





Managing bioactive amines in plant-based fermented products

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ABSTRACT

The fermentation of vegetable products is gaining interest due to its ability to extend shelf life and reduce food waste. Additionally, the perceived health benefits of certain fermented foods and the growing popularity of plant-based diets have led to greater consumption and diversification of fermented products. However, fermentation can also promote the accumulation of biogenic amines, which may pose health risks. This study investigated the content of bioactive amines in various commercial plant-based fermented products and evaluated a novel strategy to reduce biogenic amine accumulation by the addition of an active ingredient derived from lyophilised green pea sprouts containing the enzyme diamine oxidase (DAO). Among the tested products, sauerkraut and soy sauce exhibited the highest total biogenic amines levels, with the greatest variability between samples. In contrast, average biogenic amines levels in kimchi, tempeh, miso, soybean paste and a cashew-based cheese analogue were moderate with less variability. No biogenic amines were detected in kombucha. Spermidine and spermine were present in most products, reflecting their natural occurrence in plant ingredients. When the DAO-containing active ingredient was added to laboratory-scale sauerkraut, it significantly reduced biogenic amine levels after seven days: cadaverine decreased by 80 %, putrescine by 70 %, histamine by 23 % and tyramine by 11 %. When all four biogenic amines were simultaneously present in the sauerkraut, the selectivity and effectiveness of the active ingredient were maintained. This novel approach may contribute to the development of safer, higher-quality fermented plant products while benefiting histamine-intolerant consumers.

1. Introduction

Plant-based fermented products, such as cheese analogues, sauerkraut, kimchi, kombucha and fermented soybeans, are gaining popularity among consumers. This trend is driven by their potential health benefits, attributed to pre- and probiotic properties, along with the rise of flexitarian, vegetarian, and vegan diets. The significant increase in the consumption of these products has been accompanied by an exponential growth in their variety (Goksen et al., 2023). Global market data reflect this shift: since 2021, approximately 600 new fermented plant-based products have been launched annually, compared to about 250 a decade ago (Boukid et al., 2023). However, despite this rapid growth, particularly in countries like Spain, actual consumption patterns remain understudied.

Fermentation also addresses the critical issue of food waste. In industrialized countries, up to 30 % of vegetables are lost during primary production, partly due to strict aesthetic standards imposed by distributors (Spang et al., 2019). By extending shelf life, fermentation offers a sustainable solution, at the same time enhancing flavors and textures, qualities highly appreciated by consumers. Moreover, plant-based fermented foods are a source of bioactive amines, a broad category that includes both biogenic amines and polyamines. While biogenic amines are considered undesirable compounds that can compromise food safety and quality, polyamines such as spermidine and spermine, naturally present in plant-based raw materials and thus in fermented vegetables, are associated with potential health benefits (Bover-Cid et al., 2014).

Biogenic amines in fermented products originate mainly from the

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activity of fermentative microorganisms, which can produce histamine, tyramine, putrescine and cadaverine, through the decarboxylation of their corresponding precursor amino acids (EFSA, 2011). Furthermore, spoilage bacteria from raw materials and/or introduced during manufacturing processes may further contribute to biogenic amine build-up in fermented products. In addition, the rising popularity of domestic fermentation practices, where hygiene standards may not be consistently applied, can lead to higher concentrations of biogenic amines compared to commercial products, thereby increasing the risk of adverse health effects related to histamine exposure.

Concretely, histamine is associated with the highest food safety risk due to its toxicity and occurrence. At high levels, its intake can cause adverse health effects in both the general population and, more notably, in sensitive individuals (Comas-Basté et al., 2019; EFSA, 2011). The European Food Safety Authority (EFSA) and the European Centre for Disease Prevention and Control (ECDC) have consistently identified histamine intoxication as a major food safety hazard due to its health implications and impact on global trade (EFSA, 2024). From a legal perspective, the European Union has established maximum levels of 100–200 mg/kg for histamine in fish and fishery products from species with a naturally high histidine content (European Commission, 2005). No other biogenic amines or food categories have been subject to regulatory limits.

Another condition associated with histamine intake, known as histamine intolerance, is a growing concern (Hrubisko et al., 2021). This disorder is primarily caused by a deficiency of the enzyme diamine oxidase (DAO) at the intestinal level, which leads to increased sensitivity to normal or even low levels of histamine in food. The symptoms of histamine intolerance resemble those of histamine intoxication, as both are triggered by the accumulation of histamine in plasma (Lee et al., 2019). Critically, the adverse effects are not only due to the presence of histamine. Other biogenic amines (e.g., putrescine, cadaverine), while not intrinsically harmful, can compete with histamine for DAO-mediated metabolism in the intestine, thereby increasing histamine absorption and toxicity. This interaction may also extend to high levels of spermidine and spermine, albeit to a lesser extent (Chu & Bjeldanes, 1982; Sánchez-Pérez et al., 2022). Consequently, food safety depends not only on histamine content but also on the total load of biogenic amine and polyamines in a product.

The scientific community and food industry have designed various hygienic and technological strategies to minimize the formation of biogenic amines in fermented foods and beverages (Park et al., 2019). However, effective control remains challenging, requiring a multi-faceted approach. In addition to ensuring the hygienic quality of raw materials and manufacturing processes, one of the most studied and commonly applied strategies is the use of selected fermentation starter cultures composed of microorganisms lacking aminogenic activity (Bover-Cid et al., 2000; Latorre-Moratalla et al., 2012; Tabanelli et al., 2018). In addition, some authors proposed the use of bacteriocin-producing strains as starters or co-starters to inhibit amino acid decarboxylase activity in biogenic amine-forming bacteria, reducing its accumulation during product fermentation and ripening (Barbieri et al., 2025; Lim, 2022).

Over the past decade, the ability of certain microorganisms to degrade histamine has been explored as a promising alternative for producing amine-free fermented foods (Alvarez & Moreno-Arribas, 2014; Moniente et al., 2022). However, this degradation capacity is strain-dependent and not widespread among fermentative species, which limits its practical application in the agri-food industry.

Another innovative approach to controlling biogenic amines in fermented products is the addition of a food ingredient with DAO activity. This copper-containing amine oxidase can degrade histamine and other amino substrates found in food (Boulfekhar et al., 2023). Currently, porcine kidney is one of the main sources of DAO and is used in dietary supplements to manage histamine intolerance (Costa-Catala et al., 2024; Schnedl et al., 2019). From a food safety perspective, a few studies have

reported promising results following the incorporation of this animal-derived ingredient in fermented foods, even under the acidic conditions typical of fermentation (Dapkevicius et al., 2000; Moniente et al., 2022; Naila et al., 2012). More recently, germinated legume seeds have emerged as a plant-based alternative, with extracts demonstrating DAO activity equal to or even greater than those derived from porcine sources (Comas-Basté et al., 2020).

The growing popularity of plant-based fermented products, together with their potentially high biogenic amine content, highlights the need for comprehensive research into biogenic amine levels and effective strategies to control their accumulation. Therefore, the aim of this study was to analyse the occurrence of bioactive amines (i.e. biogenic amines and polyamines) across a range of commercially available plant-based fermented foods. Moreover, a pilot study was performed to evaluate a novel approach for biogenic amine control using DAO-containing green pea sprouts as a natural active ingredient in laboratory-scale sauerkraut.

2. Material and methods

2.1. Chemicals and reagents

Boric acid, acetic acid, 2-mercaptoethanol, Brij® L23 solution, 1-octanesulfonic acid sodium salt, methanol, acetonitrile, phthalaldehyde (OPA), histamine dihydrochloride, cadaverine dihydrochloride, tyramine dihydrochloride, putrescine dihydrochloride, β -phenylethylamine hydrochloride, tryptamine hydrochloride, octopamine hydrochloride, serotonin creatine sulphate, dopamine hydrochloride, agmatine sulphate salt, spermine tetrahydrochloride and spermidine trihydrochloride were purchased from Sigma-Aldrich (St. Louis, USA). Anhydrous sodium acetate and perchloric acid 70 % were acquired from PanReac Química (Castellar del Vallès, Spain). Potassium hydroxide was obtained from Thermo Fisher Scientific (Waltham, USA). A LaboStar System from Evoqua Water Technologies (Warrendale, USA) was used to produce ultrapure water (18.2 M Ω cm).

2.2. Analysis of bioactive amines in plant-based fermented products

2.2.1. Samples

A total of 88 samples were analysed, belonging to nine different categories of plant-based fermented products: sauerkraut (n = 10), kimchi (n = 11), soy sauce (n = 8), miso (n = 12), soybean paste (n = 5), tempeh (n = 7), amazake (n = 11), a cashew-based cheese analogue (n = 13) and kombucha (n = 11). Products were acquired from supermarkets and small shops in the region of Barcelona (Spain). After purchase, all food samples were stored at their recommended storage temperature in their original packaging until analysis. Table 1 summarizes the main characteristics of the commercial fermented plant-based products selected for this study.

2.2.2. Chromatographic determination of bioactive amines

Bioactive amines were determined following the method described by Latorre-Moratalla et al. (2009). Concretely, 10 g of each sample was ground, homogenised, and mixed with 10 mL of 0.6 M perchloric acid. The mixture was stirred on a magnetic plate (Agimatic-E, J.P. Selecta S. A., Barcelona, Spain) for 20 min at 700 rpm. The sample was centrifuged during 20 min at 12,500 rpm and 4 °C (Beckman Coulter AVANT J-30I, California, USA) and the supernatant was filtered and collected in a 25 ml volumetric flask. This extraction process was performed twice, and the final volume of the extract was adjusted with 0.6 M perchloric acid. All samples were filtered through a GHP 0.22 μ m filter (Water Corp., Milford, USA) and stored at 4 °C until analysis. For kombucha and soy sauce, 2 mL of homogenised sample was directly acidified with 0.6 M perchloric acid (1:1), centrifuged (12,500 rpm, 4 °C, 20 min) and filtered, as described above.

Twelve bioactive amines, including biogenic amines (histamine, tyramine, putrescine, cadaverine, agmatine, β -phenylethylamine,

Table 1
Main characteristics of the plant-based fermented products.

	Sauerkraut	Kimchi	Soy sauce	Tempeh	Miso	Soybean paste	Cashew-based cheese analogue	Amazake	Kombucha
Origin	Germany	Korean	Japan and China	Indonesian	Japan	Korea and China	China	Japan	China
Main raw material	Cabbage	Cabbage	Soybean	Soybean	Soybean	Soybean	Cashew	Rice	Tea
Fermentation agents	<i>Lactobacillus</i> , <i>Leuconostoc</i> and/or <i>Pediococcus</i>	<i>Lactobacillus</i> , <i>Leuconostoc</i> and/or <i>Weissella</i>	<i>Aspergillus oryzae</i> (koji), lactic acid bacteria, yeasts	<i>Rhizopus</i>	<i>Koji (Aspergillus oryzae or Aspergillus soyae)</i> , with <i>Saccharomyces</i> , <i>Torulopsis</i> , <i>Pediococcus</i> and/or <i>Streptococcus</i>	<i>Aspergillus oryzae</i> , <i>Bacillus subtilis</i> , lactic acid bacteria, yeasts	<i>Lactococcus</i> and <i>Penicillium</i>	<i>Koji (A. oryzae)</i>	SCOBY (symbiotic culture of bacteria and yeast)
Fermentation duration	7–21 days	3–7 days	3–6 months	24–36 h	2–6 months	6–12 months	1–7 weeks	8–12 h	5–21 days
Fermentation temperature	18–22 °C	2 - °C	15–30 °C	30–40 °C	25–30 °C	20–30 °C	20–30 °C	55–60 °C	20–30 °C
pH	3.5–4	4.2–4.5	4.5–5.5	5.5–6.5	5–5.5	5–6	4–5	5–6	2.5–4.2
References	Majcherczyk and Surówka (2019)	Jung et al. (2014)	Yongmei et al. (2009)	Park et al. (2019)	Allwood et al. (2021)	Yoon et al. (2017)	Harper et al. (2022)	Oguro et al. (2017)	Huang (2024)

tryptamine, serotonin, octopamine and dopamine) and polyamines (spermidine and spermine) were determined using ion-pair ultra-high performance liquid chromatography coupled with online post-column derivatization with OPA and fluorometric detection (UHPLC-FL). Chromatographic analyses were conducted on a Waters Acquity™ UPLC system (Waters Corp., Milford, MA, USA) using an Acquity UPLC BEH C18 1.7 μm reverse phase column (2.1 mm × 50 mm) (Waters Corp., Milford, USA) maintained at a constant temperature of 42 °C. For the

post-column derivatization of bioactive amines, an additional pump was connected to a zero-dead-volume mixing T positioned between the column outlet and the fluorescence detector. The mobile phase was delivered at a flow rate of 0.8 mL/min and consisted of eluent A, a solution of 0.1 M sodium acetate and 10 mM sodium octanesulphonate adjusted to pH 4.8 with acetic acid, and eluent B, a mixture of solvent B and acetonitrile (6.6:3.4), where solvent B was a solution of 0.2 M sodium acetate and 10 mM sodium octanesulphonate adjusted to pH 4.5

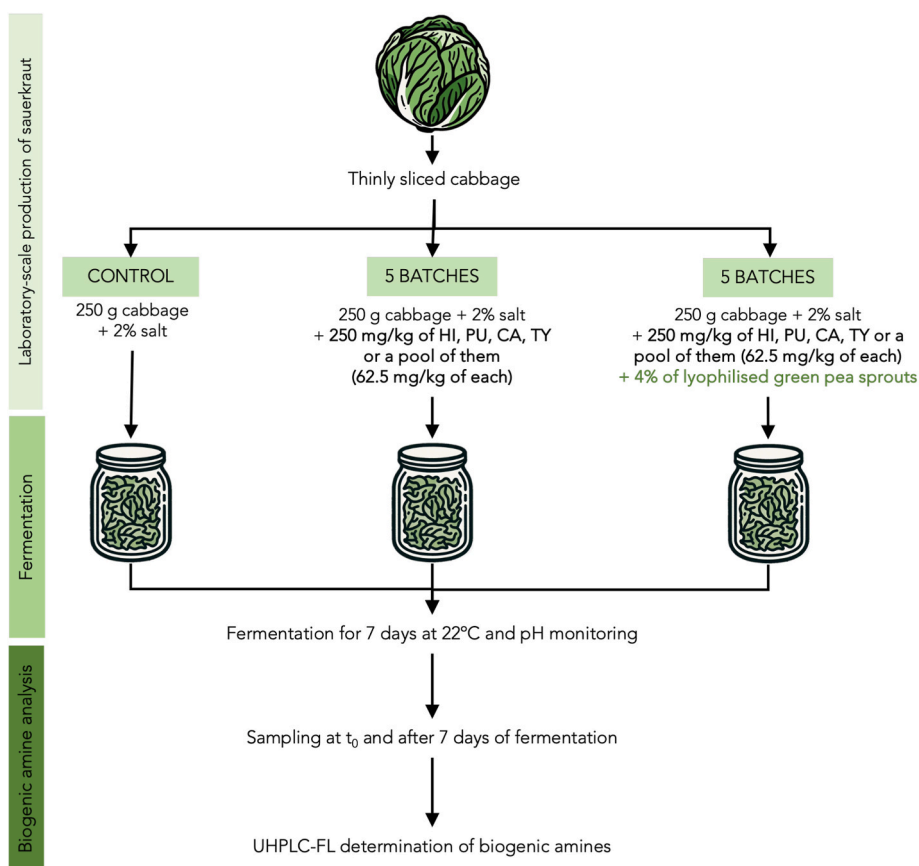


Fig. 1. Experimental procedure for the laboratory-scale production of sauerkraut samples and assessment of the effectiveness of the active ingredient in reducing biogenic amines. HI = histamine, PU = putrescine, CA = cadaverine and TY = tyramine.

with acetic acid. The post-column derivatization reagent, consisting of 0.01 % aqueous OPA solution prepared daily, was pumped at a flow rate of 0.4 mL/min. An automatic injection of 1 μ L was performed. Fluorescence detection was performed with an excitation wavelength of 340 nm and an emission wavelength of 445 nm.

2.3. Legume sprouts as a mitigation strategy for biogenic amine accumulation in sauerkraut

The active ingredient derived from green pea (*Pisum sativum* L.) sprouts was prepared following the protocol described by Costa-Catala et al. (2025). Briefly, seeds were disinfected with 70 mg/l sodium hypochlorite, rinsed, and soaked overnight in distilled water. Germination was performed in a climate-controlled chamber for four days in darkness (30 °C, 70 % relative humidity). The sprouts were then frozen, freeze-dried and ground using a domestic mill. The resulting homogenised powder was sieved to ensure a granulometry of <1 mm and stored at -20 °C until further use. The enzymatic activity of this active ingredient was verified in vitro using four different biogenic amines standards according to the method described by Comas-Basté, Latorre-Moratalla, Sánchez-Pérez, Veciana-Nogués, Vidal-Carou, et al. (2019).

To assess the effect of the active ingredient, eleven sauerkraut batches were prepared at laboratory scale (Fig. 1). Four batches were singularly spiked with initial biogenic amines (250 mg/kg each of histamine, putrescine, cadaverine, or tyramine) and a fifth batch with a pool of all four biogenic amines at 62.5 mg/kg each. Five additional batches contained the same amount of amines plus 4 % (w/w) of lyophilised green pea sprouts as the active ingredient and DAO source. A control batch with no added amines or sprouts was also included to assess the potential formation of biogenic amines by naturally present microbiota.

For each batch, 250 g of thinly sliced cabbage was mixed with 2 % (w/w) salt and transferred to a glass fermentation jar. The mixture underwent spontaneous fermentation for 7 day at 22 °C. Fermentation progress was monitored by measuring pH with a micropH 2001 CRISON (Barcelona, Spain). Biogenic amines concentrations were determined at baseline (t_0) and after seven days of fermentation using the procedure described in the previous section. The effectiveness of the active ingredient in reducing histamine and other biogenic amines was assessed by comparing biogenic amines levels in batches with and without the addition of lyophilised legume sprouts.

Table 2

Bioactive amine contents (mg/kg fresh weight) found in commercial plant-based fermented products. Data are presented as mean \pm standard deviation and minimum-maximum values.

Biogenic amine and polyamine content (mg/kg)								
	n	Histamine	Putrescine	Cadaverine	Tyramine	Spermidine	Spermine	Total
Sauerkraut	10	18.48 \pm 25.54	127.30 \pm 57.94	30.51 \pm 21.93	43.07 \pm 18.94	3.82 \pm 2.98	0.13 \pm 0.30	223.32 \pm 105.14
		1.83–87.35	40.54–207.58	4.43–75.14	23.44–81.94	1.30–11.44	nd - 0.92	110.57–453.38
Kimchi	11	5.81 \pm 8.40	45.22 \pm 66.20	14.28 \pm 28.50	19.46 \pm 24.82	4.21 \pm 1.79	nd	88.97 \pm 116.00
		nd - 25.42	0.36–222.32	nd - 96.50	nd - 75.70	1.03–7.72		4.07–405.78
Soy sauce	8	50.14 \pm 77.61	57.52 \pm 80.39	27.83 \pm 56.84	87.41 \pm 110.78	18.76 \pm 6.66	6.07 \pm 6.14	225.22 \pm 288.80
		nd - 209.93	6.98–189.98	nd - 143.28	nd - 249.74	nd - 26.38	nd - 15.50	29.03–687.52
Tempeh	7	0.35 \pm 0.64	24.32 \pm 12.88	23.47 \pm 40.33	4.36 \pm 4.63	51.41 \pm 24.31	8.27 \pm 6.04	112.18 \pm 47.73
		nd - 1.62	9.65–40.80	nd - 89.93	nd - 10.66	21.92–90.68	1.25–16.63	64.49–180.60
Miso	12	3.76 \pm 3.69	8.75 \pm 4.13	0.03 \pm 0.08	17.13 \pm 30.74	5.28 \pm 5.83	nd	34.95 \pm 34.80
		nd - 9.93	1.18–17.47	nd - 0.26	nd - 96.13	0.19–18.75		8.59–127.97
Soybean paste	5	30.23 \pm 29.68	14.13 \pm 5.09	1.43 \pm 0.28	77.48 \pm 77.73	6.28 \pm 6.58	1.28 \pm 1.05	80.87 \pm 90.76
		nd - 51.21	9.34–22.21	nd - 1.62	nd - 156.80	0.25–17.57	nd - 2.66	nd - 232.21
Cashew-based cheese analogue	13	0.65 \pm 1.67	11.19 \pm 15.39	10.18 \pm 15.39	14.24 \pm 29.01	12.21 \pm 10.64	13.16 \pm 12.40	61.64 \pm 50.19
		nd - 5.55	nd - 56.94	nd - 47.93	nd - 91.41	0.81–40.25	0.27–31.53	2.46–134.37
Amazake	11	nd	2.47 \pm 1.69	1.49 \pm 3.33	2.81 \pm 9.31	1.32 \pm 1.94	0.25 \pm 0.49	8.49 \pm 11.52
			0.68–6.45	nd - 9.36	nd - 30.89	nd - 5.56	nd - 1.37	0.71–40.98
Kombucha	11	nd	nd	nd	nd	nd	nd	nd

nd: not detected (below detection limit of 0.05 mg/kg).

2.4. Statistical analysis

Statistical analysis was performed using IBM SPSS Statistics 27.0 software (IBM Corporation, Armonk, USA). Biogenic amine and polyamine contents are reported as mean values, standard deviation (SD), and minimum and maximum values based on fresh weight. All determinations were done in triplicate, and sauerkraut production was carried out in three independent experiments. Differences in biogenic amine content among sauerkraut batches were assessed using analysis of variance (ANOVA) followed by Tukey's post-hoc test. Statistical significance was set at $p < 0.05$.

3. Results and discussion

3.1. Bioactive amine content in commercial plant-based fermented products

Table 2 presents the content of bioactive amines (i.e., biogenic amines and polyamines) detected across various categories of commercial plant-based fermented products. Considerable variation was observed not only between product categories but also among different brands within the same category. Regarding biogenic amines, only histamine, putrescine, cadaverine and tyramine were detected in the analysed samples. On the other hand, the polyamines spermidine and spermine were detected in almost all analysed samples, reflecting their natural presence in plant-based raw materials or ingredients.

Sauerkraut exhibited by far the highest bioactive amine levels and the greatest variability, and some samples exceeding 400 mg/kg. Tempeh, kimchi, cashew-based cheese analogue, miso and amazake displayed lower and more consistent bioactive amine concentrations. Notably, no bioactive amines were detected in any kombucha samples, consistent with the scarce published studies on kombucha, which also reported their absence in laboratory-scale samples (Bromley, 2021; Liao et al., 2024).

Although no specific regulation exists for plant-based fermented products, none of the samples analysed in this study showed histamine levels above the threshold established for fish and fishery products (100 mg/kg) according to European legislation. Nevertheless, it should be considered that in histamine-sensitive individuals, even lower concentrations may elicit toxic effects. Moreover, from a food safety perspective, not only histamine levels alone but also the combined presence of other biogenic amines, which can potentiate histamine-related symptoms, must be taken into account.

All analysed commercial sauerkraut samples contained histamine,

putrescine, cadaverine and tyramine (Table 2). Among these, putrescine was predominant, accounting for up to 57 % of the total mean biogenic amine content, with concentrations varying widely. Tyramine and cadaverine were present at considerably lower concentrations, while histamine occurred in the smallest quantities (Table 2 and Fig. 2). In its 2011 report on biogenic amines in fermented foods, EFSA included data on several European sauerkraut samples, showing a qualitative and quantitative amine profile consistent with the findings of the present study. Specifically, putrescine was the predominant amine, with reported levels of up to 264 mg/kg (EFSA, 2011). Other authors have corroborated these findings in sauerkraut samples from various countries around the world (Moret et al., 2005; Peñas et al., 2010; Yu et al., 2021; Świder et al., 2020). However, some studies identify tyramine as the predominant amine in sauerkraut (Kalač et al., 1999; Majcherczyk & Surówka, 2019). For example, Kalač et al. (1999) found higher mean levels of tyramine (174 mg/kg) than putrescine (146 mg/kg) in 121

sauerkraut samples from Czech and Austrian producers.

The biogenic amines in sauerkraut primarily arise from the metabolic activity of fermentative bacteria, including *Lactobacillus* spp., *Lactobacillus curvatus*, *Leuconostoc mesenteroides* and *Pediococcus damnosus* (Kalač et al., 1999; Peñas et al., 2010). While these lactic acid bacteria (LAB) are strongly associated with the formation of tyramine, some strains can also generate putrescine, cadaverine and histamine. In addition, certain aerobic mesophilic microorganisms with decarboxylase activity that proliferate during sauerkraut production may contribute to biogenic amine accumulation (Peñas et al., 2010). Besides bacterial aminogenic capacity, biogenic amines levels in sauerkraut are influenced by product-specific factors such as salt concentration, *Brassica* cultivar, and processing conditions (Świder et al., 2020).

As expected for a plant-based product, only low amounts of the polyamines spermidine and spermine were detected in the sauerkraut samples (Świder et al., 2020). Spermidine was consistently present at

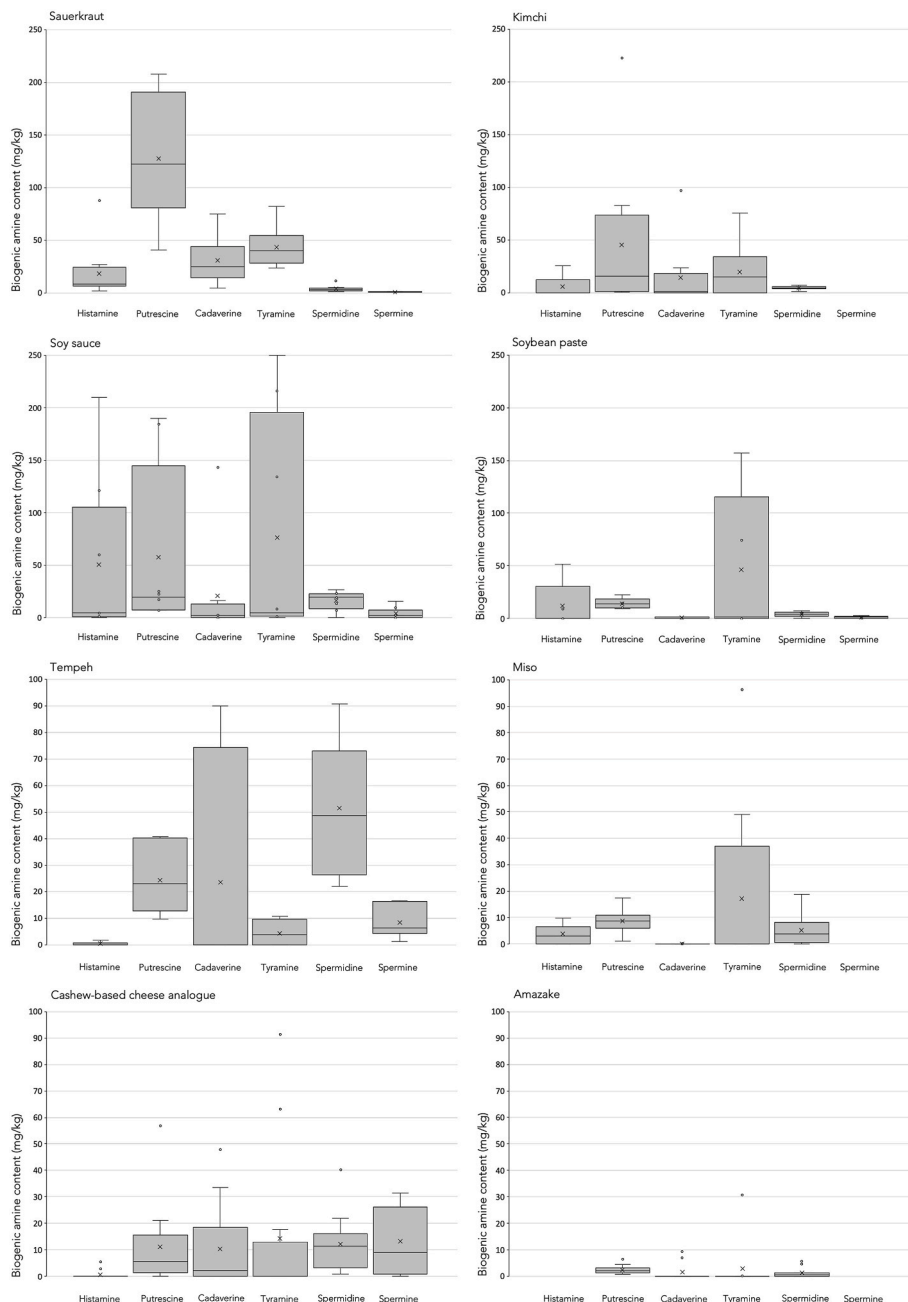


Fig. 2. Biogenic amine and polyamine content (mg/kg) of the commercial plant-based fermented products.

low concentrations, while spermine levels were negligible. The minimal inter-sample variation in polyamine content reflects their physiological origin in cabbage. Notably, the concentrations of spermidine (16 mg/kg) and spermine (1 mg/kg) reported in raw cabbage by other authors closely match the levels found in these sauerkraut samples (Muñoz-Esparza et al., 2021).

Kimchi differs from sauerkraut in its more complex preparation. While both involve lactic acid fermentation of cabbage, kimchi incorporates a wider range of ingredients, including red pepper powder, garlic, ginger, Welsh onion, radish, fermented seafood products (e.g., *Jeotgal*) and sticky rice porridge (Kim et al., 2022) (Table 1). Analysis of commercial kimchi samples revealed putrescine to be the predominant biogenic amine, followed by tyramine and cadaverine, as in the case of sauerkraut (Table 2 and Fig. 2). Although most samples contained these three amines in low to moderate levels, a few brands exhibited markedly high concentrations of putrescine (up to 222 mg/kg). Moreover, these samples with high putrescine contents also tended to have increased levels of the other amines. Histamine was detected in only five of the eleven kimchi samples, generally at low concentrations. Regarding polyamines, spermidine was detected in all kimchi samples, although at very low levels. As in sauerkraut, the polyamines in kimchi originate from cabbage, which is the main raw material in both products.

Previous studies have found wide variability in the biogenic amine content of different types of kimchi (Jin et al., 2019; Lee et al., 2019; Świder et al., 2020). While these studies consistently identified putrescine as the predominant amine, the reported concentrations (mean values ranging from 79 to 269 mg/kg) were generally higher than those observed in the present study. Similarly, histamine levels (59–155 mg/kg) in earlier reports are notably higher than those found here (Jin et al., 2019; Lee et al., 2019).

The fermentation of kimchi involves diverse LAB, mainly belonging to the genera *Leuconostoc*, *Lactobacillus* and *Weissella*, many of which have been described as strongly aminogenic (Park et al., 2019). In addition to the well-established factors influencing biogenic amine accumulation, the variety and quantity of seasonings used in the formulation of kimchi may play a significant role. In particular, seafood-based fermented ingredients, such as *Jeotgal* and *Aekjoet*, have been closely correlated with high biogenic amines contents and contribute to their final profile (Jin et al., 2019; Kim et al., 2022; Lee et al., 2019; Park et al., 2019; Świder et al., 2020). For instance, the study by Kim et al. (2022) reported that histamine in kimchi mainly derives from the fish sauce used in its preparation.

Concerning the different soy-based fermented products, soy sauce was among the categories showing high levels of biogenic amines, although substantial variability was also observed across different brands (Table 2). In these products, the predominant amines were tyramine and putrescine, with concentrations exceeding 100 mg/kg in certain samples (Fig. 2). Histamine and cadaverine were also detected, though less frequently, but in some cases at relatively high levels. By contrast, spermidine and spermine contents were consistently low across all samples, originating from the soybean raw material, and were detected at levels around 25 mg/kg.

Overall, previous studies corroborate this trend, reporting that most commercial soy sauces contain mainly tyramine, histamine, putrescine, and in some cases cadaverine, generally in moderate amounts not exceeding 100 mg/L each (Li et al., 2019; Liu et al., 2020; Yongmei et al., 2009; Zhou et al., 2023). Nonetheless, Liu et al. (2020) reported substantially higher concentrations in China commercial products, with histamine levels reaching up to 172 mg/L and tyramine up to 195 mg/L. Contrarily, the study by Toro-Funes et al. (2015), focused on soy-derived products available in the Spanish market, showed that soy sauce samples contained low biogenic amine concentrations, not exceeding 10 mg/kg for any amine. This inter-product variability could be attributed to differences in the abundance of biogenic amine-producing microorganisms, especially *Enterococcus* and LAB genera (Tan et al., 2025). In addition, previous studies have also highlighted the high salt content

characteristic of soy sauce as a crucial extrinsic factor modulating biogenic amine accumulation during fermentation (Liu et al., 2020; Tan et al., 2025; Zhou et al., 2023). Higher salt concentrations appear to exert a protective effect against amine formation, likely by selectively inhibiting decarboxylase-positive spoilage bacteria and reducing proteolytic activity (Liu et al., 2020).

In tempeh, produced through solid-state fermentation of boiled soybeans using *Rhizopus* species (Table 1), spermidine was the predominant bioactive amine, although its concentration varied considerably (Table 2). Half of the samples contained spermidine levels exceeding 50 mg/kg, with some reaching 90 mg/kg. Our findings closely align with previously reported spermidine concentrations in tempeh (Kobayashi et al., 2017; Nishimura et al., 2006; Toro-Funes et al., 2015). Its widespread presence and the consistency of these values with previously reported levels in raw soybeans strongly suggest that spermidine in tempeh primarily originates from the raw material. Spermine was also detected in all commercial samples but at levels below 20 mg/kg, in accordance with previous studies (Kobayashi et al., 2017; Muñoz-Esparza et al., 2021). It is important to highlight that the levels of polyamines found in this product would not pose a risk related to biogenic amine intake, as they are not high enough to interfere with histamine degradation mediated by the DAO enzyme (Chu & Bjeldanes, 1982; Sánchez-Pérez et al., 2022).

Moreover, all tempeh samples contained putrescine, with concentrations falling within the range previously reported for unfermented soybeans (i.e., 8–70 mg/kg) (Kobayashi et al., 2017; Muñoz-Esparza et al., 2021; Nishimura et al., 2006). This pattern indicates that putrescine in tempeh is likely of physiological rather than microbial origin, unlike in other fermented vegetables. Indeed, several plant-based foods, including soybeans and citrus fruits, naturally contain high levels of putrescine, which also serves as a metabolic precursor of spermidine.

On the other hand, cadaverine, histamine and tyramine were detected only sporadically and in a limited number of samples, which suggests that these amines likely result from the activity of spoilage microorganisms or spontaneous LAB involved in the fermentation process. In this context, Nout et al. (1993) confirmed the ability of *R. oligosporus* (the primary tempeh fermentation fungus) to produce tyramine and other amines. Additionally, *Lactiplantibacillus plantarum* and *Klebsiella pneumoniae*, microorganisms typically present in this type of product, also contribute to tyramine and cadaverine formation (Nout et al., 1993; Saaid et al., 2009).

Miso is also a traditional Japanese fermented paste produced from soybeans, rice or barley (Table 1). Spermidine and putrescine were consistently detected in all miso samples (Table 2 and Fig. 2). Previous studies confirm that commercial miso products typically contain these two amines and at similar amounts that those reported in the current study (Byun & Mah, 2012; Kirschbaum et al., 2000; Toro-Funes et al., 2015). These compounds are likely derived from the soybeans used as raw material (Byun & Mah, 2012). However, the lower concentrations compared to raw soybeans or other fermented products such as tempeh (Kobayashi et al., 2017; Park et al., 2019) likely reflect the composition of miso, which generally includes only 35–50 % soybeans. The absence of detectable spermine in all miso samples may also be attributed to this reduced soybean content.

On the other hand, tyramine was detected in only five of the 12 miso samples, showing high variability (Fig. 2). This considerable variability may be attributed to the differing fermentation times that miso products undergo, which can vary significantly, from 2 to 6 months, since this amine is strongly associated with fermentation bacteria (Allwood et al., 2021). In contrast, histamine was present in more samples but at consistently low concentrations, remaining below 10 mg/kg in all cases. These findings are broadly consistent with previous reports indicating low histamine contents in miso products (Byun & Mah, 2012; Kirschbaum et al., 2000; Lee et al., 2016), although isolated cases of significantly higher levels (up to 389 mg/kg) have been documented (Kirschbaum et al., 2000). The presence of histamine in miso is strongly

associated with spoilage bacterial activity. [Byun and Mah \(2012\)](#) confirmed that various *Bacillus* spp., considered the predominant contaminant bacteria in miso, were likely the major histamine producers.

Soybean pastes, products very similar to miso in both their main ingredient (soybeans) and type of fermentation, but with slightly different formulations depending on their country of origin, exhibited a comparable biogenic amine profile. As in miso, overall amine contents were generally low and not of particular concern. However, two samples showed noteworthy levels of tyramine and histamine, reaching up to 150 and 50 mg/kg, respectively. Putrescine and spermidine were the only amines consistently detected across all samples, which can be attributed to their physiological origin in soybeans used as raw material ([Muñoz-Esparza et al., 2021](#)). These findings are in agreement with previous reports on this type of product ([Park et al., 2019](#); [Shukla et al., 2010](#)), and the factors influencing amine content appear to be the same as those described for miso, since both rely on a similar production process and the same principal ingredient ([Park et al., 2019](#); [Shukla et al., 2010](#)).

Cashew-based cheese, a plant-based fermented product recently introduced to the market ([Table 1](#)), represents a potential source of biogenic amines, particularly tyramine, putrescine and cadaverine ([Table 2](#)). While most samples contained low or very low amine levels, five exhibited markedly higher concentrations ([Fig. 2](#)). In two of these, tyramine was the only notable amine, reaching high levels up to 91 mg/kg. In contrast, three other samples contained high levels of putrescine and cadaverine, while tyramine was undetectable, suggesting possible contamination by spoilage bacteria, including Enterobacteriaceae ([Novella-Rodríguez et al., 2003](#)). All samples contained the polyamines, spermidine and spermine, attributable to the cashew nuts (58–67 % of the product formulation), which are naturally rich in both compounds ([Muñoz-Esparza et al., 2021](#)).

To the best of our knowledge, only [Tabanelli et al. \(2018\)](#) assessed biogenic amine content in cashew-based cheese analogues, characterising home-made vegan fermented samples and highlighting the presence of low concentrations of tyramine and 2-phenylethylamine and the absence of histamine, putrescine and cadaverine. However, the observed amine profile found in the current cashew-based cheese analogues is consistent with that of traditional dairy cheeses, where tyramine is often dominant, even at much higher concentrations, likely due to the use of similar fermentative microbial species ([Bravo-Lamas et al., 2025](#); [EFSA, 2011](#)). LAB species (e.g., *Lactococcus lactis* subsp. *cremoris*) and moulds (e.g., *Penicillium camemberti*, *Penicillium roqueforti*), commonly used in the fermentation of both products, have previously been identified as tyramine producers ([Flasarová et al., 2016](#); [Natrella et al., 2024](#)). However, information about the specific bacterial strains used in the commercial products analysed here is unavailable.

Koji amazake, a traditional Japanese sweet beverage produced by fermenting rice ([Table 1](#)), showed the lowest biogenic amines levels among the analysed plant-based fermented products ([Table 2](#) and [Fig. 2](#)). Of the 11 commercial samples, only one contained detectable tyramine, together with a low amount of cadaverine. Putrescine was present in all amazake samples at low concentrations and spermidine showed a similar pattern. It is worth mentioning that rice naturally contains low levels of putrescine and spermidine, which is reflected in the concentrations found in amazake ([Hou et al., 2019](#)). Two samples were formulated with soybeans or adzuki beans in addition to rice, which may explain their slightly higher levels of putrescine and spermidine compared to amazake produced exclusively from rice. To our knowledge, no previous studies have examined the biogenic amine content of this fermented product.

3.2. Pilot study on the use of DAO-rich lyophilised green pea sprouts to reduce biogenic amines in sauerkraut

Among the various commercially available plant-based fermented

foods analysed, sauerkraut consistently showed the highest total biogenic amines concentrations ([Table 2](#)). For this reason, sauerkraut was selected as a laboratory-scale model to evaluate the efficacy of DAO-rich lyophilised green pea sprouts in mitigating biogenic amine accumulation. This active ingredient exhibited *in vitro* DAO activity towards cadaverine (11.87 mU/mg), putrescine (10.85 mU/mg), histamine (0.40 mU/mg) and tyramine (0.32 mU/mg).

The pH was monitored throughout the seven days of spontaneous fermentation. All batches showed the characteristic gradual decrease, from an initial pH of 5.3–5.5 to final values of 3.9–4.0, confirming the normal progression of cabbage fermentation. The most pronounced drop in pH occurred during the first three days, followed by a more gradual decline of 0.4–0.5 units over the remaining four days.

As expected, at time zero (prior to fermentation), only the experimentally spiked biogenic amines were detected, at their predefined concentrations ([Fig. 1](#)). It is important to note that the cabbage used as the fermentation substrate did not contain significant amounts of biogenic amines (<1.5 mg/kg); only naturally occurring spermidine and spermine were detected (3.9 ± 0.9 mg/kg and 1.6 ± 0.5 mg/kg, respectively). The batches supplemented with lyophilised green pea sprouts showed slightly higher polyamine concentrations (spermidine: 7.5 ± 1.0 mg/kg; spermine: 9.5 ± 1.1 mg/kg, respectively), attributable to the composition of the active ingredient.

After seven days of fermentation, only minimal formation of the four biogenic amines was observed in both control and spiked batches without the active ingredient (<2.5 mg/kg). This likely reflects the optimal hygienic conditions maintained during laboratory-scale fermentation and the decarboxylase-negative nature of the indigenous LAB, which inherently limits amine accumulation. Regarding the effectiveness of the active ingredient, a significant reduction in histamine, putrescine, cadaverine and tyramine levels was observed after seven days of spontaneous fermentation, although the extent of reduction varied depending on the specific amine ([Fig. 3](#)). Cadaverine and putrescine showed the most pronounced decreases, with reductions of 80 % and 70 %, respectively ($p < 0.001$). Histamine concentrations dropped from approximately 250 mg/kg to 190 mg/kg, while tyramine showed a more modest reduction of only 11 %. These differences may be attributed to the substrate selectivity of plant-based DAO, which shows the highest affinity for diamines such as putrescine and cadaverine, a slightly lower (but still relevant) affinity for histamine, and the lowest affinity for monoamines such as tyramine, as reported in previous studies ([Kivirand & Rinke, 2007](#); [Pietrangeli et al., 2007](#)).

In a more realistic scenario simulating commercial conditions, with all four biogenic amines present simultaneously, the active ingredient demonstrated comparable effectiveness ([Fig. 4](#)). The addition of lyophilised green pea sprouts reduced the total biogenic amine content by nearly half (from 250 mg/kg to 130 mg/kg) over the fermentation period ($p < 0.001$). The substrate-specific reduction pattern persisted, with cadaverine (81 %) and putrescine (74 %) showing the most significant declines, followed by histamine (33 %) and tyramine (28 %).

The content of the polyamines spermine and spermidine remained constant throughout the fermentation process, both in the control batch (4.16 ± 2.09 mg/kg and 1.5 ± 0.8 mg/kg, respectively) and in the samples with the active ingredient added (7.8 ± 1.2 and 9.5 ± 3.6, respectively). This suggests that no polyamine formation occurred during fermentation and that the catalytic effect of the active ingredient does not affect these compounds.

To the best of our knowledge, this is the first study to demonstrate the efficacy of an active ingredient based on lyophilised legume sprouts as a strategy to control the occurrence of biogenic amines in plant-based fermented foods. To date, only a few studies have explored the addition of DAO as a means of biogenic amine control in food matrices, all relying on commercial purified enzymes extracted from porcine liver or kidney. For instance, [Dapkevicius et al. \(2000\)](#) reported an 80 % reduction in histamine levels in ensiled fish slurry (initially spiked at 200 mg/l) treated with purified porcine DAO at a concentration of 7.7 %. Their

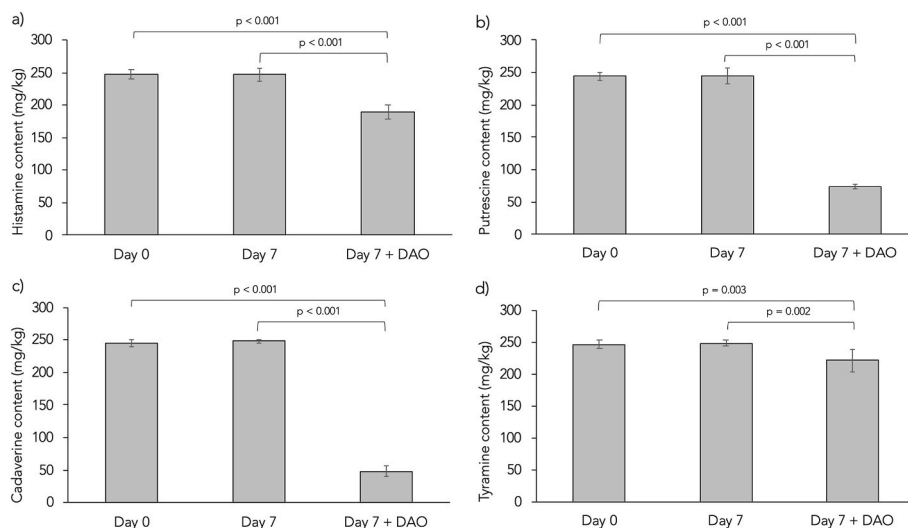


Fig. 3. Biogenic amine content (mg/kg) in sauerkraut batches spiked with 250 mg/kg of a) histamine, b) putrescine, c) cadaverine and d) tyramine, measured at day 0 and after 7 days of spontaneous fermentation, with or without the addition of 4% (w/w) lyophilised green pea sprouts as a source of diamine oxidase (DAO).

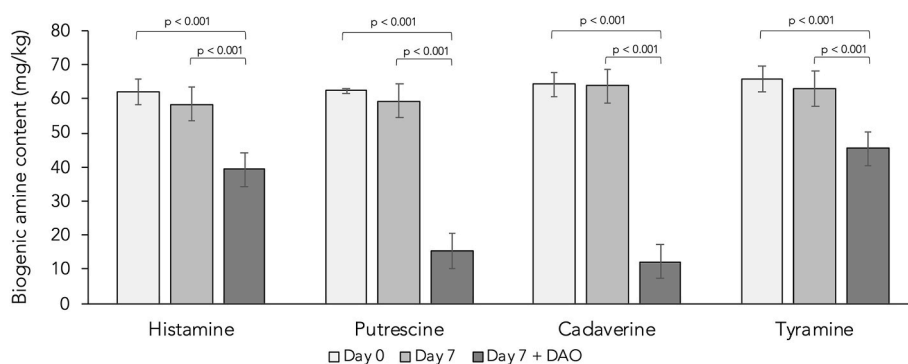


Fig. 4. Biogenic amine content (mg/kg) in sauerkraut batches spiked with 250 mg/kg of a pool of histamine, putrescine, cadaverine and tyramine (62.5 mg/kg each), measured at day 0 and after 7 days of spontaneous fermentation, with or without the addition of 4% (w/w) lyophilised green pea sprouts as a source of diamine oxidase (DAO).

study also demonstrated that DAO activity is retained under the mildly acidic conditions typical of early fermentation ($\text{pH} > 4.5$). More recently, [Moniente et al. \(2022\)](#) evaluated the effect of purified porcine kidney DAO (0.065 %) in cheese inoculated with a strong histamine-producing strain of *Lentilactobacillus parabuchneri*. Similar to our study on sauerkraut, histamine levels in the cheese were reduced by 23 % after 100 days of ripening, from an initial concentration of 771 mg/kg formed by the aminogenic starter culture. Although the DAO dose used by [Moniente et al. \(2022\)](#) was lower than here, it is important to note that they employed a highly purified commercial enzyme. In contrast, our approach offers a more affordable, natural and minimally processed plant-derived DAO alternative.

DAO application has also been explored in non-fermented matrices. For instance, [Naila et al.](#) applied porcine liver DAO (0.056 % w/v) to a fish soup used to prepare *Rihaakuru*, a traditional sauce from the Maldives ([Naila et al., 2012](#)). In that study, 500 mg/l of histamine in a sample was completely degraded within 10 h by the DAO extract. This successful elimination can be attributed to the experimental conditions, as the matrix was incubated under optimal parameters for enzymatic activity ($\text{pH} 7$ and 37°C) ([Naila et al., 2012](#)). The authors concluded that, while effective, the use of commercially purified DAO is economically unfeasible and emphasized the need for more affordable and sustainable sources. In this context, the legume-derived active ingredient evaluated in the present study could represent a promising DAO source.

4. Conclusions

This study reveals the presence and significant variability of biogenic amines in commercial plant-based fermented products. Although histamine was generally detected at low levels, its presence in some samples could potentially pose a health risk to sensitive individuals, particularly those with histamine intolerance. Regarding polyamines, they are generally present at low levels and without significant relevance. Moreover, the present study is the first to demonstrate the efficacy of a plant-derived DAO-containing ingredient in reducing biogenic amine levels, using sauerkraut as a fermentation model. This novel approach may contribute to the development of safer, higher-quality fermented plant products while benefiting histamine-intolerant consumers. Importantly, this strategy is not intended as a substitute for good hygienic practices in the handling of raw materials, as biogenic amine accumulation in these products arises mainly from fermentative rather than spoilage microbiota.

It should be acknowledged that this work was conceived as a general screening of commercially available plant-based fermented products in Spain. As such, while it provides valuable first insights into their bioactive amine content, it does not fully capture the inherent variability in production processes and raw materials among products. Regarding the control strategy, it is worth noting that the study was conducted using a single fermented food model, and different product matrices may lead to varying outcomes. In addition, the absence of sensory analyses

makes it difficult to determine how the incorporation of this active ingredient could affect consumer acceptance of the final products. Further studies are therefore warranted to optimize the amount of legume sprouts required to achieve maximal efficacy in reducing biogenic amine levels while minimizing potential effects on organoleptic properties and overall consumer acceptance. The promising results obtained here provide a basis for future studies under more realistic conditions, including longer fermentation periods, different operating conditions and a more realistic microbial ecology. Alternatively, the extraction and purification of DAO from sprouts could also be investigated as a means of reducing these potential drawbacks, or other sources of DAO with inherently lower impact on product quality could be evaluated.

CRedit authorship contribution statement

Judit Costa-Catala: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Giulia Tabanelli:** Writing – review & editing, Writing – original draft, Methodology. **Alicia Díez-González:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **M. Luz Latorre-Moratalla:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **M. Carmen Vidal-Carou:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Oriol Comas-Basté:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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