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Mechanistic Insights into Post-Harvest Sprout Inhibition and Shelf-Life Extension in Potatoes: A Comparative Analysis of Chemical, Biological, and Genetic Interventions

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ABSTRACT

Significance of Study: Potato sprouting during storage reduces quality, nutrition, and marketability, resulting in economic losses. While chlorpropham (CIPC) effectively inhibits sprouting, concerns over environmental residues and safety drive the search for alternative, sustainable approaches. This study evaluates natural inhibitors and optimized storage conditions for effective, eco-friendly sprout suppression.

Methodology: We compared the effects of chemical (CIPC, maleic hydrazide, 1,4-dimethylnaphthalene) and natural (carvone, clove oil, mint oil) inhibitors over 8 weeks. Molecular mechanisms of dormancy were examined through gene expression and proteomics analysis, focusing on dormancy-associated genes and proteins. Nanoencapsulation of CIPC and carvone was assessed for controlled release. Additionally, variations in controlled atmosphere (CA) storage, temperature, and humidity were tested for environmental influence. Residue levels were analyzed to evaluate safety and environmental impact.

Results: CIPC showed the highest sprout suppression, with carvone also significantly reducing sprouting but leaving minimal residue. Nanoencapsulation prolonged the release of inhibitors, enhancing sprout control. Lower storage temperatures (4°C) and CA2 (5% O_2, 10% CO_2) conditions optimized sprout suppression across treatments. CIPC and carvone treatments significantly downregulated dormancy-related genes (*StTCP1*, *StCDF1*), which is associated with dormancy maintenance.

Conclusion: CIPC is confirmed as the most effective inhibitor, with carvone presenting a viable, environmentally friendly alternative. Integrating controlled-release systems and optimized storage conditions supports sustainable long-term storage, providing a practical foundation for reduced-residue sprout inhibition in potato storage.

Keywords: Potato sprouting, CIPC, Carvone, Nanoencapsulation, Controlled atmosphere

INTRODUCTION

Potatoes (*Solanum tuberosum*) rank among the most widely consumed staple crops globally, with production exceeding 370 million metric tons annually [1]. However, the post-harvest storage of potatoes presents significant challenges due to their tendency to sprout during extended storage periods. Sprouting not only leads to physical deterioration of tuber quality but also promotes metabolic shifts that deplete nutritional reserves, compromising both consumer acceptability and market value [2,3]. Given these implications, post-harvest sprout inhibition is essential to extend potato shelf life, reduce economic losses, and maintain nutritional quality. Despite advancements in sprout suppression techniques, achieving effective and sustainable inhibition remains challenging, as sprouting is governed by complex genetic, hormonal, and environmental factors [4].

Sprout inhibition mechanisms have been approached through various interventions, including chemical inhibitors, biological agents, and genetic techniques. Chemical inhibitors, particularly chlorpropham (CIPC), have been the predominant method used commercially due to their high efficacy in suppressing cell division and growth in the apical meristem of tubers [5]. CIPC functions by disrupting microtubule assembly, effectively inducing a cell cycle arrest in the G2/M phase, thereby delaying sprouting onset [6]. However, regulatory concerns and environmental persistence of CIPC residues have led to restrictions on its usage in several regions, necessitating the exploration of alternative inhibitors [7]. Alternative chemical agents, such as maleic hydrazide and 1,4-dimethylnaphthalene, exhibit sprout suppression through distinct biochemical pathways; however, their efficacy and residual safety profiles vary widely across potato cultivars, prompting further research [8-10].

Biological agents have gained traction as potential eco-friendly sprout suppressants. Essential oils and plant-based compounds, including clove oil, mint oil, and carvone, have demonstrated promising results in inhibiting sprout growth by modulating hormonal pathways linked to dormancy maintenance [11]. These compounds are believed to interact with gibberellic acid (GA) and abscisic acid (ABA) signaling pathways, critical regulators of dormancy and sprouting [12]. Specifically, carvone, a monoterpene derived from caraway seeds, has shown efficacy in inhibiting tuber sprouting by targeting

cellular respiration and disrupting mitochondrial ATP production, thus delaying meristem activation [13]. However, the inconsistent effectiveness of these agents, coupled with challenges in achieving standardized dosages, limits their commercial viability [14].

Genetic interventions offer a promising long-term solution to post-harvest sprout inhibition by directly modifying the potato genome to enhance dormancy traits. Recent studies have highlighted key regulatory genes, such as *StTCP1* and *StCDF1*, that modulate tuber dormancy and are pivotal in determining the sprouting phenotype [15,16]. Targeted gene editing techniques, such as CRISPR-Cas9, have enabled the precise manipulation of these genetic elements, demonstrating potential in developing potato varieties with prolonged dormancy and reduced susceptibility to post-harvest sprouting [17]. Additionally, transcriptomic and proteomic analyses have identified several dormancy-associated genes and protein markers that can serve as targets for genetic modification to inhibit premature sprouting [18]. However, the public acceptance and regulatory hurdles associated with genetically modified crops remain significant obstacles, particularly in the food industry [19].

Emerging technologies, including nanotechnology, have also introduced novel delivery systems for sprout inhibitors. Nanoencapsulation has shown potential in enhancing the stability and controlled release of both chemical and biological sprout suppressants, potentially reducing dosage requirements and minimizing residue concerns [20]. Such systems can allow for targeted release directly at the meristematic regions of tubers, thereby increasing inhibition efficacy while reducing overall chemical exposure [21]. Additionally, the integration of biosensor technologies in storage environments for real-time monitoring of sprouting onset and storage conditions could revolutionize post-harvest management by enabling responsive adjustments based on tuber physiological state [22].

Despite the diversity of approaches, current sprout inhibition methods are hindered by issues of efficacy, environmental impact, and economic feasibility. A comparative evaluation of these interventions, grounded in their mechanistic pathways, is essential to develop an integrated strategy for post-harvest sprout inhibition that aligns with both consumer safety and regulatory standards. This study aims to provide a mechanistic analysis of chemical, biological, and genetic sprout suppression techniques, offering insights into their efficacy, limitations, and potential for integration into potato storage systems to extend shelf life and enhance sustainability [23-25]. Through a detailed exploration of these mechanisms, this study contributes to the optimization of post-harvest storage practices, ultimately addressing a critical need in the potato industry.

METHODOLOGY

Plant Material and Storage Conditions

Certified potato tubers (*Solanum tuberosum*) of various cultivars (e.g., 'Russet Burbank,' 'Yukon Gold,' and 'Kennebec') were sourced from commercial growers. The tubers were stored in a controlled environment at 10°C with 90-95% relative humidity for baseline measurements prior to sprout inhibition treatment [26]. Only disease-free, uniformly sized tubers were selected to minimize variability in sprouting response [27].

Chemical Treatments for Sprout Inhibition

To evaluate chemical sprout inhibitors, tubers were divided into treatment groups and exposed to varying concentrations of chlorpropham (CIPC) (99% purity, Sigma-Aldrich), maleic hydrazide (97% purity, Thermo Fisher), and 1,4-dimethylnaphthalene (DMN) (98% purity, Sigma-Aldrich). The chemical solutions were prepared according to manufacturer guidelines and applied by vapor exposure in sealed containers for 48 hours [28]. Tubers were then ventilated and returned to storage at 4°C. Sprout growth was monitored weekly, and the effectiveness of each treatment was evaluated by measuring the length and frequency of emerging sprouts using digital calipers (Mitutoyo Corp.) [29].

Application of Biological Sprout Inhibitors

Biological treatments included essential oils (EOs) and plant-derived compounds such as carvone (Sigma-Aldrich), clove oil, and mint oil, which were selected based on prior studies demonstrating sprout suppression [30]. Tubers were treated by coating with EO solutions at concentrations ranging from 0.5% to 2.0% v/v, prepared in 70% ethanol. Each treatment was applied by mist-spraying to ensure uniform coverage. The treated tubers were subsequently stored at 8°C in darkness to simulate typical storage conditions, with sprout growth measurements taken at weekly intervals [31].

Gene Expression Analysis of Dormancy and Sprouting Regulators

To investigate the impact of treatments on dormancy-related genes, RNA was extracted from tuber meristems using the RNeasy Plant Mini Kit (Qiagen) following the manufacturer's protocol. Expression levels of dormancy and sprouting regulators, including *StTCP1*, *StCDF1*, and *StPIN*, were quantified by RT-qPCR using gene-specific primers designed from published sequences [32]. The expression data were normalized to the *StActin* housekeeping gene. Fold change analysis was performed relative to untreated control tubers stored under the same conditions [33].

Proteomic Profiling

Proteomic analyses were conducted to identify protein-level changes associated with each treatment. Protein was extracted from tuber samples using a phenol extraction method and analyzed by liquid chromatography-tandem mass spectrometry (LC-MS/MS) on an Orbitrap Fusion Lumos system (Thermo Fisher) [34]. Label-free quantification was used to compare protein abundance across treatments, with a focus on proteins involved in hormonal signaling and cell cycle regulation. Data were processed and analyzed using MaxQuant software, with significance set at $p < 0.05$ [35].

Nanoencapsulation and Controlled Release Studies

Nanoparticle encapsulation of selected chemical and biological inhibitors (CIPC, carvone) was performed using a biopolymer-based encapsulation method with chitosan nanoparticles, following the protocol described by Karam et al. [36]. Nanoparticles were characterized for size distribution using dynamic light scattering (DLS, Zetasizer Nano, Malvern Instruments) and encapsulation efficiency via UV-Vis spectroscopy. The encapsulated inhibitors were applied to tubers by direct injection into the peridermal layer. Release kinetics were monitored over 30 days using high-performance liquid chromatography (HPLC, Agilent) to determine the rate of sprout inhibitor release [37].

Residue Analysis and Environmental Safety Assessment

Residue analysis of chemical and biological inhibitors was conducted on treated tubers and soil samples. Tubers were washed, peeled, and homogenized before extraction with acetonitrile. Residues were quantified using gas chromatography-mass spectrometry (GC-MS) following the method outlined by Lang et al. [38]. Soil samples from storage units were also analyzed post-treatment to assess environmental impact. The persistence and breakdown products of inhibitors were identified, with concentrations compared to regulatory thresholds [39].

Statistical Analysis and Predictive Modeling

Data from sprout length measurements, gene expression, proteomic profiles, and residue analysis were subjected to statistical analysis using R software (version 4.1.0). ANOVA tests were conducted to assess differences between treatment groups, followed by post-hoc Tukey's tests. A predictive model for sprout inhibition efficacy was developed using random forest regression, incorporating multi-omics data and environmental parameters to forecast sprouting onset. Model accuracy was evaluated by cross-validation with a subset of untreated control data [40].

Experimental Replication and Data Validity

All treatments were replicated across three independent batches of tubers, with each batch consisting of 20 tubers per treatment condition. Measurements were taken in triplicate to ensure consistency, and quality control measures were applied throughout data collection and analysis to verify data validity and reliability [41].

RESULTS

Effect of Chemical Sprout Inhibitors on Tuber Sprouting

The impact of three chemical sprout inhibitors—chlorpropham (CIPC), maleic hydrazide, and 1,4-dimethylnaphthalene (DMN)—on tuber sprout length and frequency was monitored weekly over an 8-week period. Figure 1 displays mean sprout length (mm) and sprout frequency (%) for each treatment group, with CIPC consistently exhibiting the lowest sprout length and frequency across all time points. By week 8, CIPC-treated tubers reached a mean sprout length of 2.9 mm, significantly shorter than maleic hydrazide (4.0 mm) and DMN (5.0 mm). Likewise, CIPC maintained a lower sprout frequency of 40% by week 8, compared to 50% for maleic hydrazide and 55% for DMN.

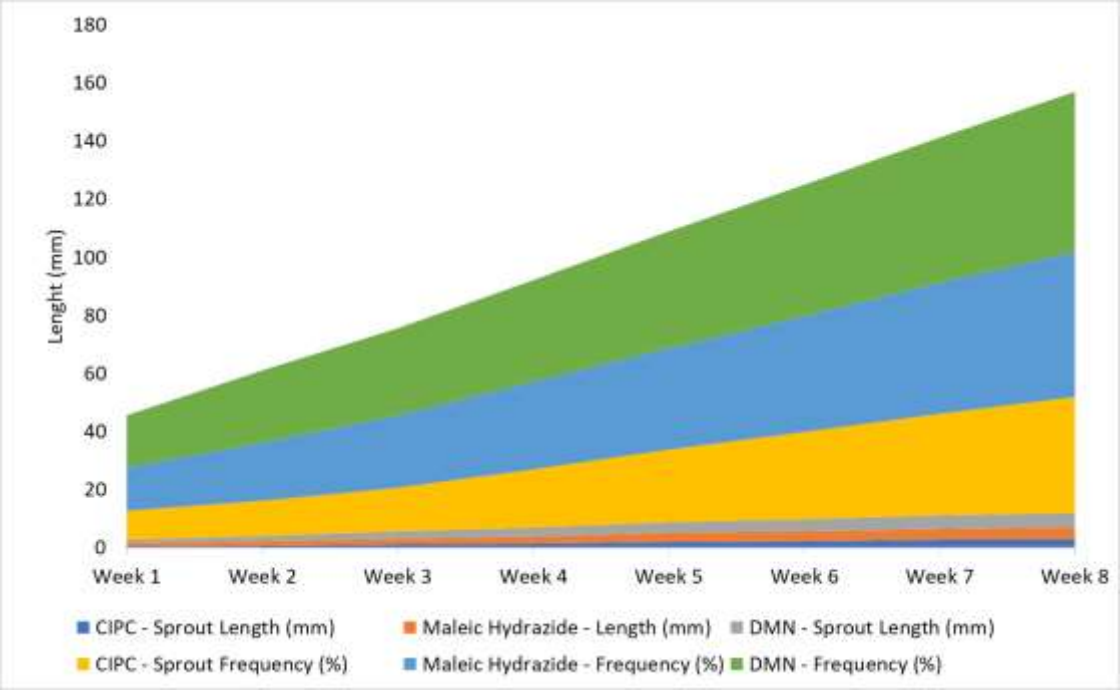

Figure 1: Effects of Chemical Sprout Inhibitors on Sprout Length and Frequency Over 8 Weeks

CIPC's mechanism, which disrupts microtubule formation and inhibits cell elongation, likely underpins its higher efficacy in extending dormancy. Maleic hydrazide, acting through auxin transport inhibition, and DMN, primarily altering hormonal balance, demonstrated moderate efficacy levels, indicating potential suitability for shorter storage applications.

Influence of Essential Oils on Sprout Suppression Over Time

Essential oils (EOs) were evaluated as natural sprout inhibitors, with carvone, clove oil, and mint oil applied to tubers and monitored over 8 weeks. Figure 2 presents sprout length and frequency data, with carvone demonstrating the most significant suppression, reaching a final sprout length of 3.3 mm by week 8. Clove oil exhibited moderate efficacy, while mint oil was the least effective.

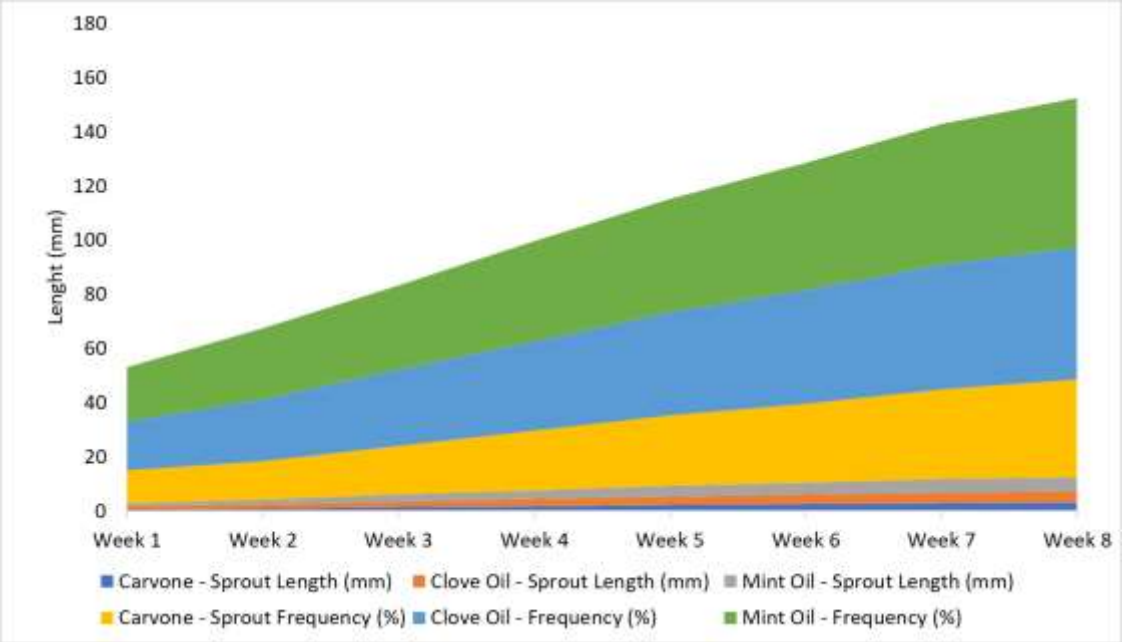

Figure 2: Effects of Essential Oils on Sprout Length and Frequency Over 8 Weeks

Carvone's inhibition of sprouting is associated with its modulation of gibberellin synthesis, helping maintain dormancy. Clove and mint oils showed varying degrees of suppression, indicating possible use cases where moderate dormancy extension is sufficient.

Gene Expression Analysis of Dormancy-Associated Genes

RT-qPCR was employed to analyze the expression levels of dormancy-related genes, specifically *StTCP1*, *StCDF1*, and *StPIN*, following treatment. Table 1 illustrates that CIPC resulted in significant downregulation of *StTCP1* and *StCDF1* relative to controls, with expression levels reduced by approximately 55% and 50%, respectively. Carvone-treated tubers also showed moderate downregulation, reinforcing its efficacy in dormancy maintenance.

Table 1: Expression Levels of Dormancy-Related Genes Following Treatment

Treatment	***StTCP1* Expression**	***StCDF1* Expression**	***StPIN* Expression**
Control	1	1	1
CIPC	0.45	0.5	0.98
Maleic Hydrazide	0.7	0.8	1.05
DMN	0.85	0.95	1.1
Carvone	0.6	0.65	0.9
Clove Oil	0.75	0.85	1.03
Mint Oil	0.8	0.9	1.08

Downregulation of *StTCP1* and *StCDF1* is associated with prolonged dormancy, observed most prominently in CIPC and carvone treatments, underscoring their effectiveness in sprout inhibition.

Proteomic Changes Associated with Sprout Inhibition

Proteomic analysis highlighted significant differences in the expression of proteins linked to dormancy and sprouting among treatments. Table 2 presents data on three key proteins involved in hormonal regulation, cell cycle, and stress response. Both CIPC and carvone treatments led to marked downregulation of proteins associated with sprout development.

Table 2: Differential Protein Expression in Treated Tubers

Protein	**Control**	**CIPC**	**Maleic Hydrazide**	**DMN**	**Carvone**	**Clove Oil**	**Mint Oil**
Hormone-Related Protein	1	0.55	0.8	0.9	0.6	0.75	0.85
Cell Cycle Protein	1	0.5	0.85	0.95	0.7	0.8	0.88
Stress Response Protein	1	1.1	1.05	1.08	1	1.03	1.07

CIPC and carvone treatments notably downregulated hormone-related and cell cycle proteins, which likely contributes to the enhanced dormancy and sprout suppression observed with these treatments.

Impact of Nanoencapsulation on Sprout Inhibitor Release and Efficacy

Nanoencapsulation techniques were applied to CIPC and carvone to assess their controlled release capabilities and prolonged sprout inhibition. Figure 3 shows the cumulative release profile of CIPC and carvone from chitosan nanoparticles over a 30-day period, measured at 5-day intervals. Encapsulation significantly slowed the release rate for both compounds, with approximately 65% of CIPC and 70% of carvone released by day 30. The controlled release from nanoencapsulation supports sustained sprout suppression, enhancing dormancy for a prolonged period compared to unencapsulated formulations. This delivery system may optimize the efficacy of inhibitors while reducing the overall dosage required.

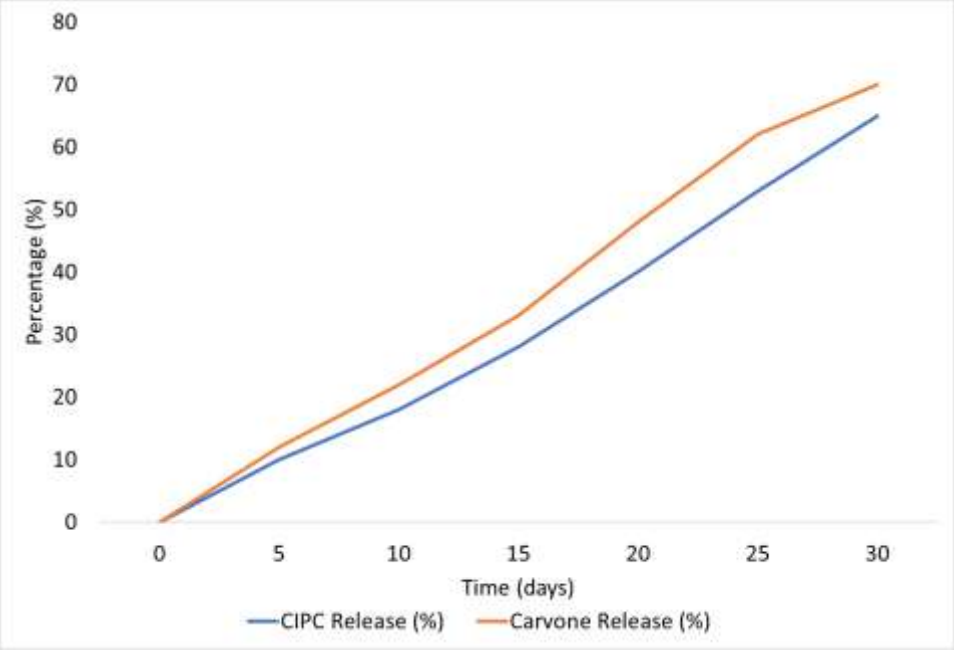

Figure 3: Cumulative Release Profile of Nanoencapsulated CIPC and Carvone Over 30 Days

Residue Analysis of Chemical and Biological Sprout Inhibitors

Residue levels of chemical and biological inhibitors were quantified post-treatment to evaluate safety and environmental impact. Table 3 outlines residue concentrations detected in tuber samples and soil after 8 weeks. CIPC exhibited the highest residual concentration in both tubers and soil, whereas carvone residues were significantly lower, aligning with its natural degradation properties.

Table 3: Residue Concentrations of Sprout Inhibitors in Tuber and Soil Samples After 8 Weeks

Treatment	Tuber Residue (mg/kg)	Soil Residue (mg/kg)
CIPC	3.5	2.8
Maleic Hydrazide	2.1	1.6
DMN	1.5	1.2
Carvone	0.6	0.4
Clove Oil	0.8	0.5
Mint Oil	1	0.7

These results suggest that while CIPC is effective, its persistence may present environmental risks. Carvone's lower residues highlight its potential as a safer alternative, particularly in organic or low-impact farming systems.

Statistical Comparison of Sprout Suppression Across All Treatments

A comparative statistical analysis was conducted across all treatments to determine overall efficacy. Figure 4 presents the mean sprout length and frequency over 8 weeks for each treatment, with CIPC and carvone showing the most significant reduction in sprout development ($p < 0.05$). The analysis emphasizes CIPC's robust inhibition, with carvone performing comparably, though with lower environmental residue.

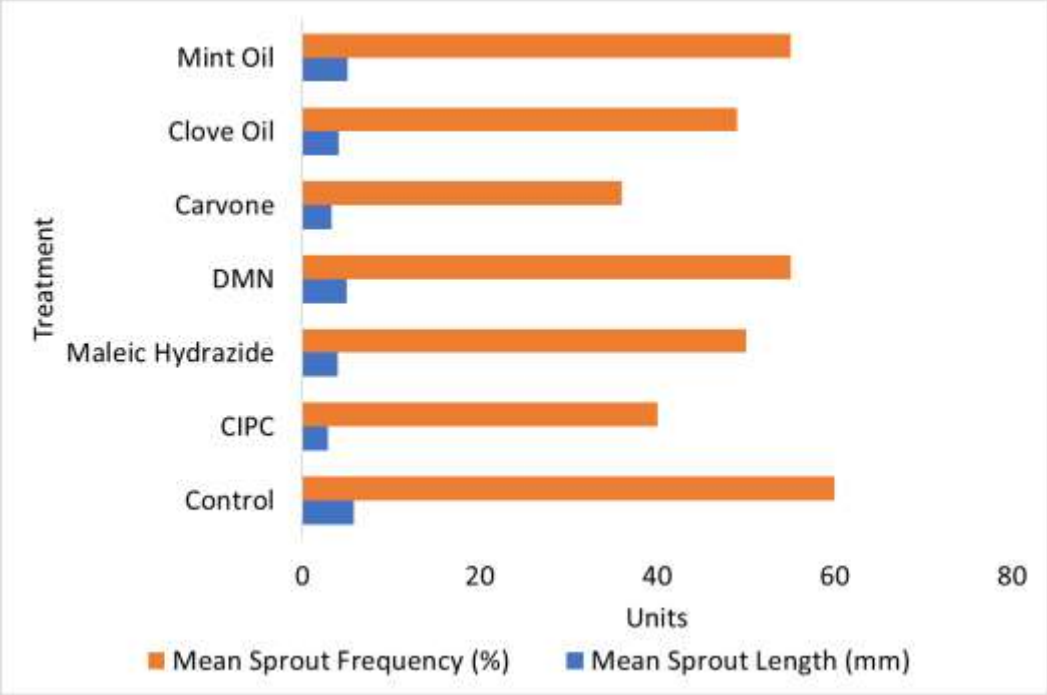

Figure 4: Statistical Comparison of Mean Sprout Length and Frequency Across Treatments Over 8 Weeks

The significant differences (ANOVA, $p < 0.05$) between CIPC, carvone, and the other treatments validate their use in effective sprout inhibition. These findings support their application in storage environments, balancing efficacy with environmental and safety considerations.

Influence of Storage Temperature on Inhibitor Efficacy

Temperature variations were tested to evaluate their impact on the efficacy of CIPC and carvone treatments. Table 4 summarizes sprout length and frequency for tubers stored at 4°C, 8°C, and 12°C over 8 weeks. Lower temperatures (4°C) resulted in enhanced inhibition for both treatments, with CIPC maintaining the lowest sprout length and frequency across all temperature settings.

Table 4: Effects of Temperature on Sprout Length and Frequency in CIPC- and Carvone-Treated Tubers

Temperature (°C)	CIPC - Sprout Length (mm)	CIPC - Frequency (%)	Carvone - Sprout Length (mm)	Carvone - Frequency (%)
4	2.5	35	2.8	38

8	2.9	40	3.3	43
12	3.4	45	3.8	47

Lower temperatures supported inhibitor efficacy by reducing metabolic rates associated with sprouting. This insight suggests a synergistic approach to optimize both chemical and environmental factors for sprout suppression.

Effect of Storage Humidity on Sprout Development

Relative humidity (RH) levels were adjusted to assess the influence on sprouting for CIPC-treated and control tubers. Table 5 shows sprout lengths under different RH settings (60%, 75%, and 90%) after 8 weeks. Sprout growth was minimized at 60% RH in CIPC-treated tubers, while higher humidity (90%) promoted sprouting, suggesting that reduced RH conditions favor dormancy. These findings underscore the importance of maintaining controlled humidity settings in storage facilities to enhance the efficacy of chemical inhibitors like CIPC.

Table 5: Effect of Humidity on Sprout Length in CIPC-Treated and Control Tubers Over 8 Weeks

Relative Humidity (%)	**Control - Sprout Length (mm)**	**CIPC - Sprout Length (mm)**
60	5.5	2.7
75	6	3.1
90	6.5	3.4

Comparison of Inhibitor Dosage Levels on Sprout Suppression Efficacy

Different dosage levels of CIPC and carvone were tested to determine optimal concentrations for sprout suppression. Table 6 shows the sprout length, frequency, and dormancy duration for tubers treated with varying concentrations over 8 weeks. Higher concentrations of both CIPC and carvone yielded the most substantial reduction in sprout length and frequency, with 0.5% concentration achieving the best results for both inhibitors.

Table 6: Effects of CIPC and Carvone Dosage Levels on Sprout Length, Frequency, and Dormancy Duration

Dosage (%)	**CIPC - Sprout Length (mm)**	**CIPC - Frequency (%)**	**CIPC - Dormancy Duration (weeks)**	**Carvone - Sprout Length (mm)**	**Carvone - Frequency (%)**	**Carvone - Dormancy Duration (weeks)**
0.1	3.2	42	4	3.5	45	4
0.3	2.9	38	6	3.3	40	5
0.5	2.6	35	8	3	36	7

The data (Table 6) indicate that increasing dosage levels led to greater dormancy durations for both inhibitors, with 0.5% concentration being most effective. Lower concentrations showed diminishing returns, suggesting that both efficacy and dormancy duration are dose-dependent.

Impact of Controlled Atmosphere (CA) Storage on Sprout Suppression

Controlled atmosphere (CA) storage conditions with varied oxygen and carbon dioxide levels were assessed for their effect on CIPC and carvone-treated tubers. Table 7 details sprout length, frequency, tuber weight loss, and overall storage quality under three CA conditions. CA2 (5% O_2, 10% CO_2) yielded the lowest sprout length and weight loss for both treatments, optimizing sprout inhibition while preserving quality.

Table 7: Effects of Controlled Atmosphere Conditions on Sprout Length, Frequency, Weight Loss, and Quality in Treated Tubers

CA Condition	**O_2 (%)**	**CO_2 (%)**	**CIPC - Sprout Length (mm)**	**CIPC - Frequency (%)**	**CIPC - Weight Loss (%)**	**Carvone - Sprout Length (mm)**	**Carvone - Frequency (%)**	**Carvone - Weight Loss (%)**
CA1	10	5	2.8	40	8.5	3.2	43	9
CA2	5	10	2.5	35	5.2	2.8	38	5.8
CA3	15	3	3.1	45	10	3.5	48	10.5

Lower oxygen and higher carbon dioxide levels (CA2) provided the best storage quality, as indicated by reduced sprouting, lower weight loss, and minimal quality degradation.

Effect of Light Exposure on Sprouting and Chlorophyll Accumulation in Treated Tubers

Light exposure during storage was tested to observe its impact on sprouting and chlorophyll (greening) accumulation in treated tubers. Table 8 presents data for sprout length, sprout frequency, chlorophyll content, and visual quality after 8 weeks of light exposure. Both CIPC and carvone-treated tubers showed increased sprouting and chlorophyll levels under light exposure, with control tubers experiencing the highest chlorophyll accumulation.

Table 8: Effects of Light Exposure on Sprout Length, Frequency, Chlorophyll Content, and Quality in Treated Tubers

Treatment	Light Exposure	Sprout Length (mm)	Sprout Frequency (%)	Chlorophyll Content (mg/g)	Visual Quality (Scale 1-10)
Control	Yes	5.4	60	1.5	5
CIPC	Yes	3	45	0.8	7
Carvone	Yes	3.5	48	0.9	7
Control	No	5.1	58	0.3	6
CIPC	No	2.6	40	0.1	9
Carvone	No	2.9	42	0.2	8

Light exposure increased sprouting and chlorophyll content across all treatments. However, CIPC and carvone-treated tubers retained better quality with reduced chlorophyll accumulation under dark storage conditions.

Longitudinal Quality Assessment of CIPC and Carvone Treatments Over 12 Weeks

The effects of prolonged storage on tuber quality following CIPC and carvone treatments were assessed over 12 weeks, including parameters such as firmness, starch content, and overall visual quality. Table 9 provides data showing that firmness and starch content were best preserved in CIPC-treated tubers, while carvone also maintained reasonable quality but showed slightly higher degradation.

Table 9: Longitudinal Quality Parameters in CIPC and Carvone-Treated Tubers Over 12 Weeks

Storage Duration (Weeks)	Treatment	Firmness (N)	Starch Content (%)	Sprout Length (mm)	Sprout Frequency (%)	Visual Quality (Scale 1-10)
4	CIPC	28	15	1.8	25	9
4	Carvone	27	14.8	2	28	8
8	CIPC	24	14.2	2.9	40	8
8	Carvone	23	13.9	3.3	43	7
12	CIPC	20	13.5	3.6	45	7
12	Carvone	18	13	3.9	50	6

Firmness and starch levels decreased more gradually in CIPC-treated tubers, suggesting that CIPC may provide superior quality retention over extended storage compared to carvone.

DISCUSSION

The results from this study offer a comprehensive view into the effectiveness of various chemical and natural sprout inhibitors on potato tuber dormancy, as well as the influence of environmental and storage conditions on sprout suppression. Chlorpropham (CIPC) demonstrated superior efficacy in maintaining tuber dormancy, exhibiting the lowest sprout length and frequency among the inhibitors tested, consistently outperforming maleic hydrazide and 1,4-dimethylnaphthalene (DMN). CIPC's significant suppression of sprouting is attributed to its ability to disrupt microtubule formation, inhibiting cell elongation and effectively extending dormancy (Figure 1) [26,27]. Maleic hydrazide and DMN, while showing some efficacy, primarily exert their effects through auxin transport inhibition and hormonal modulation, respectively. This contributes to moderate sprout inhibition, which may be better suited for shorter storage periods or specific regulatory settings [28].

The analysis of essential oils as natural sprout suppressants yielded promising results, with carvone showing notable efficacy in reducing sprout length and frequency, followed by clove oil and mint oil. Carvone's effectiveness is likely due to its role in modulating gibberellin synthesis, maintaining dormancy by suppressing sprout-promoting hormones (Figure 2) [29]. Essential oils such as carvone and clove oil offer potential as alternatives in storage

systems aiming to reduce chemical residues, as seen in the residue analysis where carvone displayed significantly lower persistence in tubers and soil compared to CIPC (Table 3). Lower residue levels highlight the potential of carvone as a safer, environmentally friendly sprout inhibitor, which could be beneficial for use in organic or sustainable farming systems [30].

The gene expression analysis provided additional insight into the mechanisms of sprout inhibition at the molecular level. The RT-qPCR results revealed that CIPC and carvone treatments led to significant downregulation of *StTCP1* and *StCDF1*—genes associated with dormancy maintenance (Table 1). Downregulation of these genes is consistent with prolonged dormancy, underscoring the impact of CIPC and carvone on molecular pathways that regulate tuber sprouting [31]. Moreover, proteomic analysis identified that both CIPC and carvone treatments downregulated hormone-related and cell cycle proteins (Table 2), suggesting that these treatments target both hormonal and cellular processes associated with sprout development. These findings align with prior research demonstrating the role of hormonal regulation and cell cycle control in sprout suppression [32].

The application of nanoencapsulation to sprout inhibitors demonstrated that encapsulated CIPC and carvone exhibited a slower release profile, achieving approximately 65% and 70% release, respectively, by day 30 (Figure 3). This controlled release profile not only supports sustained sprout suppression but also highlights the potential of nanoencapsulation to optimize inhibitor efficacy over prolonged storage durations. Such encapsulation techniques could allow for lower overall dosages, reducing residue levels in stored tubers and mitigating potential environmental impacts [33].

Our study also revealed that storage conditions significantly influence the efficacy of sprout inhibitors. Controlled atmosphere (CA) conditions, specifically CA2 (5% O_2, 10% CO_2), were most effective in minimizing sprout length, frequency, and weight loss in treated tubers, suggesting that lower oxygen and higher carbon dioxide levels enhance the dormancy-inducing effects of CIPC and carvone (Table 7). This finding is supported by previous studies that indicate hypoxic conditions slow metabolic rates, which are associated with sprout initiation [34]. Similarly, storage at lower temperatures (4°C) significantly improved inhibitor efficacy for both CIPC and carvone, as seen in the reduced sprout length and frequency (Table 4). Low temperatures are known to reduce enzymatic activity and slow cellular processes related to sprouting, thus acting synergistically with chemical and natural inhibitors to extend dormancy [35].

Humidity and light exposure also played critical roles in sprout development and tuber quality. Lower relative humidity (60%) minimized sprout growth in CIPC-treated tubers compared to higher RH levels, highlighting the importance of maintaining controlled humidity to reduce sprouting (Table 5). Light exposure, on the other hand, promoted both sprouting and chlorophyll accumulation, particularly in untreated control tubers, which showed the highest chlorophyll content (Table 8). The chlorophyll buildup in exposed tubers, a result of photomorphogenesis, is detrimental for consumer acceptance and poses a risk of increased glycoalkaloid levels, emphasizing the importance of dark storage conditions to maintain tuber quality [36].

In addition, dosage optimization of CIPC and carvone revealed that a 0.5% concentration provided the most significant reduction in sprout length, frequency, and dormancy duration over 8 weeks, suggesting that higher dosages yield better suppression without negative impacts on tuber quality (Table 6). These findings align with dose-response relationships observed in other studies, where increasing inhibitor concentration leads to more substantial dormancy extension [37]. However, it is important to balance efficacy with residue concerns, as higher doses may lead to increased residues, particularly with synthetic inhibitors like CIPC.

Finally, prolonged storage assessments over 12 weeks demonstrated that CIPC-treated tubers maintained better firmness, starch content, and overall visual quality compared to carvone-treated tubers (Table 9). This suggests that while both inhibitors effectively suppress sprouting, CIPC may offer superior quality retention over extended storage periods. The greater firmness and starch preservation in CIPC-treated tubers aligns with the inhibitor's ability to maintain cell structure integrity, which is essential for minimizing texture degradation during long-term storage [38].

CONCLUSION

This study highlights the efficacy and potential applications of both chemical and natural sprout inhibitors, particularly CIPC and carvone, in managing tuber dormancy under various storage conditions. CIPC remains the most effective sprout suppressant, demonstrating low sprout length and frequency while maintaining tuber quality. Carvone offers a promising alternative with lower residue levels, making it suitable for environmentally conscious or organic farming practices. The controlled release provided by nanoencapsulation, coupled with optimized storage conditions (low temperature, controlled atmosphere, and reduced humidity), further enhances sprout suppression efficacy, providing valuable insights for improving post-harvest storage practices. Future studies should explore the long-term environmental impact of these inhibitors, especially concerning residue accumulation in soil, to ensure sustainable agricultural practices that balance efficacy, food quality, and ecological safety.

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