of the inoculated areas. This

method was employed to identify differences in soft rot resistance across various sections of the sweet potato tubers and to evaluate the efficacy of 0.5% CAC w/v treatment in enhancing resistance to soft rot.

2.3.2. Effect of 0.5% w/v CAC on Textural Characteristics

The textural attributes of sweet potato slices were evaluated using a Texture Profile Analysis (TPA) analyzer (model TMS-PRO, Food Technology Corporation, Dranesville, VA, USA) as per the methodology described by Aiessandrini et al. [14]. The TPA settings were configured as follows: pre-test speed: 30 mm min^{-1}, test speed: 60 mm min^{-1}, post-test speed: 90 mm min^{-1}, compression ratio: 60%, force detection range: 0–500 N, cylindrical probe diameter: 5 mm, dwell time: 5 s, and a trigger force: 0.2 N.

2.3.3. Effect of 0.5% w/v CAC on Defense-Related Enzyme Activities

Enzyme extraction procedure: Sweet potato tuber samples, each weighing 1.0 g, were homogenized in 1 mL of precooled phosphate buffer solution (PBS, 50 mM, pH 7.8) using a chilled mortar and pestle. The resulting homogenate was then transferred into a 15 mL centrifuge tube and supplemented with an additional 4 mL of the same PBS. This mixture was centrifuged at 12,000× g for 10 min at 4 °C, after which the supernatant was carefully collected for the assessment of peroxidase (POD) and ascorbate peroxidase (APX) activities. To determine the activity of catalase (CAT), fresh sweet potato tuber samples (1.0 g) were homogenized in 1 mL of precooled boric acid–borax buffer (50 mM, pH 8.8). The homogenate was then supplemented with 4 mL of the same buffer and centrifuged under the above conditions. The supernatant was subsequently collected for the CAT activity assay. To determine the activity of polyphenol oxidase (PPO), fresh sweet potato tuber samples (1.0 g) were homogenized in 1 mL of precooled acetate–sodium acetate buffer (0.05 M, pH = 5.5). The homogenate was then supplemented with 4 mL of the same buffer and centrifuged under the above conditions. The supernatant was subsequently collected for the PPO activity assay. Crude enzyme extracts for chitinase (CHI) and β-1,3-glucanase (GLU) activities were prepared by homogenizing sweet potato tuber samples (1.0 g) in 1 mL of a precooled sodium acetate buffer solution (100 mM, pH 5.0) containing 1 mM EDTA, polyvinylpolypyrrolidone (PVPP, 2% w/v), and 5 mM β-mercaptoethanol. This homogenate was centrifuged at 12,000× g for 20 min at 4 °C, and the supernatant was retained as the crude enzyme extract for subsequent analysis.

POD activity assay: The method of Wu et al. was adapted for POD activity determination [15]. The reaction mixture consisted of 0.1 mL enzyme extract, 0.1 mL 1.5% (v/v) guaiacol, 2.7 mL 50 mM phosphate buffer (pH 7.8), and 0.1 mL 0.3 mM hydrogen peroxide (H_2O_2). Absorbance at 470 nm was monitored using a water blank. The POD activity was expressed as U kg^{-1}, where U = 0.01 OD_{470} min^{-1}.

APX activity assay: The method of Apiamu and Asagba [16] was adapted for APX activity determination. The reaction mixture included 0.1 mL enzyme extract, 0.1 mL 0.3 mmol L^{-1} H_2O_2, 0.1 mL 7.5 mmol L^{-1} ascorbic acid, and 2.7 mL 50 mmol L^{-1} phosphate buffer (pH 7.8). Absorbance at 290 nm was monitored using a water blank. The APX activity was expressed as U kg^{-1}, where U = 0.01 OD_{290} min^{-1}.

CAT activity assay: The CAT activity was determined using a reaction mixture comprising 0.1 mL enzyme extract, 0.1 mL 0.3 mmol L^{-1} H_2O_2, and 2.8 mL 150 mmol L^{-1} phosphate buffer (pH 7.8). A water blank was used as a control. The CAT activity was expressed as U kg^{-1}, where U = 0.01 OD_{240} min^{-1}.

PPO activity assay: The PPO activity was determined using a reaction mixture comprising 0.1 mL enzyme extract, 0.5 mL 50 mmol L^{-1} catechol solution, and 2 mL 50 mmol L^{-1}

acetate buffer (pH 5.5) [17]. A water blank was used as a control. The PPO activity was expressed as U kg^{-1}, where U = 0.01 OD_{420} min^{-1}.

CHI activity assay: CHI activity was determined using a commercial assay kit (Beijing Solarbio Technology Co., Ltd., Beijing, China), with absorbance measured at 585 nm. One unit (U) of CHI activity was defined as the amount of enzyme required to release 1 μg of N-acetylglucosamine from chitin per hour per gram of fresh sample. CHI activity is expressed as U kg^{-1}.

GLU activity assay: The GLU activity assay was adapted from Zong et al. [18]. The reaction mixture contained 0.1 mL enzyme extract and 0.1 mL 10 g L^{-1} laminarin solution. The mixture was incubated at 37 °C for 40 min, followed by the addition of 3 mL 3,5-dinitrosalicylic acid reagent and incubation at 100 °C for 5 min. Absorbance was measured at 540 nm. One unit (U) of GLU activity represented the amount of enzyme releasing 1 mg glucose from laminarin per hour per gram fresh weight. GLU activity is expressed as U kg^{-1}.

2.3.4. Effect of 0.5% CAC on Cell Wall-Degrading Enzyme Activity

Enzyme extraction procedure: The tubers of sweet potato (1.0 g) were aseptically ground to pulp with a precooled mortar and pestle in the presence of 1 mL of 95% v/v ethanol. After centrifugation at 8000× g for 10 min at 4 °C, the pellet was carefully collected. Repeat the procedures of the extraction and centrifugation cycle. The final pellet was then resuspended in 5 mL of precooled extraction buffer containing 1.8 M NaCl and incubated on ice for 16 min to ensure complete solubilization of the enzymes. After centrifugation, the supernatant was carefully collected and stored at 4 °C for later use.

Polygalacturonase (PG) activity assay: The procedure for determining PG activity was modified based on the work of Zdunek et al. [19]. The reaction mixture was composed of 1 mL of 50 mM acetate buffer (pH 5.5), 0.5 mL of 10 g L^{-1} polygalacturonic acid solution, and 0.5 mL of enzyme extract. This mixture was incubated at 37 °C for 1 h, after which 3 mL of 3,5-dinitrosalicylic acid (DNS) reagent was introduced. The mixture was then heated to boiling for 5 min and allowed to cool before being diluted to a final volume of 25 mL with distilled water. The absorbance was recorded at 540 nm, with a control reaction lacking enzyme included for comparison. PG activity was quantified as the amount of enzyme necessary to release 1 mg of reducing sugars per gram of fresh sample per hour. The PG activity was expressed as U kg^{-1}.

Cellulase (Cx) Activity Assay: The method for assessing Cx activity was adapted from Abu-Goukh [20]. A reaction mixture, consisting of 1.5 mL of a 10 g L^{-1} carboxymethyl cellulose (CMC) solution and 0.5 mL of enzyme extract, was incubated at 37 °C for 1 h. Following this, 3 mL of 3,5-dinitrosalicylic acid (DNS) reagent was added, and the mixture was brought to a boil for 5 min before dilution with distilled water to a final volume of 25 mL. The absorbance was measured at 540 nm. Cx activity was calculated as the quantity of enzyme required to release 1 mg of reducing sugars per gram of fresh sample per hour. The Cx activity was expressed as U kg^{-1}.

2.3.5. Effect of 0.5% w/v CAC on Phenylpropane Metabolism

Phenylalanine ammonia-lyase (PAL) activity assay: The assay method for PAL activity was adapted from Lister et al. [21]. The reaction mixture contained 0.5 mL enzyme extract, 0.5 mL 20 mmol L^{-1} L-phenylalanine, and 3 mL 50 mmol L^{-1} boric acid–borax buffer (pH 8.8). The mixture was incubated at 37 °C for 1 h. Absorbance at 290 nm was measured using a water blank. The PAL activity was expressed as U kg^{-1}, where U = 0.01 OD_{290} h^{-1}.

Total phenol content: The method by Zhou et al. [22] was adapted for measuring total phenolic content. Fresh sweet potato tuber tissue (1.0 g) was homogenized with 1 mL of a

1% v/v hydrochloric acid–methanol solution in a precooled mortar. This homogenate was then transferred to a 15 mL centrifuge tube and diluted to a final volume of 5 mL with the same solvent. Following centrifugation at 12,000× g for 15 min at 4 °C, the supernatant was collected. The total phenolic content was assessed by measuring the absorbance at 280 nm using a 1% v/v hydrochloric acid–methanol solution as a blank, with results expressed as OD_{280} kg^{-1}.

Flavonoid Content: The method for determining flavonoid content is parallel to the method for determining total phenol content. The absorbance was measured at 325 nm against a 1% v/v hydrochloric acid–methanol blank. The flavonoid content was expressed as OD_{325} kg^{-1}.

2.3.6. Effect of 0.5% w/v CAC on Nutritional Quality Indexes

Protein and soluble sugar content analysis: Near-infrared spectroscopy (NIRS) was utilized to assess protein and soluble sugar content in sweet potato root powder samples using a FOSS Analytical A/S DS2500 instrument. Samples were analyzed in triplicate, and results were reported as g kg^{-1} of root powder.

2.4. Comprehensive Assessment of CAC Effects on Sweet Potato Quality

Principal component analysis (PCA): PCA was conducted to simplify the dataset's dimensionality and evaluate the significance of various quality attributes. Key indicators of sweet potato quality included hardness, cohesion, protein content, soluble sugar levels, total phenols, and flavonoids. The PCA technique was modified based on the approach detailed by Sun et al. [23].

2.5. Statistical Analysis

Data organization and analysis: The data were organized utilizing Microsoft Excel 2016 (Microsoft Corporation, Redmond, WA, USA). Statistical analysis employed one-factor analysis of variance, and Duncan's method was utilized for mean comparisons within treatments at a significance level of $p < 0.05$. Principal component analysis and comprehensive assessments were executed within the SPSS 20.0 software (International Business Machines Corporation, Armonk, NY, USA). Correlation analyses and data visualization were accomplished using Origin software, version 2021 (OriginLab Corporation, Northampton, MA, USA). Each experimental treatment was replicated three times biologically and three times technically.

3. Results and Discussion

3.1. Effect of 0.5% w/v CAC on the Activity of Rhizopus stolonier

The colony diameter of *Rhizopus stolonifer* increased progressively with extended storage. However, the group treated with 0.5% w/v CAC showed a markedly reduced colony diameter in comparison to the CK group (Figure 1A). The suppressive impact of 0.5% w/v CAC on colony expansion was sustained, achieving a 32.54% decrease in size relative to the CK after 120 h (Figure 1B(f,l)). After a 5 day incubation period, the mycelial morphology of *Rhizopus stolonifer* was examined under a microscope at 400× magnification. The mycelium of the CK group was smooth in texture, with intact cell contents and vigorous growth (Figure 2A). On the contrary, those cells treated with 0.5% w/v CAC showed darkening, vacuolization, and significant alteration of internal structure (Figure 2B).

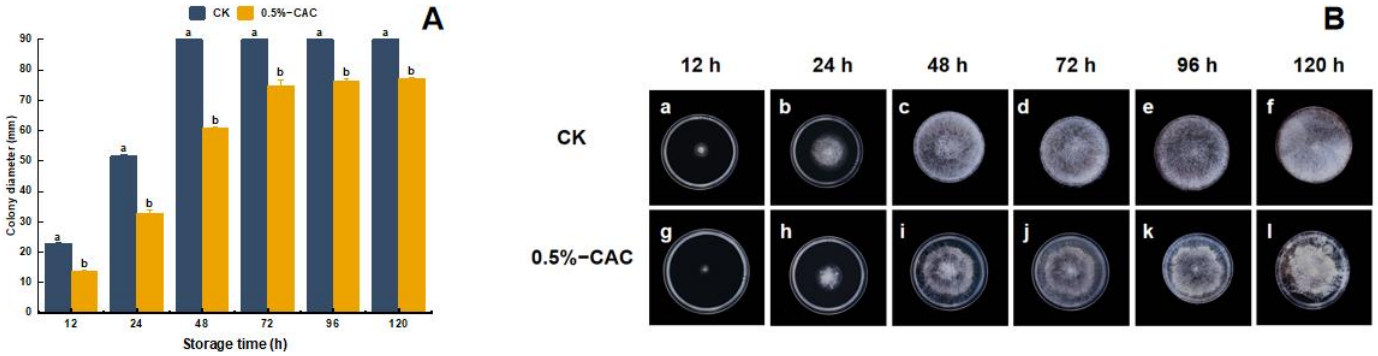

Figure 1. Colony diameter (**A**) and growth (**B**) of *Rhizopus stolonifer* on PDA medium at 12 (**a**,**g**), 24 (**b**,**h**), 48 (**c**,**i**), 72 (**d**,**j**), 96 (**e**,**k**), and 120 h (**f**,**l**). The significant difference between the means in the (**A**) ($p < 0.05$) is indicated by letters above the histogram bars.

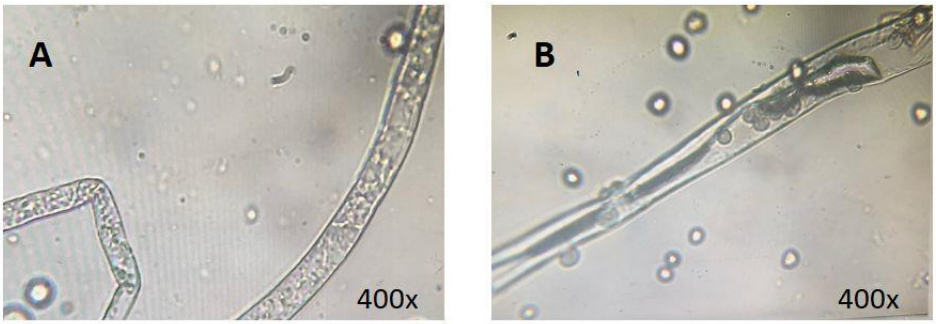

Figure 2. Assessment of mycelial morphology in *Rhizopus stolonifer* following 5 day incubation. Comparison between CK (**A**) and 0.5% *w*/*v* CAC (**B**) treatment groups.

Rhizopus stolonifer propagates through the formation of spores and the growth of mycelia. Disrupting the structure of *Rhizopus stolonifer* is an effective strategy to reduce its vitality and impair its physiological processes. Wang et al. [24] demonstrated that 1-octen-3-ol could inhibit *Rhizopus stolonifer* by increasing membrane permeability, altering mycelial morphology, and disrupting organelle structure. Likewise, Nickerson and Leastman [25] described in detail the inhibitory effects of cyanobacteria on the mitochondrial biosynthesis of *Rhizopus stolonifer*, which resulted in impaired sporulation and germ tube formation. In this study, the 0.5% CAC treatment can reduce fungal activity by destroying the mycelial structure and inhibiting mycelial growth. Thus, we conclude that the 0.5% CAC treatment could effectively prevent the occurrence of soft rot in sweet potato.

3.2. Physiological Response of Sweet Potato to Soft Rot After 0.5% w/v CAC Treatment

3.2.1. Effect of 0.5% *w*/*v* CAC Pretreatment on the Infection Process of *Rhizopus stolonifer*

Phenotype is a direct reflection of the genetic traits and environmental conditions of organisms. The assessment of disease management, preservation, and storage efficacy can be effectively conducted through phenotypic observation [26]. The progression of disease in various sweet potato tissues following *Rhizopus stolonifer* infection was examined. Upon examination of the longitudinal sections, it was observed that the propagation of sweet potato disease spots was minimal, with the primary mode of infection being lateral rather than vertical (Figure 3A). A cross-sectional examination of the inoculated sites in sweet potato tubers disclosed distinct patterns of disease advancement. Specifically, at the 3 day mark post-inoculation, brown discoloration emerged at the extremities of the tubers within the CK, with the central region remaining unaffected. By the 7th day, signs of rot became evident at both ends, and the middle part showed signs of browning. Subsequent to the 0.5% *w*/*v* CAC treatment, the expansion of lesions was curtailed across all tuber sections, in contrast to the CK tubers which had escalating lesion progression, tissue discoloration,

and eventual internal decay (Figure 3B). In this study, the results underscore the potency of 0.5% *w*/*v* CAC in mitigating *Rhizopus stolonifer* infections and curtailing the incidence of soft rot. It is hypothesized that the variation in disease spot size might be attributed to the delayed activation of some defense mechanisms in sweet potato immediately after the 0.5% CAC treatment.

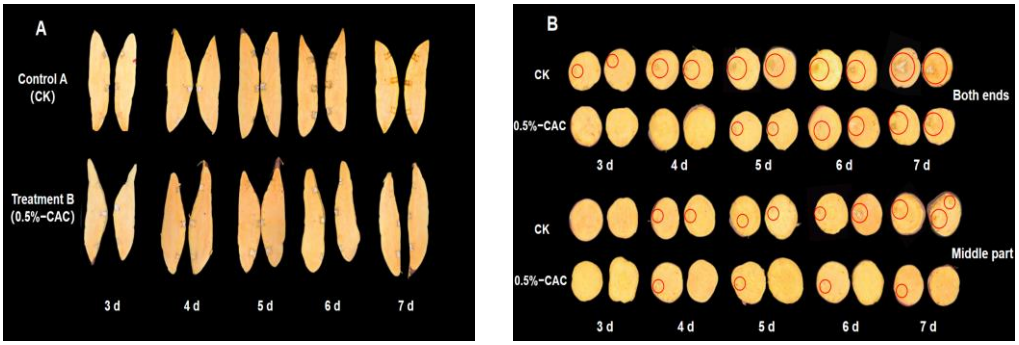

Figure 3. Phenotypes and lesion progression in distinct sweet potato tuber sections post-*Rhizopus stolonifer* inoculation. Vertical phenotypes (**A**) and cross-sectional lesion expansion (**B**).

3.2.2. Effect of 0.5% *w*/*v* CAC Pretreatment on Texture Characteristics Under Soft Rot Stress

Hardness and cohesiveness are key indicators of texture, signifying a material's resistance to deformation and its internal binding strength. Zhao et al. [27] found that greater hardness in sweet potato was associated with stronger resistance to soft rot. In this study, similar findings were observed (Figure 4). The CK experienced a rapid decrease in textural attributes after 2 day, whereas the group treated with 0.5% *w*/*v* CAC exhibited a slower rate of textural degradation, with significant softening only after 3 day. By the 7th day, sweet potato subjected to the 0.5% *w*/*v* CAC treatment retained 3.57% and 4.88% greater cohesiveness in the middle part and both ends, respectively, than those in the CK (Figure 4A). Correspondingly, hardness in the CAC-treated tubers was elevated by 12.58% and 10.42% in the middle and both end sections compared to the CK (Figure 4B). Sweet potato treated with 0.5% *w*/*v* CAC exhibited better texture characteristics, speculating that this treatment can improve the soft rot resistance by maintaining the texture characteristics.

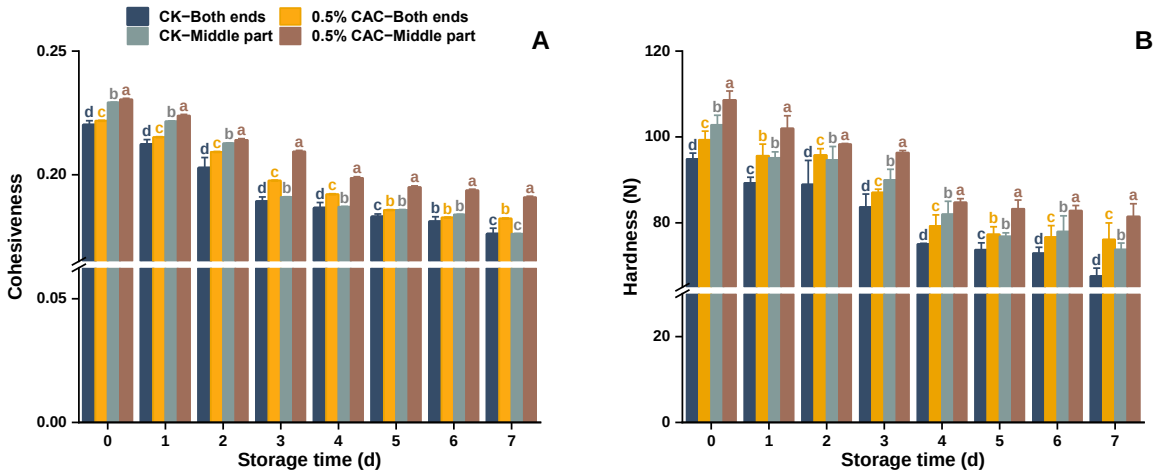

Figure 4. Cohesiveness (**A**) and hardness (**B**) changes in various sweet potato tuber sections during a 7 day *Rhizopus stolonifer* infection. Significant differences ($p < 0.05$) between means are indicated by letters above the histogram bars.

3.2.3. Effect of 0.5% *w*/*v* CAC Pretreatment on the Activity of Defense-Related Enzymes Under Soft Rot Stress

POD is an important oxidoreductase that plays a crucial role in the response to pathogen attack, oxidative stress, and other challenges. It facilitates the conversion of tissue carbohydrates into lignin. This process enhances lignification, thereby contributing to plant protection [28]. In this study, the application of 0.5% *w*/*v* CAC significantly boosted POD activity when compared to the CK (Figure 5A). POD activity in sweet potato tubers demonstrated a biphasic trend, peaking on the fifth day post-treatment. Specifically, on the fifth day, the POD activity in the middle of the CK exceeded that of both ends by 11.08%, while in the 0.5% *w*/*v* CAC treated group, the middle part showed a 2.14% higher activity than both ends. On the fifth day, the POD activity in both ends and the middle part of the CAC-treated tubers was notably higher, being 2.74 and 2.52 times greater, respectively, than that of the CK. Liu et al. [9] and Wang et al. [29] reported similar results and showed that enhanced POD activity could improve disease resistance. It is postulated that the 0.5% *w*/*v* CAC treatment activates defense mechanisms, triggers lignification, and strengthens the cell wall, thereby enhancing sweet potato resistance and impeding *Rhizopus stolonifer* infection.

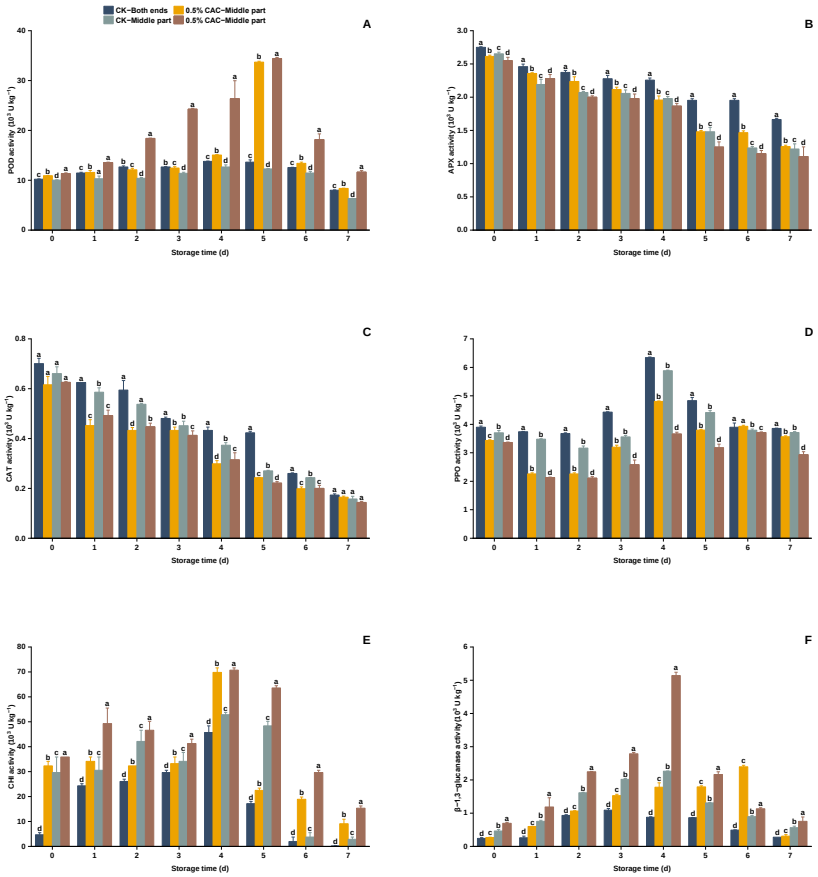

Figure 5. Defense-related enzyme activities were assessed in different treatment groups of sweet potato over 7 day of storage. The enzymes analyzed included POD (**A**), APX (**B**), CAT (**C**), PPO (**D**), CHI (**E**), and GLU (**F**). Significant differences ($p < 0.05$) between means are indicated by letters above the histogram bars.

H_2O_2 is a key component of the disease resistance mechanism in fruits and vegetables. A decrease in the activities of APX and CAT facilitates the accumulation of H_2O_2, which aids in the lignification process of damaged tissues, thereby creating a barrier that can mitigate the spread of pathogens [30,31]. The role of APX and CAT in induced resistance can vary among different plant species or even among different tissues within the same plant [32].

Zhu et al. [33] found that methyl jasmonate enhances the expression and activity of CAT and APX, which scavenges excess H_2O_2 and reduces protein oxidative damage, leading to induced resistance against gray mold in tomatoes. Conversely, Wang et al. [34] reached the different conclusion in rice. In this study, the activities of APX and CAT generally declined across all treatment groups. The treatment with 0.5% w/v CAC notably reduced APX and CAT activities compared to the CK. Specifically, on the 7th day of storage, APX activity was reduced by 24.44% and 9.29% at the ends and middle of CAC-treated sweet potato, respectively, compared to the CK (Figure 5B). Correspondingly, CAT activity in these sections was respectively reduced by 5.04% and 8.80% (Figure 5C). It is hypothesized that the enhancement of sweet potato disease resistance is mediated by the inhibition of APX and CAT activities, thus promoting H_2O_2 accumulation and potentially contributing to the plant defense response.

PPO is a pivotal enzyme in the browning process of fruits and vegetables; increased activity of PPO correlates with enhanced browning, softening, and accelerated senescence in fruits and vegetables [35,36]. Sweet potato treated with 0.5% w/v CAC exhibited superior phenotypic qualities compared to the CK upon infection, delaying the onset of browning (Figure 3). During storage, PPO activity in sweet potato tubers followed a biphasic trend, peaking on the fourth day of the observation period. Notably, the application of 0.5% w/v CAC significantly dampened PPO activity across all sections compared to the CK (Figure 5D). Specifically, on the fourth day, PPO activity decreased by 24.26% in the end sections and by 37.77% in the middle sections of the CAC-treated tubers. Lin et al. [37] reported similar results and showed that enhancing PPO activity through ε-poly-L-lysine treatment could suppress postharvest diseases in passion fruit caused by *Lasiodiplodia theobroma*. It is inferred that the 0.5% w/v CAC treatment may bolster the sweet potato's disease resistance by curbing phenol oxidation via PPO.

CHI and GLU, as pathogenesis-related (PR) proteins, are integral to the plant's defense mechanism against fungal pathogens. These enzymes degrade the cell walls of invading fungi, thereby providing a direct line of defense [38,39]. CHI is commonly found in fruits and vegetables and enhances resistance to disease by breaking down chitin, a component of fungal cell walls. Meanwhile, GLU activity is closely associated with the postharvest disease resistance of fruits and vegetables, as it is influenced by various abiotic and biotic factors [40]. Zhang et al. [41] reported that oleanolic and ursolic acids can enhance fruit resistance to gray mold by increasing CHI and GLU activities, thus slowing down fruit rot. This correlation between enhanced disease resistance and elevated CHI and GLU activities was further supported by Ye et al. [42] and Zhou et al. [43] in their respective studies. Similar results were found in this experiment. CHI activity displayed a biphasic trend, reaching its zenith on the fourth day before in comparison to the CK (Figure 5E). Specifically, on the fourth day of storage, CHI activity in both ends and the middle sections of the CAC-treated sweet potato was increased by 52.73% and 33.78%, respectively, relative to the CK. Similarly, GLU activity reflected a biphasic pattern, peaking on the fourth day. Throughout the storage period, the 0.5% w/v CAC treatment group consistently demonstrated significantly higher GLU activity in comparison to the CK. On the fourth day, the GLU activity in both ends and the middle sections of the CAC-treated sweet potato was 1.03 and 1.28 times, respectively, higher than that observed in the CK group (Figure 5F). This study underscores the potential of CAC treatment in strengthening the defensive capabilities of sweet potato against soft rot, likely through the modulation of PR protein activity, which could have significant implications for postharvest management and food security.

In conclusion, the 0.5% w/v CAC treatment changed the activity of defense-related enzymes and improved the resistance of sweet potato to soft rot.

3.2.4. Effect of 0.5% *w*/*v* CAC Pretreatment on the Cell Wall-Degrading Enzymes Under Soft Rot Stress

PG and Cx are pivotal cell wall-degrading enzymes that play a significant role in the deterioration of plant tissue [44,45]. Cao et al. [46] established a correlation between elevated activities of these cell wall enzymes and the accelerated spoilage of sweet potato. During storage, PG activity increased with storage period in both treatment groups. However, it remained consistently lower in the 0.5% CAC group in comparison to the CK (Figure 6A). Specifically, on the 7th day, the PG activity in both ends and the middle sections of the CAC-treated sweet potato was reduced by 16.62% and 13.49%, respectively, compared to the CK. The activity of Cx showed a biphasic pattern, reaching its peak on the fourth day of storage across both treatment groups. Nevertheless, the Cx activity was consistently lower in the 0.5% CA-treated group compared to the CK group (Figure 6B). On the critical fourth day, the Cx activity decreased by 24.47% and 18.61% in the ends and middle sections of the CAC-treated sweet potato, respectively, compared to the CK. This suggests that the 0.5% *w*/*v* CAC treatment can effectively inhibit the activity of cell wall-degrading enzymes and delay spoilage of sweet potato. This conclusion mirrors the findings shown in Figure 3. It is hypothesized that the modulation of PG and Cx activity through CAC treatment could be a strategic approach to enhance the durability of sweet potato against postharvest diseases.

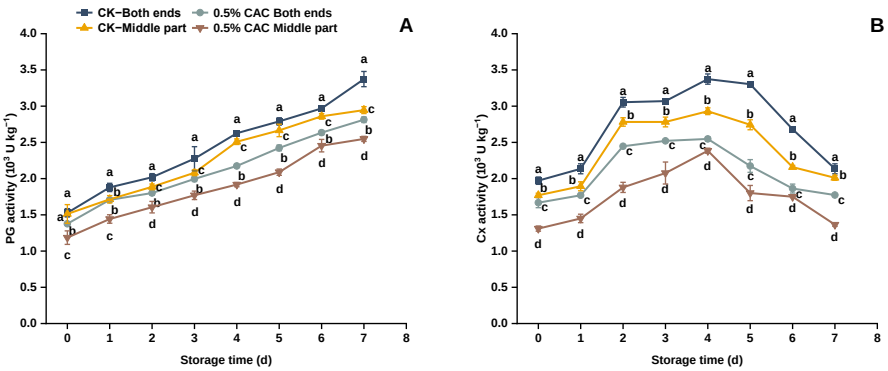

Figure 6. PG activity (**A**) and Cx activity (**B**) in different treatment groups of sweet potato over 7 day of storage. Significant differences between the means ($p < 0.05$) are indicated by the letters above the line chart.

3.2.5. Effect of 0.5% *w*/*v* CAC Pretreatment on the Phenylpropane Metabolic Pathway Under Soft Rot Stress

The phenylpropanoid metabolic pathway plays a key role in plant defense mechanisms [47,48]. PAL is the rate-limiting enzyme in the phenylalanine pathway and catalyzes the conversion of L-phenylalanine to antimicrobial compounds, including phenols and flavonoids. This pathway is upregulated in response to plant stress, enhancing disease resistance [49]. Phenolic compounds and flavonoids are recognized for their antioxidant and antimicrobial properties [50,51]. These compounds accumulate in plant tissues upon pathogen invasion, forming a protective barrier [52]. In this study, it was found that all parts of the tuber activated the phenylpropanoid metabolic pathway following 0.5% CAC *w*/*v* treatment. The activity of PAL exhibited a biphasic pattern, initially increasing to reach a peak on the fourth day. In all treatment groups, the PAL activity was lower at both ends of the sweet potato than in the middle section. The treatment with 0.5% *w*/*v* CAC significantly increased PAL activity compared to the CK (Figure 7A). In particular, on the fourth day, the PAL activity in the end and middle sections of the CAC-treated sweet potato was increased by 72.49% and 56.09%, respectively, compared with the CK. The 0.5% *w*/*v* CAC treatment significantly increased the total phenol content in comparison to the CK (Figure 7B). In particular, on the fourth day, the total phenol content in both ends and the middle sections

of the CA-treated sweet potato was increased by 13.21% and 13.08%, respectively. Similarly, the 0.5% w/v CAC treatment also significantly augmented the flavonoid content when compared to the CK (Figure 7C). On the fifth day, the flavonoid content in both ends and the middle sections of the CAC-treated sweet potato was increased by 4.43% and 10.56%, respectively, relative to the CK. These findings align with Liu et al. [9], who reported similar results regarding the activation of the phenylpropanoid pathway. It is hypothesized that the modulation of the metabolic pathway of phenylpropane through CAC treatment could be a strategic approach to enhance the durability of sweet potato against postharvest diseases.

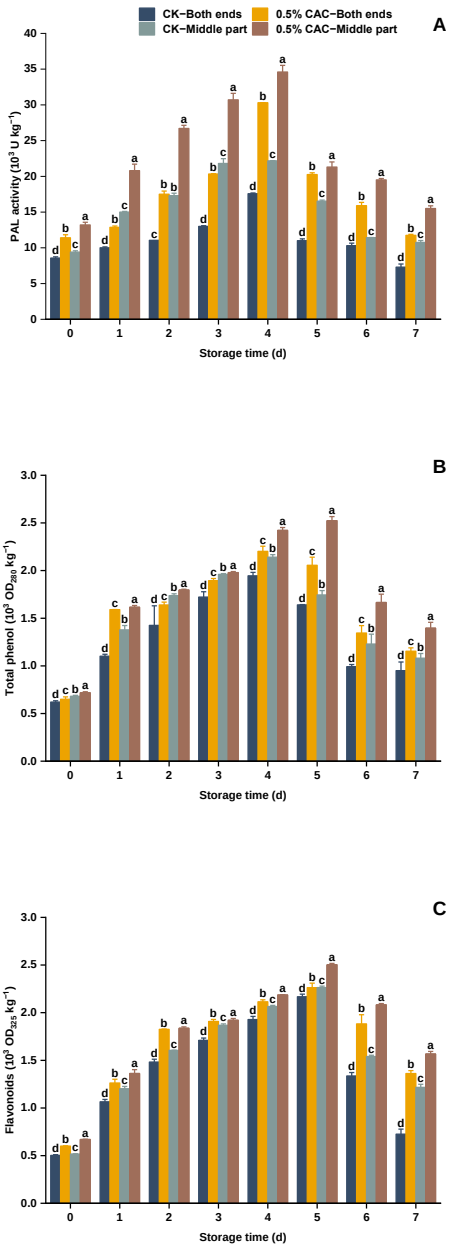

Figure 7. Changes in PAL (**A**), total phenol (**B**), and flavonoid (**C**) content in different treatment groups of sweet potato over 7 day of storage. Significant differences ($p < 0.05$) between means are indicated by letters above the histogram bars.

3.2.6. Effect of 0.5% w/v CAC Pretreatment on the Nutritional Quality Under Soft Rot Stress

Protein and soluble sugar content are critical nutritional parameters in sweet potato, significantly influencing both nutritional value and organoleptic properties [53]. The group

treated with 0.5% *w*/*v* CAC consistently maintained higher protein and soluble sugar content levels than the CK (Figure 8A,B). On the 7th day, the protein content of the 0.5% CAC group increased by 33.87% overall compared to the CK, with the protein content in the center increasing by 9.45%. On the 7th day, the soluble sugar content was 1.76% higher overall and 5.27% higher in the middle section of the 0.5% *w*/*v* CAC group relative to the CK. The protein content showed a decline during the storage period in both treatment groups, which may be related to the deterioration of protein after the attack of disease during storage. The soluble sugar content of both groups showed an increasing trend during storage, which may be related to the saccharification reaction during storage [54]. Building on the work of Chandrajith et al. [55], this study demonstrated that postharvest treatment with 0.5% *w*/*v* CAC was effective in preserving these key nutrients. This finding is particularly important for optimizing storage strategies to ensure the retention of essential dietary components.

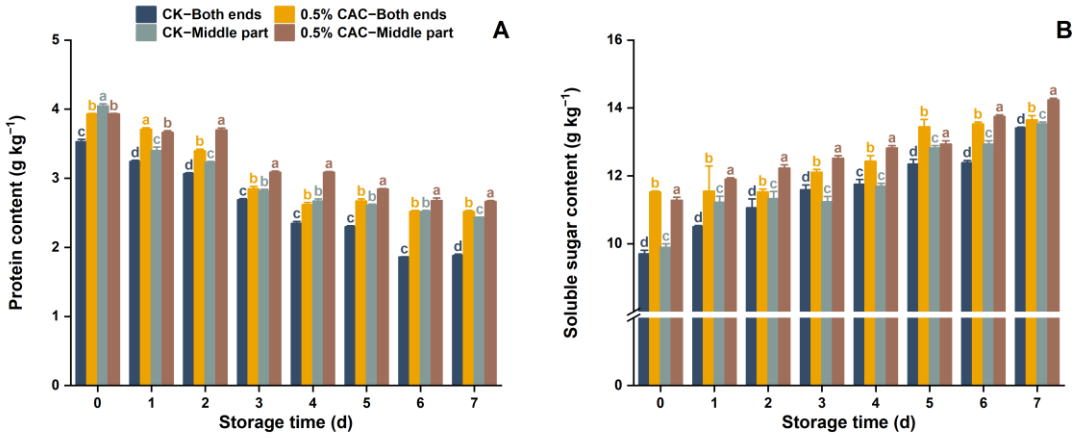

Figure 8. Changes in protein (**A**) and soluble sugar (**B**) content in different sweet potato tuber sections over 7 day of storage under CK and 0.5% *w*/*v* CAC treatment conditions. Significant differences ($p < 0.05$) between means are indicated by letters above the histogram bars.

3.3. Principal Component Analysis and Comprehensive Evaluation of Storage Quality of Sweet Potato Treated with 0.5% w/v CAC

Assessing postharvest fruit quality is a complex task that often requires the evaluation of multiple parameters, presenting a challenge for comprehensive assessments [11]. PCA has established itself as an invaluable tool in the analysis of biological shapes and postharvest studies [56]. Chu et al. [57] effectively employed PCA to create a comprehensive quality evaluation model for lilies, highlighting the benefits of steam blanching and CAC treatment in preventing browning and maintaining nutritional value. To ascertain the impact of a 0.5% *w*/*v* CAC treatment on enhancing the resistance to soft rot in sweet potato, PCA was applied in this study to assess tuber quality. Each index is simplified into three principal components (Table 1). Flavonoids and total phenols showed the highest loadings on PC1, mainly reflecting the accumulation of antimicrobial compounds. Hardness, cohesion, and protein exhibited the highest loadings on PC2, suggesting that this component primarily elucidated the textural properties of the samples. PC3 was most affected by the loading of soluble sugar, indicating its role in contributing to the overall nutritional quality (Table 2). The characteristic vector of the principal component coefficient is derived by dividing the load coefficient by its corresponding characteristic root, as detailed in Table 3. The linear variances of the three principal components and a comprehensive evaluation equation are obtained as follows:

$$F_1 = -0.33\,X_1 - 0.02\,X_2 + 0.45\,X_3 - 0.65\,X_4 + 1.58\,X_5 + 3.01\,X_6 \quad (1)$$

$$F_2 = -0.43\ X_1 - 0.56\ X_2 + 0.63\ X_3 + 0.22\ X_4 - 0.08\ X_5 + 0.56\ X_6 \quad (2)$$

$$F_3 = 0.21\ X_1 + 0.45\ X_2 + 0.42\ X_3 - 0.79\ X_4 + 0.22\ X_5 - 0.80\ X_6 \quad (3)$$

$$F_{all} = 0.40\ F_1 + 0.27\ F_2 + 0.18\ F_3 \quad (4)$$

Table 1. Principal component analysis of variance.

Indicators	Eigenvalues	Variance Contribution Rate (%)	Cumulative Variance Contribution Rate (%)
Hardness	2.39	39.81	39.81
Cohesion	1.36	22.64	62.44
Protein	1.08	17.97	80.41
Soluble sugar	0.70	11.70	92.11
Flavonoids	0.36	6.42	98.53
Total Phenol	0.09	1.47	100.00

Table 2. Principal component load matrix.

Indicators	PC1	PC2	PC3
Hardness	−0.51	0.66	0.32
Cohesion	−0.02	−0.66	0.52
Protein	0.46	0.66	0.43
Soluble sugar	−0.47	0.18	0.67
Flavonoids	0.95	−0.05	−0.13
Total Phenol	0.89	0.17	−0.24

Table 3. Principal component feature vectors.

Indicators	PC1	PC2	PC3
Hardness	−0.33	0.43	0.21
Cohesion	−0.02	−0.56	0.45
Protein	0.45	0.63	0.42
Soluble sugar	−0.56	0.22	−0.79
Flavonoids	1.58	−0.08	0.22
Total Phenol	3.01	0.56	−0.80

The comprehensive score of each treatment was calculated according to Equation (4). Throughout the storage period, scores were consistently higher in the 0.5% *w*/*v* CAC treatment group relative to the CK. In each treatment group, the middle sections of the tubers exhibited higher scores than those at both ends (Figure 9A). These findings indicated that after infection by *Rhizopus stolonifer*, the middle tissue maintained better quality than the two ends and that 0.5% *w*/*v* CAC treatment maintained better quality than CK.

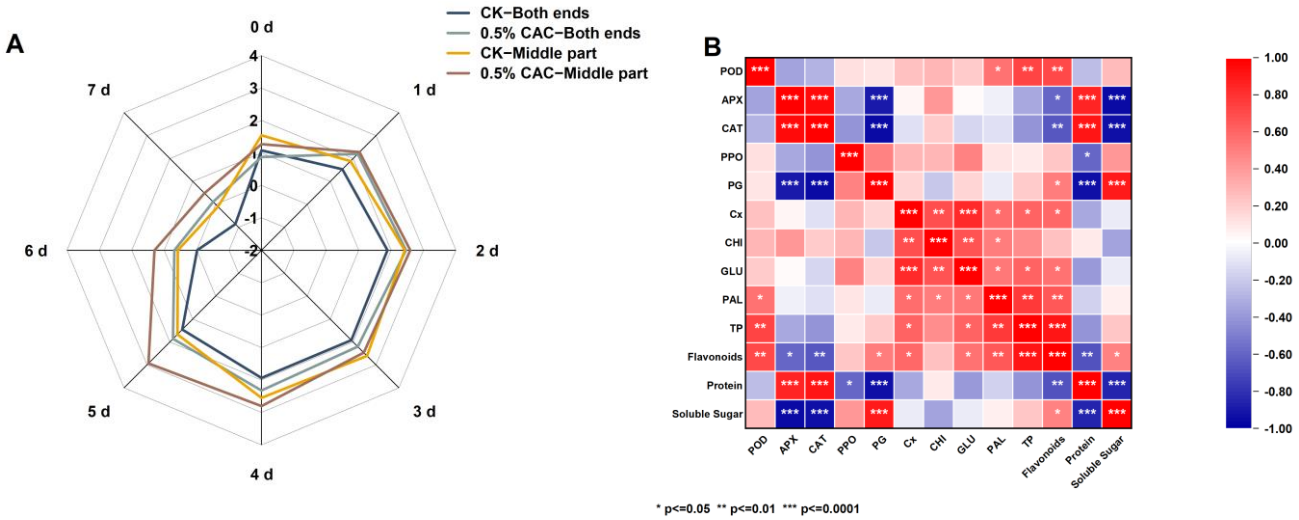

Figure 9. Comprehensive score (**A**) of storage characteristics of sweet potato in different treatment groups. Correlation analysis (**B**) between independent indicators.

3.4. Correlation Analysis of Storage Quality of Sweet Potato Treated with 0.5% CAC

Plant disease resistance is a complex process that involves numerous metabolic pathways, some of which may work synergistically, while others may have inhibitory effects [58]. Conducting a correlation analysis of each index can help elucidate the mechanisms underlying resistance to soft rot, which is induced by 0.5% *w*/*v* CAC. Correlation analysis revealed that POD levels were positively associated with phenylpropane metabolism. APX activity correlated positively with CAT and inversely with PG. These enzymes exhibited positive relationships with flavonoids and soluble sugar but a negative one with proteins. Phenylpropane metabolism was positively correlated with Cx, CHI, and GLU. Protein was negatively correlated with soluble sugar (Figure 9B). The results indicated that during the 0.5% *w*/*v* CAC-induced resistance to soft rot in sweet potato, there is a cooperative relationship between the phenylpropanoid metabolic pathway, the cell wall metabolic pathway, pathogenesis-related (PR) proteins, and antioxidant enzymes. This relationship provides a direction for further understanding of the mechanism of sweet potato soft rot resistance and is significant for developing disease-resistant crop varieties.

4. Conclusions

This study has conclusively demonstrated that a 0.5% *w*/*v* CAC treatment significantly inhibits the growth and development of *Rhizopus stolonifer*, the causative agent of sweet potato soft rot. Notably, the middle part of the sweet potato tuber exhibited a heightened innate resistance to infection compared to both ends, highlighting the importance of standardized sampling for accurate assessment. Furthermore, the 0.5% *w*/*v* CAC treatment enhances sweet potato resistance to soft rot through multiple mechanisms. The application of the 0.5% *w*/*v* CAC treatment induced the accumulation of defense-related compounds, including phenolics and flavonoids, while also suppressing the activity of cell wall-degrading enzymes. These synergistic effects were crucial for maintaining the nutritional quality and textural integrity of sweet potato during storage. Due to its efficacy and environmental friendliness, the 0.5% *w*/*v* CAC treatment emerges as a promising strategy for extending the shelf life of sweet potato and for managing soft rot. The findings from this study provide valuable insights that can inform the refinement of preservation and storage practices for sweet potato, potentially influencing future horticultural and postharvest strategies.

Author Contributions: Investigation: Y.C., L.P., J.B., W.Y., Y.Z., M.S.G. and G.L.; writing—original draft: Y.C., L.P. and G.L.; data curation: Y.C., L.P., J.B., W.Y. and G.L.; methodology: Y.Z., M.S.G. and Z.L.; writing—editing: Y.C., L.P. and G.L.; funding acquisition: G.L. and Z.L.; formal analysis: Z.L.; methodology: Y.Z., M.S.G. and Z.L. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest.

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