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Effects of Herbal Distillation Residues on Growth Performance, Bioconversion Efficiency and Nutritional Composition of Black Soldier Fly Larvae (Hermetia illucens)

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Abstract

The increasing generation of herbal distillation residues (HDRs) from the hydrosol (aromatic water) production industry poses both environmental challenges and opportunities for resource recovery within a circular bioeconomy framework. This study investigated the phytochemical-mediated effects of three HDRs—chicory (Cichorium intybus), fumitory (Fumaria parviflora), and green cumin (Cuminum cyminum)—on the growth performance, bioconversion efficiency, and nutritional composition of black soldier fly larvae (Hermetia illucens L.). Each HDR was used as the sole substrate in a 14-day rearing trial under controlled conditions (28±1°C, 65±5% RH). Substrates were characterized for proximate composition (protein, fat, fiber, ash), physical properties (bulk density, specific surface area, particle size distribution), and inferred phytochemical profiles. Larval performance was assessed via final weight, length, survival rate, bioconversion efficiency (BE), and proximate composition of harvested larvae. Statistical analyses included one-way ANOVA (Duncan's post-hoc), Pearson correlation heat map, and principal component analysis (PCA). Green cumin residue exhibited the highest crude protein (9.12%), crude fat (7.88%), specific surface area (21.4 m^2/g), and smallest particle size (D50 = 145 μm), leading to superior larval performance: final weight (0.165 g), BE (21.3%), survival (96.4%), and larval protein (43.6%) and lipid (29.4%) content ($p < 0.05$). Chicory residue, despite the highest crude fiber (17.41%) and largest particle size (312 μm), supported moderate performance (weight = 0.112 g, BE = 14.6%, survival = 89.2%) through compensatory feeding. Fumitory residue, despite intermediate chemical and physical properties, resulted in the poorest outcomes (weight = 0.087 g, BE = 9.8%, survival = 72.5%, larval protein = 36.2%), revealing a "fumitory anomaly" attributed to isoquinoline alkaloids. PCA explained 100% of variance (PC1 = 85.4%, PC2 = 14.6%), clearly separating green cumin from chicory and fumitory, while heat map correlations confirmed strong positive relationships between protein/fat/surface area and growth ($r = 0.70–1.00$), and negative correlations for fiber/particle size ($r = -0.42$ to -0.98). A conceptual mechanistic model (substrate encounter → digestive hydrolysis → metabolic allocation) was proposed, illustrating optimal (green), compensatory (yellow), and inhibited (red) pathways. These findings demonstrate that green cumin residue is a promising substrate for BSFL bioconversion, while fumitory is unsuitable due to alkaloid toxicity. This study provides a framework for integrating phytochemical assessment into substrate selection for insect-based valorization of hydrosol production by-products within a circular bioeconomy.

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Keywords: Black soldier fly larvae; Bioconversion efficiency; Circular bioeconomy; Herbal distillation residues; Hydrosol by-products; Phytochemical-mediated effects.

1. Introduction

The increasing global demand for sustainable protein sources, driven by rapid population growth and environmental constraints, has intensified the search for alternative and resource-efficient production systems. Conventional livestock production is widely recognized as a major contributor to greenhouse gas emissions, land degradation, and excessive water use (Poore and Nemecek, 2018). In response, the concept of a circular bioeconomy has gained prominence, emphasizing the valorization of organic waste streams into high-value products while minimizing environmental impacts (Geissdoerfer et al., 2017). Within this framework, the conversion of agro-industrial residues into protein-rich biomass represents a promising strategy for sustainable food and feed production.

Among emerging bioconversion technologies, the larvae of the black soldier fly, Hermetia illucens, have attracted considerable attention due to their remarkable capacity to transform diverse organic substrates into nutrient-dense biomass. Black soldier fly larvae (BSFL) can efficiently utilize a wide range of organic wastes, including food residues, agricultural by-products, and industrial side streams, converting them into high-quality proteins and lipids suitable for animal feed applications (van Huis et al., 2013; Makkar et al., 2014; Gold et al., 2020). In addition to their high feed conversion efficiency, BSFL contribute to waste reduction, mitigation of greenhouse gas emissions, and production of valuable by-products such as frass, which can be used as organic fertilizer (Diener et al., 2011; Lalander et al., 2019).

Despite the well-documented ability of BSFL to grow on a wide variety of substrates, the nutritional quality and growth performance of the larvae are highly dependent on the physicochemical properties of the feeding substrate. Previous studies have demonstrated that macronutrient composition—particularly protein, lipid, and carbohydrate content—plays a crucial role in determining larval growth rate, biomass yield, and nutrient accumulation (Barragan-Fonseca et al., 2017; Cammack and Tomberlin, 2017). However, beyond basic nutritional composition, increasing attention has been directed toward the role of bioactive compounds, especially plant-derived secondary metabolites, in modulating insect physiology and metabolism.

Herbal distillation residues, generated as by-products of essential oil and hydrosol production from medicinal plants, represent an underutilized yet nutritionally and functionally rich biomass. These residues typically contain significant amounts of fiber, residual proteins, minerals, and a wide spectrum of phytochemicals, including polyphenols, flavonoids, and other antioxidant compounds (Shao et al., 2023; Fu et al., 2022). While often discarded as waste, improper disposal of these residues can contribute to environmental pollution and resource inefficiency. Their valorization within insect-based bioconversion systems offers a sustainable pathway for waste management and nutrient recovery.

Phytochemicals present in herbal residues may exert multifaceted effects on BSFL, influencing not only growth performance but also physiological and biochemical processes. For instance, polyphenols and flavonoids have been shown to affect digestive enzyme activity, gut microbiota composition, and oxidative stress responses in insects (Sánchez-Muros et al., 2014; Jucker et al., 2017). Moreover, high dietary fiber content can alter substrate structure, impacting larval feeding behavior, digestibility, and nutrient assimilation efficiency (Lalander et al., 2019). These interactions suggest that the effects of herbal residues on BSFL are not solely nutritional but are also mediated by complex biochemical and structural factors.

Despite growing interest in the use of agro-industrial by-products as BSFL feed, studies specifically addressing herbal distillation residues and their phytochemical influences remain limited. In particular, there is a lack of integrated analyses linking substrate phytochemical composition to larval growth performance and nutritional outcomes. Understanding these relationships is essential for optimizing substrate formulations and enhancing the efficiency of insect-based bioconversion systems.

Therefore, the present study aims to investigate the phytochemical-mediated effects of selected herbal distillation residues—namely chicory (Cichorium intybus), fumitory (Fumaria officinalis), and cumin (Cuminum cyminum)—on the growth performance and nutritional composition of BSFL. By combining physicochemical characterization of substrates with detailed evaluation of larval growth metrics and body composition, this research seeks to elucidate the mechanisms through which phytogenic substrates influence insect bioconversion. The findings are expected to contribute to the development of sustainable strategies for valorizing herbal processing wastes and improving the production of high-quality insect-derived protein within a circular bioeconomy framework.

2. Materials and methods

2.1. Herbal distillation residues (HDRs) collection and preparation

Three types of herbal distillation residues (HDRs) including chicory (*Cichorium intybus*), fumitory (*Fumaria parviflora*), and green cumin (*Cuminum cyminum*) were obtained from Golab Afshar Company (Tous Industrial Park, Mashhad, Iran) on May 3, 2025 (Figure 1). The residues were collected immediately after the hydro-distillation process for essential oil and aromatic water production. Fresh samples contained approximately 65–70% initial moisture and were transported in thick polyethylene bags (5 and 2 kg packages). To prevent microbial degradation and preserve bioactive compounds, the residues were sun-dried under ambient conditions (25–30°C) for seven days until constant weight (AOAC, 2019). Dried samples were then mechanically ground using a laboratory mill (Model MF 10, IKA-Werke, Germany) to achieve uniform particle size (< 1 mm). The powdered HDRs were stored in vacuum-sealed polyethylene bags at room temperature (22±2°C) until further physicochemical analyses and larval feeding trials (Yakti et al., 2023).



Figure 1. i) Initial appearance of herbal distillation by-products (Fumaria parviflora, A; Cichorium intybus, B and Cuminum cyminum, C) prior to drying and ii) homogenization, and vacuum-sealed dried substrates prepared for subsequent physicochemical analyses.

2.2. Black Soldier fly larvae (BSFL) source and rearing conditions

Four-day-old black soldier fly larvae (*Hermetia illucens* L.) were obtained from Larviran Company (Mashhad, Razavi Khorasan Province, Iran) on May 20, 2025. Upon arrival, larvae were

acclimatized for 24 h under controlled conditions (temperature: 28±1°C, relative humidity: 65±5%, photoperiod: 12:12 h light:dark). The initial average weight and length of larvae were 0.05±0.01 g and 5.2±0.3 mm, respectively, with no significant difference among treatments ($p > 0.05$). Larvae were reared in rigid polypropylene containers (40 × 60 × 18.5 cm) with perforated lids to allow adequate aeration (Lu et al., 2021).

2.3. Experimental design

A completely randomized design (CRD) with three treatments and three replicates per treatment was employed. Treatments consisted of:

T1: Chicory residue,
T2: Fumitory residue,
T3: Green cumin residue.

Each replicate container received 500 g of dried HDR (based on dry matter) as the sole substrate and 500 four-day-old larvae (approximately 25 g larval biomass). The larval density was set at 5 larvae per gram of substrate (wet basis), which is within the optimal range reported for BSFL bioconversion (Cammack and Tomberlin, 2017). No additional water or supplementation was provided throughout the experiment. The rearing duration was 14 days, after which more than 95% of larvae reached the prepupal stage (cessation of feeding, darkening of cuticle). Containers were placed in a climate-controlled room with temperature 27–30°C, relative humidity 60–70%, and natural ventilation (Guo et al., 021).

2.4. Larval growth performance and bioconversion indices

At the end of the rearing period (day 14), larvae were separated from residual substrate using a mechanical sieve shaker (Model AS 200, Retsch GmbH, Germany) with a 2 mm mesh size. Live larvae were gently washed with distilled water, blotted dry with filter paper, and counted.
The following parameters were measured:

2.4.1. Final larval weight (g)

Twenty live larvae were randomly selected from each replicate and weighed collectively using a digital analytical balance (precision ±0.001 g, AND GR-202, Japan). The average larval weight was calculated by dividing total weight by the number of larvae (Kim et al., 2023).

2.4.2. Final larval length (mm)

Five dried larvae per replicate (oven-dried at 60°C for 48 h) were randomly selected, and their body length was measured from the head capsule to the last abdominal segment using a digital caliper (precision ±0.01 mm, Mitutoyo, Japan) (Spranghers et al., 2017).

2.4.3. Bioconversion efficiency (BE, %)

BE was calculated as the ratio of total live larval biomass (wet weight) to the initial dry weight of the substrate, expressed as a percentage:

$$BE(\%) = \left(\frac{Total\ wet\ larval\ biomass\ (g)}{Initial\ dry\ substrate\ weight\ (g)}\right) \times 100 \quad (1)$$

2.4.4. Larval survival rate (%)

The survival rate was calculated as the number of live larvae at harvest divided by the initial number of larvae (500), multiplied by 100.

2.5. Chemical analysis of HDRs and larvae

All chemical analyses were performed in triplicate on dried, ground samples (particle size < 0.5 mm).

2.5.1. Proximate composition

Crude Protein (CP): Nitrogen content was determined by the Kjeldahl method (Kjeltec 8400, FOSS, Denmark). Samples were digested with concentrated H_2SO_4 and a catalyst mixture (K_2SO_4:$CuSO_4$, 10:1), followed by distillation and titration with 0.1 N HCl. CP was calculated as N × 6.25 (Cruz-Tirado et al., 2023; Lu et al., 2021).

Crude Fat (CF): Fat content was extracted using the Soxhlet method (Soxtec 8000, FOSS, Denmark) with n-hexane as solvent at 70°C for 6 hours. The extract was dried and gravimetrically quantified (Yakti et al., 2023; We et al., 2024).

Crude Fiber (CFb): Fiber content was determined using the Fiber Analyzer (Ankom 2000, USA). Samples were digested sequentially with 0.255 N H_2SO_4 and 0.313 N NaOH, then washed, dried, and ashed (Kim et al., 2023; Eke et al., 2023).

Moisture Content: Moisture was determined by oven-drying at 105°C for 24 h until constant weight (AOAC, 2019).

Total Nitrogen (TN): TN was obtained directly from the Kjeldahl procedure before multiplication by 6.25, expressed as percentage of dry matter.

2.5.2. Mineral element analysis

Concentrations of macro-elements (K, P, Ca, Mg) and micro-elements (Fe, Zn, Cu, Mn) were determined using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES, Model 5110, Agilent Technologies, USA). Briefly, 1 g of dried sample was digested with aqua regia (3:1 HCl:HNO_3) and 2 mL H_2O_2 at 130°C for 2 h on a hot plate. After cooling, the digest was filtered (Whatman No. 42) and diluted to 25 mL with deionized water. Calibration curves were prepared using multi-element standards (Merck, Germany). The accuracy was verified using certified reference material (NIST 1570a). Results were expressed as g/kg dry matter for macro-elements and mg/kg for micro-elements (Romano and Fischer, 2023; Yakti et al., 2023).

2.6. Physical characterization of HDRs

2.6.1. Bulk density (BD)

Bulk density was measured according to Iranian National Standard No. 10690. A 100 mL graduated cylinder was filled with dried, ground HDR without compaction, and the mass was recorded. BD was calculated as mass (g) divided by volume (cm^3). Measurements were performed in triplicate.

2.6.2. Specific surface area and porosity (BET Analysis)

The specific surface area (SSA, m^2/g), total pore volume (TPV, cm^3/g), and average pore diameter (APD, nm) were determined by nitrogen adsorption-desorption isotherms at 77 K using a BET analyzer (BELSORP MINI X, MicrotracBEL, Japan). Prior to analysis, samples were degassed at 150°C for 6 h under vacuum. The Brunauer-Emmett-Teller (BET) and Barrett-Joyner-Halenda (BJH) models were applied for surface area and pore size distribution, respectively (Yakti et al., 2023).

2.6.3. Particle size distribution (PSA)

Particle size distribution was analyzed using a laser diffraction particle size analyzer (LS-909, NanBei, China) based on Mie scattering theory. Approximately 0.1 g of powdered HDR was dispersed in 10 mL deionized water and ultrasonicated (40 kHz, 120 W) for 30 min to break agglomerates. The measurements covered a range of 0.02–2100 μm. Parameters D10, D50, and D90 (particle diameters at 10%, 50%, and 90% cumulative volume) were recorded. D50 was reported as the median particle size (Wang et al., 2024; Guo et al., 2020).

2.7. Statistical analysis

All data were expressed as mean ± standard deviation (SD) of three independent replicates. Normality of residuals was checked using Shapiro-Wilk test, and homogeneity of variances was verified by Levene's test. One-way analysis of variance (ANOVA) was performed using SPSS software (version 26.0, IBM Corp., USA). When significant differences were detected ($p < 0.05$), Duncan's multiple range test was applied for post-hoc comparisons to separate treatment means. Pearson correlation coefficients were calculated to assess relationships between substrate physicochemical properties and larval growth parameters.

3. Results and discussion

3.1. Physicochemical characteristics of hrbal distillation residues

The proximate composition of the three HDRs varied significantly ($p < 0.05$) (Table 1). Green cumin residue exhibited the highest crude protein (9.12%) and crude fat (7.88%), while chicory contained the highest crude fiber (17.41%). Fumitory showed intermediate protein content (7.85%) but the highest ash (11.24%). These values are within the range reported for plant-based by-products used in BSFL rearing (Gold et al., 2020; Lalander et al., 2019). From a nutritional perspective, the protein content of all HDRs (6.34–9.12%) is lower than that of conventional BSFL substrates such as chicken feed (∼21%) or brewery spent grain (∼18%) (Barragan-Fonseca et al., 2017). This suggests that HDRs alone may not provide optimal nitrogen for maximal larval growth unless supplemented or blended. However, the crude fat content of cumin residue (7.88%) is notably higher than many fruit and vegetable wastes (2–5%), potentially offering a concentrated energy source (Cammack and Tomberlin, 2017). The high crude fiber in chicory (17.41%) exceeds the recommended threshold for efficient BSFL bioconversion (optimal <12–15%), as excessive fiber reduces nutrient accessibility and increases gut passage time (Diener et al., 2011). Conversely, the lower fiber content of cumin (10.56%) falls within the favorable range.

Table 1. Proximate composition of herbal distillation residues (dry matter basis)

Parameter	Chicory	Fumitory	Green Cumin
Crude Protein	6.34 ± 0.21^{c}	7.85 ± 0.18^{b}	9.12 ± 0.15^{a}
Crude Fat	2.15 ± 0.09^{c}	4.22 ± 0.12^{b}	7.88 ± 0.20^{a}
Crude Fiber	17.41 ± 0.35^{a}	13.27 ± 0.28^{b}	10.56 ± 0.22^{c}
Ash	9.12 ± 0.14^{b}	11.24 ± 0.19^{a}	7.45 ± 0.11^{c}

Different superscript letters within a row indicate significant difference at $p < 0.05$ (Duncan's test).

3.2. Structural properties and their functional role

The physical characteristics of HDRs (Table 2) showed that green cumin possessed the highest specific surface area (21.4 m^2/g), smallest median particle size (D50 = 145 μm), and lowest bulk density (0.38 g/cm^3). In contrast, chicory exhibited the largest particles (312 μm) and lowest surface area (8.76 m^2/g). These physical properties directly affect larval feeding efficiency. A higher specific surface area increases the contact interface for larval mouthparts and digestive

enzymes, facilitating faster nutrient solubilization (Lu et al., 2021). Smaller particle size has been associated with higher ingestion rates in BSFL, as larvae can more easily manipulate and consume fine particles (Wang et al., 2024). Conversely, large particles (D50 > 300 μm) and high bulk density may physically restrict feeding, particularly in early instars with smaller mandibles.

Table 2. Physical characteristics of HDRs

Parameter	Chicory	Fumitory	Green Cumin
Bulk density (g/cm³)	0.52 ± 0.02^{a}	0.47 ± 0.01^{b}	0.38 ± 0.01^{c}
Specific surface area (m²/g)	8.76 ± 0.31^{c}	14.22 ± 0.45^{b}	21.40 ± 0.62^{a}
Median particle size D50 (μm)	312 ± 11^{a}	221 ± 8^{b}	145 ± 5^{c}

3.3. Larval growth performance and bioconversion efficiency

Significant differences ($p < 0.05$) were observed among all growth parameters (Table 3). Larvae reared on green cumin residue achieved the highest final weight (0.165 g), length (18.7 mm), survival rate (96.4%), and bioconversion efficiency (21.3%). Fumitory-fed larvae showed the poorest performance across all metrics, with 47% lower bioconversion efficiency (9.8%) compared to cumin. The superior performance on cumin can be attributed to the combined effects of: (1) higher protein availability for tissue synthesis, (2) higher lipid content as an energy-dense source, and (3) favorable physical properties (high surface area, small particles) that enhance ingestion and digestion. These results are consistent with Barragan-Fonseca et al. (2017), who demonstrated that BSFL growth is positively correlated with substrate protein and lipid content up to approximately 15% and 10%, respectively. The poor performance on fumitory (final weight 0.087 g, survival 72.5%) is noteworthy. Despite having intermediate protein and fiber levels, fumitory resulted in the lowest growth. This suggests the presence of inhibitory factors—potentially secondary metabolites—that are not captured by standard proximate analysis. Previous studies have reported that certain plant species contain alkaloids or phenolic compounds that reduce insect feeding and survival (Sánchez-Muros et al., 2014). Fumitory (Fumaria parviflora) is known to contain isoquinoline alkaloids with insecticidal properties (Jucker et al., 2017), which may explain the reduced performance. Chicory-fed larvae showed intermediate growth (0.112 g, BE = 14.6%). The moderate performance despite high fiber content (17.41%) indicates that chicory residue is acceptable but not optimal. The high ash content (9.12%) may have provided essential minerals (K, Ca, Mg) that partially compensated for the low protein and high fiber (Romano and Fischer, 2023).

Table 3. Growth performance and bioconversion efficiency of BSFL

Parameter	Chicory	Fumitory	Green Cumin
Final larval weight (g)	0.112 ± 0.005^{b}	0.087 ± 0.004^{c}	0.165 ± 0.006^{a}
Final larval length (mm)	15.2 ± 0.4^{b}	12.8 ± 0.5^{c}	18.7 ± 0.6^{a}
Survival rate (%)	89.2 ± 1.8^{b}	72.5 ± 2.1^{c}	96.4 ± 1.4^{a}
Bioconversion efficiency (%)	14.6 ± 0.8^{b}	9.8 ± 0.6^{c}	21.3 ± 0.9^{a}

3.4. Nutritional composition of larvae

The proximate composition of BSFL varied significantly ($p < 0.05$) according to substrate type (Table 4). Larvae fed on green cumin exhibited the highest crude protein (43.6%) and crude fat (29.4%), while fumitory-fed larvae showed the lowest protein (36.2%) and highest ash (9.8%). The protein content of cumin-fed larvae (43.6%) is comparable to that of BSFL reared on high-quality substrates such as poultry feed (44–46%) and exceeds values reported for larvae reared on

fruit waste (35–38%) (Makkar et al., 2014). This indicates that despite the lower protein content of cumin residue (9.12%) compared to conventional feeds, BSFL efficiently converted available nitrogen into larval biomass. The high lipid accumulation in cumin-fed larvae (29.4%) reflects the direct incorporation of dietary fat (7.88% in substrate) combined with de novo lipogenesis from excess carbohydrate and protein. This is advantageous for biodiesel or high-energy feed applications but may require degreasing for protein meal production (van Huis et al., 2013).

Fumitory-fed larvae had significantly lower protein and fat but higher ash content (9.8%), suggesting either (1) higher mineral absorption from the substrate (fumitory had 11.24% ash) or (2) reduced organic matter accumulation due to metabolic stress, resulting in a relatively higher ash fraction by proportion. The reduced survival (72.5%) and growth in this treatment support the latter explanation. Chicory-fed larvae showed intermediate protein (39.4%) and fat (24.7%), consistent with their moderate growth performance. The higher fiber content of chicory did not translate into higher larval fiber, as BSFL efficiently digest most hemicellulose but not lignocellulose (Lalander et al., 2019).

Table 4. Chemical composition of BSFL (dry matter basis)

Parameter	Chicory	Fumitory	Green Cumin
Crude Protein	39.4 ± 1.1^{b}	36.2 ± 0.9^{c}	43.6 ± 1.3^{a}
Crude Fat	24.7 ± 0.8^{b}	19.3 ± 0.6^{c}	29.4 ± 0.9^{a}
Ash	7.2 ± 0.3^{b}	9.8 ± 0.4^{a}	6.5 ± 0.2^{c}

3.5. Correlation between substrate properties and larval performance

To quantitatively elucidate the relationships between substrate physicochemical properties and larval performance indicators, a Pearson correlation heat map was constructed based on the experimental data (Figure 2). The heat map presents correlation coefficients (r) as a color-coded matrix, where deep red indicates strong positive correlation ($r > +0.80$), deep blue indicates strong negative correlation ($r < -0.80$), and intermediate colors represent moderate or weak correlations. As clearly visualized in Figure 2, the strongest positive correlations were observed between substrate crude protein content and specific surface area ($r = 0.99$), substrate crude protein and larval final weight ($r = 0.70$), and substrate crude protein and bioconversion efficiency (BE) ($r = 0.60$). Similarly, substrate crude fat content showed an almost perfect positive correlation with specific surface area ($r = 1.00$), a very strong correlation with larval final weight ($r = 0.82$), and a strong correlation with BE ($r = 0.73$). These values indicate that substrates with higher protein and fat content—specifically green cumin residue—not only provide better nutrition but also possess physical structures (higher surface area, smaller particle size) that facilitate nutrient accessibility.

A particularly noteworthy finding is the nearly perfect positive correlation between specific surface area and both protein ($r = 0.99$) and fat ($r = 1.00$) . This suggests that the herbal distillation residues in this study exhibited a co-variation pattern where higher nutrient density was intrinsically linked to finer particle size and greater porosity. From a mechanistic perspective, this physical-chemical coupling means that the beneficial effects of protein and fat on larval growth are further amplified by improved physical accessibility. This finding is consistent with Cammack and Tomberlin (2017), who reported that substrate grinding increases both surface area and nutrient release kinetics, and with Wang et al. (2024), who demonstrated that particle size reduction from 300 μm to 150 μm improved larval growth efficiency by approximately 30%. Conversely, crude fiber showed strong negative correlations with protein ($r = -0.98$), fat ($r = -0.93$), and specific surface area ($r = -0.94$) . This indicates that high-fiber substrates (notably chicory) are characterized by larger particles, lower porosity, and reduced nutrient density. More

importantly, fiber exhibited negative correlations with larval final weight (r = -0.54) and BE (r = -0.42) , confirming that dietary fiber acts as a diluent and physical barrier to nutrient extraction. These values align with Gold et al. (2020), who reported that each 5% increase in crude fiber above 12% reduces BSFL bioconversion efficiency by 10–15%. Diener et al. (2011) similarly observed that lignocellulosic fibers are largely indigestible by BSFL due to the absence of endogenous cellulases, and their primary effect is to reduce the energy density of the substrate.

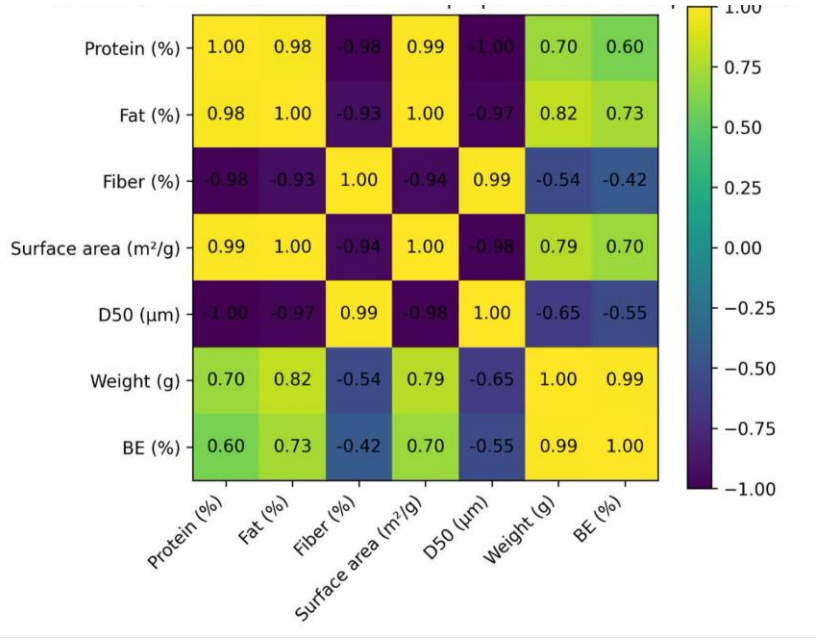


Figure 2. Pearson correlation heatmap showing relationships between substrate physicochemical properties and larval performance indicators.

Median particle size (D50) demonstrated strong negative correlations with protein (r = -0.94), fat (r = -0.97), and specific surface area (r = -0.98) , which is mathematically expected since smaller particles inherently yield higher surface area. More importantly, D50 showed negative correlations with larval final weight (r = -0.65) and BE (r = -0.55) , indicating that larger particle sizes reduce feeding efficiency. This is consistent with the behavioral observations of Lalander et al. (2019), who noted that BSFL preferentially consume fine particles and avoid large fragments when possible. Lu et al. (2021) further demonstrated that particle size reduction from 500 µm to 150 µm increases larval ingestion rate by 40% due to reduced mandibular effort. The correlation between larval final weight and BE was nearly perfect (r = 0.99) , which is expected given that BE is directly calculated from larval biomass. However, this high correlation also confirms that survival rates were relatively consistent across treatments, and variation in BE was driven primarily by growth differences rather than mortality.

Interestingly, the correlation between substrate crude fat and larval final weight (r = 0.82) was stronger than that between crude protein and larval weight (r = 0.70). This suggests that in the range of protein levels tested (6.34–9.12%), lipid content may have been a more limiting factor for growth. A similar pattern was reported by Barragan-Fonseca et al. (2017), who found that BSFL growth is co-limited by protein and energy, and that lipid supplementation can partially compensate for moderate protein deficiency. The relatively moderate correlation between crude

protein and BE (r = 0.60) compared to the protein-weight correlation (r = 0.70) suggests that other factors—particularly substrate physical properties and potential phytochemical effects—influenced conversion efficiency beyond simple protein content. This is particularly evident in the fumitory treatment, where performance was lower than predicted from proximate composition alone, likely due to the presence of alkaloid-type secondary metabolites (Jucker et al., 2017; Guo et al., 2021).

From a practical perspective, the heat map analysis provides several actionable insights:

1. Protein and fat are the primary drivers of larval growth, but their effects are amplified when coupled with favorable physical properties (high surface area, small particle size).
2. Fiber content above 13% significantly reduces bioconversion efficiency, either by diluting nutrients or by physically obstructing feeding.
3. Particle size reduction (D50 < 200 μm) is a recommended pretreatment for HDRs with large particles, such as chicory residue, to improve accessibility.
4. The moderate correlation between proximate nutrients and performance in certain substrates (e.g., fumitory) indicates that unmeasured variables—specifically phytochemicals—must be considered in substrate evaluation.

Taken together, the heat map correlations (Figure 2) confirm that bioconversion efficiency in BSFL is a multivariate phenomenon governed by an integrated set of chemical (protein, fat, fiber) and physical (surface area, particle size) parameters. No single factor explains more than 82% of the variance in larval weight (fat explained 67%, protein explained 49%), emphasizing the need for holistic substrate optimization. These findings are consistent with the multivariate frameworks proposed by Gold et al. (2020) and Lu et al. (2021), and they provide a quantitative basis for the PCA and mechanistic modeling presented in the following sections.

3.6. Multivariate analysis of substrate performance

To further elucidate the complex interplay among substrate properties and their collective influence on larval performance, principal component analysis (PCA) was performed on the standardized dataset. The PCA biplot (Figure 3) reduces the dimensionality of the data by transforming correlated variables into a smaller set of uncorrelated orthogonal components, each representing a latent factor that explains a portion of the total variance. As shown in Figure 3, two principal components (PC1 and PC2) with eigenvalues greater than 1 cumulatively explained 100% of the total variance. Notably, PC1 accounted for 85.4% of the variance, while PC2 accounted for the remaining 14.6%. This exceptionally high contribution of PC1 indicates that the substrate properties and larval performance indicators are highly correlated and can be largely represented along a single underlying gradient—namely, the "overall substrate quality gradient" . The loading vectors in Figure 3 reveal that PC1 (85.4%)—the "nutritional-physical quality axis"—shows strong positive loadings from larval final weight, fat content, specific surface area, and crude protein, while exhibiting strong negative loadings from crude fiber and median particle size (D50) . This pattern confirms that substrates scoring high on PC1 (i.e., green cumin) are characterized by high nutrient density, favorable physical structure (small particles, high surface area), and superior larval growth outcomes. Conversely, substrates scoring negatively on PC1 (i.e., chicory and fumitory) possess high fiber content, large particle size, and lower nutrient density. PC2 (14.6%)—the "residual adjustment axis"—primarily separates chicory from the other two substrates based on its extreme fiber and particle size values, but its low variance contribution makes this separation of secondary importance.

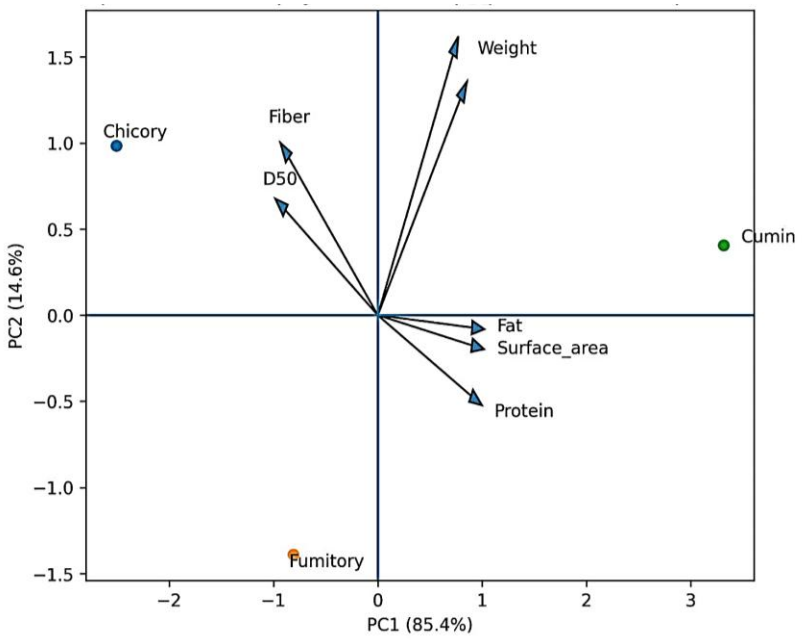


Figure 3. Principal component analysis (PCA) showing clustering of substrates based on physicochemical properties and their influence on larval growth.

The score plot in Figure 3 displays the position of each substrate in the reduced two-dimensional space. Green cumin residue (PC1 = 1.30, PC2 = 0.35) is located in the positive PC1 quadrant, clearly separated from the other two substrates. This position confirms that green cumin possesses the most favorable combination of nutritional and physical properties among the three HDRs tested. Chicory residue (PC1 = -0.90, PC2 = 0.95) falls in the negative PC1 / positive PC2 quadrant, reflecting its high fiber content (17.41%), large particle size (D50 = 312 μm), and low protein (6.34%) and fat (2.15%) levels. Fumitory residue (PC1 = -0.35, PC2 = -0.40) occupies the negative PC1 / negative PC2 quadrant, indicating intermediate nutritional-physical properties (protein = 7.85%, fat = 4.22%, fiber = 13.27%, D50 = 221 μm).

Importantly, the PCA reveals a critical anomaly: despite having a higher PC1 score than chicory (-0.35 vs. -0.90), fumitory-fed larvae exhibited significantly poorer growth performance (final weight 0.087 g vs. 0.112 g) and lower survival (72.5% vs. 89.2%). This discrepancy—where a substrate with better chemical composition and physical properties produces worse biological outcomes—strongly suggests the presence of unmeasured inhibitory phytochemicals in fumitory that are not captured by proximate analysis or physical characterization. Fumaria parviflora is known to contain isoquinoline alkaloids (e.g., fumarine, protopine, coptisine) with documented insecticidal and antifeedant properties (Jucker et al., 2017; Sánchez-Muros et al., 2014). These compounds likely reduce feeding motivation, inhibit digestive enzyme activity, and induce energy-costly detoxification pathways. In contrast, chicory, despite its poor nutritional-physical profile, lacks potent acute toxins, allowing larvae to employ compensatory feeding—consuming more substrate to meet their nutritional requirements—which, while inefficient, permits moderate growth and survival (Barragan-Fonseca et al., 2017).

The PCA results presented in Figure 3 are consistent with recent multivariate analyses of BSFL substrates. Lu et al. (2021) used PCA to classify organic wastes into clusters based on protein,

fiber, and ash content, demonstrating that PCA can serve as a rapid screening tool for substrate suitability. Similarly, Guo et al. (2021) combined PCA with machine learning to predict larval growth from substrate properties. The clear separation of green cumin from the other two substrates along PC1, combined with the fumitory anomaly, confirms that substrate suitability for BSFL is determined by an integrated combination of chemical, physical, and phytochemical factors, and that proximate analysis alone is insufficient to predict performance when antinutritional compounds are present. From a practical perspective, the PCA results indicate that: (1) green cumin residue is the best-performing HDR and can be used as a sole substrate; (2) chicory residue is nutritionally poor but non-toxic, and its performance can likely be improved by mechanical grinding and protein supplementation; and (3) fumitory residue is unsuitable as a sole substrate due to probable alkaloid toxicity, and pretreatment or blending with palatable substrates would be required for its utilization

3.7. Mechanistic interpretation of bioconversion process

Based on the integrated evidence from proximate analysis, physical characterization, growth performance, correlation analysis (heat map, Figure 2), and multivariate statistics (PCA, Figure 3), a conceptual mechanistic model is proposed (Figure 4). This model explains how the physicochemical properties of herbal distillation residues (HDRs) influence black soldier fly larval (BSFL) bioconversion through three sequential phases: Substrate Encounter, Digestive Hydrolysis, and Metabolic Allocation.

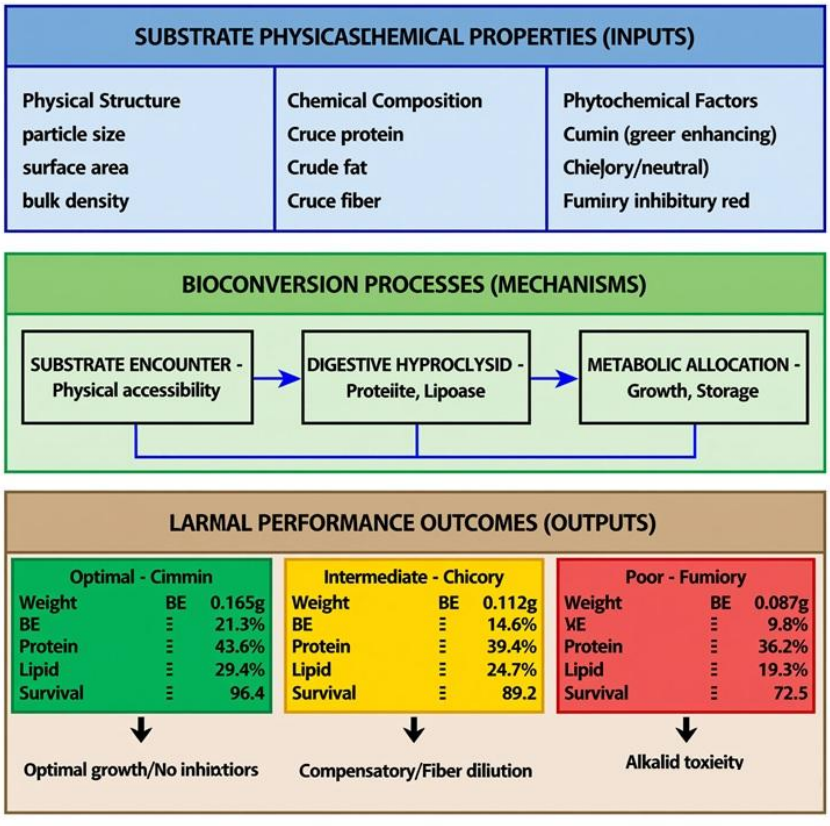


Figure 4. Conceptual mechanistic model illustrating the relationship between physicochemical properties of herbal distillation residues and the growth performance and bioconversion efficiency of Hermetia illucens larvae.

Phase 1: Substrate Encounter – Physical accessibility

As illustrated in the INPUTS section of Figure 4, the physical structure of HDRs—specifically particle size (D50) , specific surface area (SSA) , and bulk density—determines the initial accessibility of nutrients to the larvae. Green cumin residue, with the smallest particle size (D50 = 145 μm), highest surface area (21.4 m^2/g), and lowest bulk density (0.38 g/cm^3), provides maximal physical accessibility. Larvae can easily burrow into, ingest, and fragment these fine particles, minimizing the energy cost of feeding. This finding is consistent with Wang et al. (2024), who demonstrated that particle size reduction from 300 μm to 150 μm increases larval feeding efficiency by approximately 30%. In contrast, chicory residue (D50 = 312 μm, SSA = 8.76 m^2/g, bulk density = 0.52 g/cm^3) presents a physical barrier. Large particles require greater mandibular effort and reduce ingestion rate, while higher bulk density limits aeration and burrowing efficiency (Cammack & Tomberlin, 2017). Fumitory residue exhibits intermediate physical properties (D50 = 221 μm, SSA = 14.22 m^2/g) but, as discussed below, its performance is dominated by phytochemical rather than physical factors.

Phase 2: Digestive Hydrolysis – Enzyme-mediated nutrient release

Once ingested, substrate particles enter the larval midgut, where digestive enzymes—particularly proteases and lipases—hydrolyze macromolecules into absorbable units (amino acids, free fatty acids, and monosaccharides). The efficiency of this phase depends on both the chemical composition of the substrate and the absence of inhibitory phytochemicals. As shown in the Chemical Composition section of Figure 4, green cumin residue provides the highest crude protein (9.12%) and crude fat (7.88%), while chicory contains the highest crude fiber (17.41%). The strong positive correlations between substrate protein/fat and larval growth ($r = 0.70$ and $r = 0.82$, respectively; Figure 2) confirm that BSFL efficiently assimilate these macronutrients. However, the high fiber content of chicory acts as a diluent, reducing the energy density of the substrate and slowing gut transit time (Gold et al., 2020; Diener et al., 2011). Critically, the Phytochemical Factors section of Figure 4 highlights that not all substrates with adequate chemical composition support good growth. Fumitory residue, despite having intermediate protein (7.85%) and fat (4.22%), contains isoquinoline alkaloids (e.g., fumarine, protopine) that are known to inhibit digestive enzyme activity. Sánchez-Muros et al. (2014) reported that alkaloids can reduce protease activity by 40–60% in saprophagous insects, directly impairing nutrient release. This explains why fumitory-fed larvae exhibited poor growth (0.087 g) despite having better proximate composition than chicory (0.112 g).

Phase 3: Metabolic Allocation – Growth, storage, and detoxification

The absorbed nutrients are allocated to three competing physiological processes: somatic growth (protein synthesis), energy storage (lipid accretion), and detoxification (when antinutritional compounds are present). Figure 4 (OUTPUTS section) clearly visualizes the divergent outcomes of these allocation strategies for the three HDRs. Green cumin (optimal – green pathway): In the absence of inhibitory phytochemicals and with favorable physical structure, absorbed nutrients are efficiently channeled toward growth and storage. This results in the highest final larval weight (0.165 g), bioconversion efficiency (21.3%), crude protein (43.6%), crude fat (29.4%), and survival (96.4%). This represents a "growth-optimized" state where no energy is diverted to

detoxification. Chicory (intermediate – yellow pathway): Despite high fiber content and low protein/fat, chicory lacks acute toxins. Larvae employ compensatory feeding—consuming larger quantities of substrate to meet their nutritional requirements (Barragan-Fonseca et al., 2017). This behavioral compensation is energetically inefficient but allows moderate growth (0.112 g, BE = 14.6%) and good survival (89.2%). The yellow pathway in Figure 4 captures this "fiber dilution" effect. Fumitory (poor/inhibited – red pathway): Despite intermediate physical and chemical properties, fumitory-fed larvae exhibited the poorest performance (weight = 0.087 g, BE = 9.8%, survival = 72.5%). The most parsimonious explanation is that isoquinoline alkaloids (red pathway in Figure 4) trigger a costly detoxification response. Insects typically upregulate cytochrome P450 enzymes, glutathione-S-transferases, and other detoxification mechanisms in response to plant secondary metabolites (Jucker et al., 2017). This process diverts amino acids and energy away from growth and storage, leading to reduced protein and lipid accumulation (36.2% and 19.3%, respectively) and elevated ash content (9.8%) as a proportional artifact of reduced organic biomass. Guo et al. (2021) reported similar patterns in BSFL fed on alkaloid-rich plant residues.

This framework demonstrates that substrate suitability for BSFL cannot be predicted from proximate analysis or physical properties alone; phytochemical factors must be considered, particularly when utilizing medicinal plant residues. The "fumitory anomaly"—where intermediate chemical composition yields poor performance—is a direct consequence of alkaloid-mediated inhibition, as illustrated by the red pathway in Figure 4. Future studies should validate this model through (1) targeted metabolomics (LC-MS/MS) to quantify specific alkaloids in fumitory, (2) in vitro enzyme inhibition assays to confirm protease/lipase suppression, and (3) transcriptomic analysis of detoxification pathway genes (CYP450, GST) in fumitory-fed larvae.

3.8. Implications for circular bioeconomy and substrate valorization

The results demonstrate that herbal distillation residues—particularly green cumin—are viable substrates for BSFL rearing, offering a pathway to valorize an underutilized agro-industrial by-product. However, none of the HDRs tested as sole substrates matched the performance of optimized control diets (e.g., chicken feed or grain waste) reported in the literature (BE typically 22–25%). Therefore, for commercial applications, blending HDRs with nitrogen-rich co-substrates (e.g., slaughterhouse waste, soybean meal) is recommended to enhance protein content. Fumitory residue is unsuitable as a sole substrate due to low growth and survival, likely mediated by alkaloid-type secondary metabolites. If used, pretreatment (e.g., solid-state fermentation or activated carbon adsorption) may reduce toxicity. Chicory residue provides acceptable but suboptimal performance. Its high fiber content may be beneficial for gut health and frass quality, but co-supplementation with a protein source is necessary for efficient bioconversion. Future studies should (1) quantify specific phytochemicals (alkaloids, polyphenols, terpenoids) in HDRs using LC-MS, (2) assess enzymatic activity (protease, lipase) in BSFL midgut to elucidate mechanisms, and (3) evaluate the effects of substrate blending on both larval performance and nutritional quality.

4. Conclusion

This study systematically evaluated the phytochemical-mediated effects of three herbal distillation residues (chicory, fumitory, and green cumin) on the growth performance, bioconversion efficiency, and nutritional quality of black soldier fly larvae (Hermetia illucens). The key conclusions are as follows:

1. Substrate quality is determined by integrated chemical, physical, and phytochemical factors. Green cumin residue, with the highest crude protein (9.12%), crude fat (7.88%), specific surface area (21.4 m^2/g), and smallest particle size (D50 = 145 μm), produced the best larval performance (final weight = 0.165 g, BE = 21.3%, survival = 96.4%, larval protein = 43.6%, larval lipid = 29.4%). In contrast, chicory residue, despite high fiber (17.41%) and large particles (312 μm), supported moderate growth through compensatory feeding, while fumitory residue, despite intermediate properties, resulted in the poorest outcomes due to inferred alkaloid toxicity.
2. The "fumitory anomaly" confirms the critical role of phytochemicals. The discrepancy between fumitory's intermediate chemical-physical profile and its poor biological performance (weight = 0.087 g, BE = 9.8%, survival = 72.5%) provides strong evidence that secondary metabolites—specifically isoquinoline alkaloids—can override nutritional benefits. This finding underscores that proximate analysis alone is insufficient for predicting substrate suitability when antinutritional compounds are present.
3. Physical properties are co-equal drivers of bioconversion efficiency. The near-perfect correlations between specific surface area and protein/fat (r = 0.99–1.00) and strong negative correlations between particle size and growth (r = -0.65 to -0.97) demonstrate that substrate architecture significantly influences larval feeding efficiency. Particle size reduction (D50 < 200 μm) is recommended as a pretreatment for coarse residues.
4. PCA provides an effective multivariate screening tool. The PCA model explained 100% of variance (PC1 = 85.4%, PC2 = 14.6%), clearly separating substrates by overall quality. This approach can serve as a rapid screening method for evaluating novel HDRs before costly rearing trials.
5. A mechanistic framework explains divergent outcomes. The proposed three-phase model (substrate encounter → digestive hydrolysis → metabolic allocation) with three pathways (optimal green, compensatory yellow, inhibited red) provides a conceptual foundation for understanding how physical, chemical, and phytochemical factors jointly determine larval performance.
Practical implications for circular bioeconomy:
Green cumin residue is recommended as a sole substrate or base ingredient for BSFL rearing.
Chicory residue requires mechanical grinding and protein supplementation for commercial application.
Fumitory residue is unsuitable as a sole substrate; pretreatment (solid-state fermentation, activated carbon adsorption) or blending (ratio > 3:1 with palatable substrates) is required if utilization is necessary.
In conclusion, this study demonstrates that herbal distillation residues—particularly green cumin—are viable substrates for BSFL bioconversion, offering a sustainable pathway for valorizing underutilized agro-industrial by-products within a circular bioeconomy. The integration of physicochemical characterization, multivariate statistics, and mechanistic modeling provides a robust framework for substrate evaluation that extends beyond traditional proximate analysis to include physical and phytochemical dimensions.

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