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Research Article

Identification of flavonoid glycosides from *Moringa oleifera* leaves that suppress *Saccharomyces cerevisiae* metabolic activity

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Abstract

Moringa oleifera leaves are highly valued as a functional food ingredient due to their exceptional nutritional profile and diverse biological activities. *M. oleifera*'s bioactive components have also attracted increasing attention for their applicability to food biotechnology and functional food development. However, addition of *M. oleifera* leaf powder to bread dough suppresses dough expansion during fermentation, by reducing CO_2 production mediated by *Saccharomyces cerevisiae*, although the responsible compounds remain unidentified. We aimed to identify the compounds in *M. oleifera* leaves that inhibit the metabolic activity of *S. cerevisiae*. Fractionation was performed using a WST-8 assay as a bioassay-guided indicator, and the active constituents were identified by liquid chromatography–mass spectrometry and nuclear magnetic resonance spectroscopy. Quercetin-3-*O*-glucoside (Q3G) and kaempferol-3-*O*-glucoside (K3G) were identified as the principal inhibitory flavonoid glycosides. Both compounds suppressed yeast metabolic activity in a concentration-dependent manner, without affecting cell viability. Furthermore, their aglycones, quercetin and kaempferol, showed weaker inhibitory effect, indicating that *O*-glycosylation is essential for the activity. This study provides the first evidence that specific flavonoid glycosides from *M. oleifera* leaves directly inhibit yeast metabolic activity, highlighting the structural importance of glycosylation in their mode of action and offering insights into quality design in Moringa-fortified baked products.

Keywords

Moringa oleifera, quercetin-3-*O*-glucoside, kaempferol-3-*O*-glucoside, *Saccharomyces cerevisiae*, metabolic activity

Abbreviations

HPLC – high-performance liquid chromatography; MS – mass spectrometry; NMR – nuclear magnetic resonance; ODS – octadecylsilyl; SAR – structure–activity relationship; WST-8 – water-soluble tetrazolium salt

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Introduction

Moringa oleifera, belonging to the family Moringaceae, is a flowering plant native to tropical and subtropical regions and has been highly valued for its exceptional nutritional and functional properties (Verdcourt 1985). It is widely cultivated as an important food resource and its leaves, seeds, and pods are incorporated into diverse cuisines depending on local traditions, including vegetable dishes, curries, stir-fried meals, and condiments. In particular, the leaves of *M. oleifera* are rich in protein, calcium, iron, potassium, vitamins C and E, and β-carotene (Jongrungruangchok et al. 2010; Oduro et al. 2008; Sánchez-Machado et al. 2010; Yameogo et al. 2011), making them a valuable resource for nutritional supplementation and medicinal foods, especially in regions suffering from malnutrition. Numerous studies on the functionality of *M. oleifera* leaves have identified a variety of bioactive constituents, including flavonoid glycosides with quercetin and kaempferol as aglycones (Manguro and Lemmen 2007), phenolic glycosides, and unique pyrrole alkaloids (Sahakitpichan et al. 2011), which have contributed to its designation as the "miracle tree". While these bioactive compounds contribute to the nutritional and medicinal value of *M. oleifera*, they may influence microbial activity in food processing systems, although their specific effects remain unclear.

In recent years, *M. oleifera* leaf powder has been incorporated into baked products to enhance their nutritional and functional properties. However, when added to bread dough, it reportedly *suppresses* dough expansion during fermentation (Sengev et al. 2013). Bread expansion occurs when yeast metabolizes sugars to produce carbon dioxide, which creates gas bubbles that are retained by the viscoelastic gluten network (Yano 2019). A previous study demonstrated that supplementation with *M. oleifera* leaf powder suppresses bread expansion not by impairing gluten formation but rather by reducing carbon dioxide production by yeast (Koriyama et al. 2023). This suppression limits the widespread industrial application of the highly nutritious leaf powder, highlighting a crucial knowledge gap in its food utilization. The specific compounds responsible for this phenomenon, however, have not yet been identified.

The successful identification and characterization of these constituents represent a novel research effort that will enable targeted modification of the leaf powder for optimal use in baking and other fermentation-dependent food processes. We hypothesized that one or more specific pyrrole or phenolic compounds, which are known to be abundant in *M. oleifera* leaves, are responsible for the potent inhibition of *S. cerevisiae* metabolic function. Hence, the present study aimed to isolate and identify these constituents. We used the WST-8 reduction bioassay to assess *S. cerevisiae* metabolic activity to guide fractionation for active compound isolation and to sensitively evaluate their inhibitory effects on yeast metabolism because this assay specifically reflects dehydrogenase-dependent metabolic activity rather than cell viability.

Materials and Methods

Materials and chemicals. Moringa powder was purchased from Irodori LCC (Saitama, Japan). Dry yeast (standard baking *S. cerevisiae*, containing emulsifier and vitamin C) was procured from Nisshin Seifun Welna Inc. (Tokyo, Japan). *n*-Hexane, ethyl acetate, *n*-butanol, and CD_3OD were obtained from FUJIFILM Wako Pure Chemical Corporation (Tokyo, Japan). Quercetin and kaempferol were purchased from Tokyo Chemical Industry Co., Ltd. (Tokyo, Japan). LC-MS-grade 0.1% HCOOH in CH_3CN and 0.1% HCOOH in water were obtained from Thermo Fisher Scientific (Waltham, MA, USA).

Extraction of Moringa powder. Moringa powder (1.0 g) was extracted with 100 mL of methanol (25°C, 24 h). The extract was filtered through paper, and the solvent was evaporated to yield the residue (291.5 mg), which was used as the Moringa powder extract.

Assessment of *S. cerevisiae* metabolic activity in the presence of Moringa powder extract. The WST-8 assay was employed to quantify the functional metabolic activity and hence, the fermentative capacity, of the yeast. The WST-8 reagent is reduced by dehydrogenases in the yeast cells, producing a water-soluble orange formazan, and the resulting color intensity serves a proxy for metabolic activity (Tsukatani et al. 2009). One hundred milligrams of dry yeast ground in a mortar was mixed with 10 mL of ion-exchanged water. One

milliliter of the mixture was transferred to a 1.5 mL microcentrifuge tube. Moringa powder extract was added, and the mixture was incubated at 25℃ for 1h. Then, 500 µL of the solution was transferred to a 1.5 mL microcentrifuge tube, 10 µL of WST-8 reagent was added, and the reaction mixture was incubated at 40℃ for 3 h. The tubes were then centrifuged (13,000 rpm, 5 min), the supernatant was dispensed in 100 µL aliquots into 96-well microplates, and the absorbance at 450 nm was measured.

S. cerevisiae metabolic activity (%) was calculated as follows:

$$S.\ cerevisiae\ \text{activity}\ (\%) = \frac{\text{Abs (ME + SC + WST)} - \text{Abs (ME + SC)}}{\text{Abs (SC + WST)} - \text{Abs (SC)}} \times 100$$

where Abs (ME+SC+WST) is the absorbance of a *S. cerevisiae*-containing Moringa powder extract solution treated with WST-8, Abs (ME+SC) is the absorbance of a corresponding blank without WST-8, Abs (SC+WST) is the absorbance at 450 nm of a *S. cerevisiae* solution treated with WST-8, and Abs (SC) is the absorbance of a corresponding blank without WST-8.

***S. cerevisiae* metabolic activity-guided isolation of compounds from Moringa powder.** The methanol extract was sequentially partitioned in water, *n*-hexane, ethyl acetate, and *n*-butanol, resulting in *n*-hexane (66.5 mg), ethyl acetate (7.7 mg), *n*-butanol (24.3 mg), and water extracts (176.6 mg). The effect of each extract on *S. cerevisiae* activity was assessed as described above. The *n*-butanol extract was further fractionated using water, 50% methanol, and methanol elution with a Sep-Pak cartridge (Waters), yielding three fractions: water (12.7 mg), 50% methanol (15.5 mg), and methanol (1.3 mg). The 50% methanol fraction was subjected to additional fractionation *via* preparative high-performance liquid chromatography (HPLC; column, Mightysil ODS, 10 × 250 mm; solvent, H_2O-MeOH (1:1); flow rate, 2.5 mL. min^{-1}; detection, 270 nm) to obtain five fractions: Fraction 1 (4.0 mg), Fraction 2 (2.2 mg), Fraction 3 (4.1 mg), Fraction 4 (0.6 mg), and Fraction 5 (4.1 mg). Fractions 3 and 4 were further purified, yielding Compounds **1** and **2**, which were subjected to structural analysis using spectral techniques.

Spectral analysis. One-dimensional (^1H and ^{13}C) nuclear magnetic resonance (NMR) spectra were recorded on a JEOL AL-300TLS instrument (JEOL, Tokyo, Japan). Methanol-d_4 (CD_3OD) served as the solvent, and methanol (^1H: 3.31 ppm, ^{13}C: 49.0 ppm) was utilized as the internal standard. Liquid chromatography–mass spectrometry (LC-MS) was conducted employing a Waters Acquity/SynaptG2 system (Waters, Milford, MA, USA) equipped with a Waters BEH C18 column (2.1 × 100 mm, 1.7 µm diameter), yielding high-resolution electrospray ionization (HRESI) mass spectra. Solvents included 0.1% HCOOH in CH_3CN and 0.1% HCOOH in water.

***S. cerevisiae* cell counts.** To assess the effects of isolated active compounds on *S. cerevisiae* cell viability, live *S. cerevisiae* cells were counted using a dye exclusion method reported by Aloysius et al. (2024), with modifications. Briefly, 100 mg of dry yeast was ground in a mortar and mixed with 10 mL of ion-exchanged water. One milliliter of the suspension was transferred to a 1.5 mL microcentrifuge tube, and 0.5 mg of a test compound was added. After an initial 1 h incubation at 25℃, the mixture was transferred to an incubator at 40℃ and incubated for another 6 h for time-course analysis. Every 2 h (i.e., at 0, 2, 4, and 6 h), 10 µL was collected, diluted 1: 100 with ion-exchanged water, and mixed in a 1: 1 ratio with Trypan blue stain (Nacalai Tesque, Inc.). Live *S. cerevisiae* cells were counted using a hemocytometer (Watson). Cell count percentage was determined as follows:

$$S.\ cerevisiae\ \text{cell count}\ (\%) = \frac{\text{Live cell count in treated sample (cells/mL)}}{\text{Live cell count in untreated sample (cells/mL)}} \times 100$$

Statistical analysis. Data are expressed as the mean ± standard error of the mean (SEM) from triplicate experiments. Significant differences in values were analyzed using one-way analysis of variance (ANOVA) in the SPSS statistical software (version 29.0.2.0, IBM, Armonk, NY, USA). Tukey's method was used for multiple comparisons, with statistical significance set at $p < 0.05$.

Results and Discussion

Results

Evaluation of assay conditions and the effect of *M. oleifera* extract on *S. cerevisiae* metabolic activity. In this study, "metabolic activity" refers to *S. cerevisiae* intracellular dehydrogenase activity as measured by the WST-8 assay, whereas "cell viability" was determined based on Trypan blue dye exclusion. Koriyama et al. (2023) reported that direct supplementation of *M. oleifera* leaf powder to *S. cerevisiae* cultures decreased metabolic activity as measured by the WST-8 assay; however, the responsible compounds were not identified. In the present study, we re-examined the suppressive effect using the WST-8 assay and extracts prepared from *M. oleifera* leaves. Reaction product absorbance increased linearly with the volume of WST-8 reagent added within the range of 5-20 µL, without signal saturation. Therefore, a reagent volume of 10 µL was selected as the optimal volume. Using the assay with the optimal reagent volume, we found that *M. oleifera* leaf extract suppressed *S. cerevisiae* metabolic activity in a concentration-dependent manner (Fig. 1).

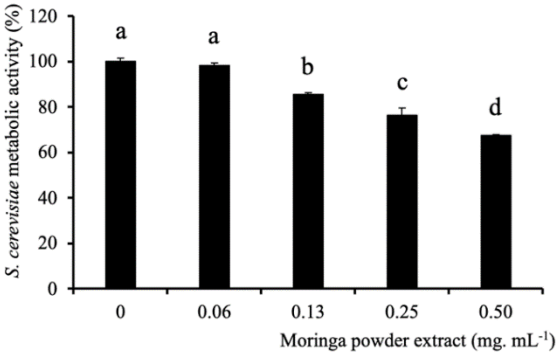


Figure 1. Inhibitory effect of a Moringa leaf methanol extract on *S. cerevisiae* metabolic activity – Values are expressed relative to the untreated control (0 mg. mL^{-1}, *S. cerevisiae* in the presence of the extraction solvent) and shown as mean ± standard error of the mean (n = 3). Different letters (a, b, c, d) indicate statistically significant differences among groups (p < 0.05; ANOVA followed by Tukey tests). Groups sharing the same

Isolation of *M. oleifera* extract compounds that suppress *S. cerevisiae* metabolic activity. Given the concentration-dependent suppression of *S. cerevisiae* metabolic activity (Fig. 2) by the crude Moringa leaf methanol extract, fractionation guided by *S. cerevisiae* metabolic activity was performed using to identify the specific inhibitory constituents in the extract.

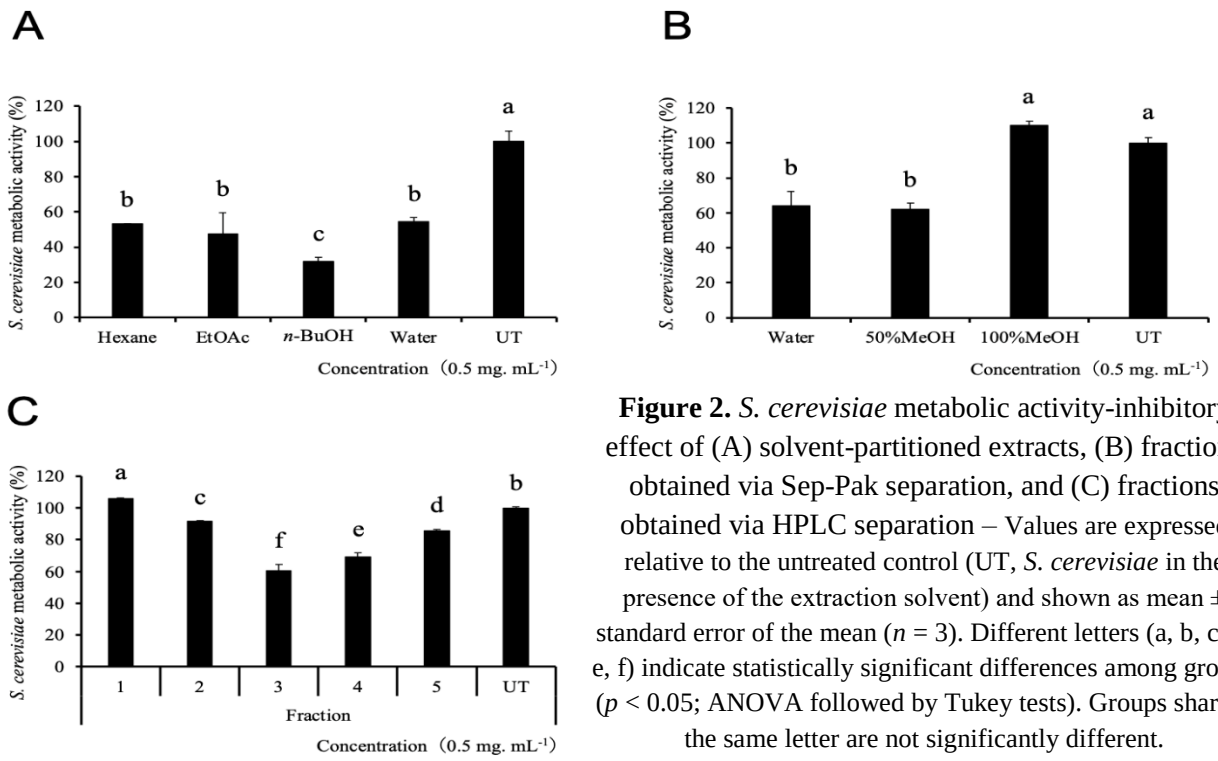


Figure 2. *S. cerevisiae* metabolic activity-inhibitory effect of (A) solvent-partitioned extracts, (B) fractions obtained via Sep-Pak separation, and (C) fractions obtained via HPLC separation – Values are expressed relative to the untreated control (UT, *S. cerevisiae* in the presence of the extraction solvent) and shown as mean ± standard error of the mean (n = 3). Different letters (a, b, c, d, e, f) indicate statistically significant differences among groups (p < 0.05; ANOVA followed by Tukey tests). Groups sharing the same letter are not significantly different.

All WST-8 assay screenings were carried out at a sample concentration of 0.5 mg.mL^{-1}. All fractions obtained by liquid–liquid partitioning exhibited inhibitory effects to *S. cerevisiae* metabolic activity (Fig. 2A), with the *n*-butanol fraction showing the strongest activity. This fraction was subsequently further separated using a Sep-Pak cartridge, yielding subfractions. Among them, the water and 50% methanol fractions displayed pronounced inhibitory effects (Fig. 2B). The 50% methanol fraction was purified using ODS column HPLC, resulting in the separation of five components. Of these, Fractions 3 and 4 exhibited the strongest inhibitory activity (Fig. 2C) and were designated as Compounds **1** and **2**, respectively.

Structural analysis of the isolated compounds. Compound **1** was obtained as a yellow amorphous solid. High-resolution electrospray ionization mass spectrometry (HRESI-MS) analysis established its molecular formula as $C_{21}H_{20}O_{12}$. Analysis of the ^{1}H- and ^{13}C-NMR spectra in CD_3OD indicated that the compound was a glucose-conjugated quercetin derivative, identified as quercetin-3-*O*-glucoside (Q3G). This assignment was supported by comparison with reported data (Yamauchi et al. 2014) (Fig. 3A). Compound **2** was also isolated as a yellow amorphous solid. HRESI-MS determined its molecular formula as $C_{21}H_{18}O_{11}$, which is 16 amu smaller than that of Compound **1**, suggesting the replacement of a hydroxyl group by a hydrogen atom.

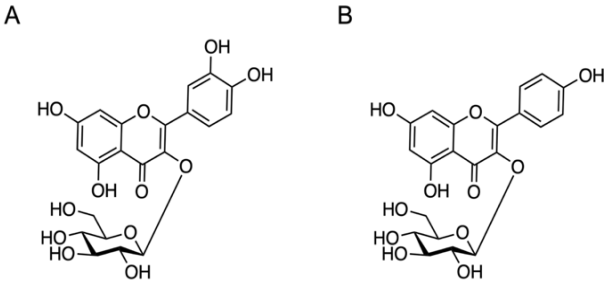


Figure 3. Chemical structures of (A) quercetin-3-*O*-glucoside (Q3G) and (B) kaempferol-3-*O*-glucoside (K3G).

Subsequent ^{1}H- and ^{13}C-NMR analyses identified Compound **2** as kaempferol-3-*O*-glucoside (K3G), and this was confirmed by comparison with reported data (He et al. 2010) (Fig. 3B).

Both Compounds **1** and **2** have been previously reported as constituents of *M. oleifera* leaves (Bennett et al. 2003).

Inhibitory effects of Q3G and K3G on *S. cerevisiae* metabolic activity and structure–activity relationships. Q3G and K3G, isolated from *M. oleifera* extract, both inhibited *S. cerevisiae* metabolic activity in a concentration-dependent manner (Fig. 4), with half-maximal inhibitory concentration (IC_{50}) values of 0.34 and 0.43 mg. mL^{-1}, respectively (Table 1).

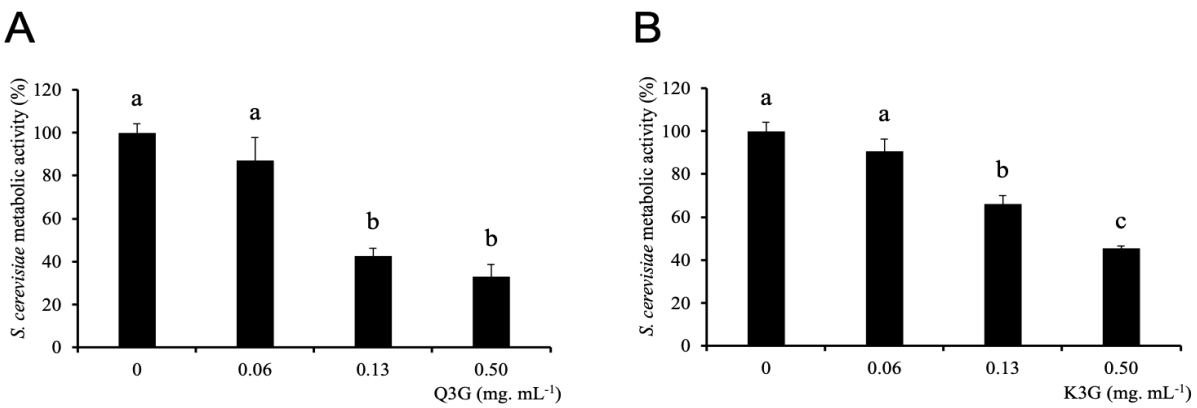


Figure 4. Effects of Q3G and K3G at various concentrations on *S. cerevisiae* metabolic activity as measured using the WST-8 assay. Data are expressed as mean ± standard error of the means (n = 3). Different letters (a, b, c) indicate statistically significant differences among groups ($p < 0.05$; ANOVA followed by Tukey tests). Groups sharing the same letter are not significantly different.

Table 1. Inhibitory effects of the isolated compounds on *S. cerevisiae* metabolic activity

Compound	IC_{50} (mg/mL)	*S. cerevisiae* metabolic activity at 0.5 mg/mL (%)
Quercetin-3-*O*-glucoside	0.34 ± 0.00	33.0 ± 0.67
Kaempferol-3-*O*-glucoside	0.43 ± 0.02	45.6 ± 0.10
Quercetin	>0.5	91.7 ± 0.26
Kaempferol	>0.5	94.2 ± 0.31

As the two compounds exhibited comparable potencies, the number of hydroxyl groups on the B ring was unlikely to contribute to the inhibitory effect. To evaluate the contribution of glycosylation, the corresponding aglycones quercetin and kaempferol were tested. Neither compound showed inhibitory activity at 0.5 mg. mL^{-1}, indicating that glycosylation is essential for the suppression of *S. cerevisiae* metabolic activity. Although the WST-8 assay is sometimes used as a proxy for cell viability, it actually measures metabolic activity (i.e., intracellular dehydrogenase function). In this study, parallel Trypan blue staining confirmed that decreased WST-8 signals (indicating reduced dehydrogenase function) were not due to cell death, but due to a specific reduction in *S. cerevisiae* metabolic activity. The proportion of dead cells in Q3G- and quercetin-treated groups did not differ significantly from that in the control group, and no increase in cell death was observed (Fig. 5A). Hence, Q3G does not kill *S. cerevisiae* cells but only reduces their metabolic activity. Furthermore, metabolic activity, as an indicator of fermentative capacity, decreased in a concentration-dependent manner (Fig. 5B). Taken together, these results indicate that Q3G suppresses *S. cerevisiae* metabolic activity without reducing cell viability.

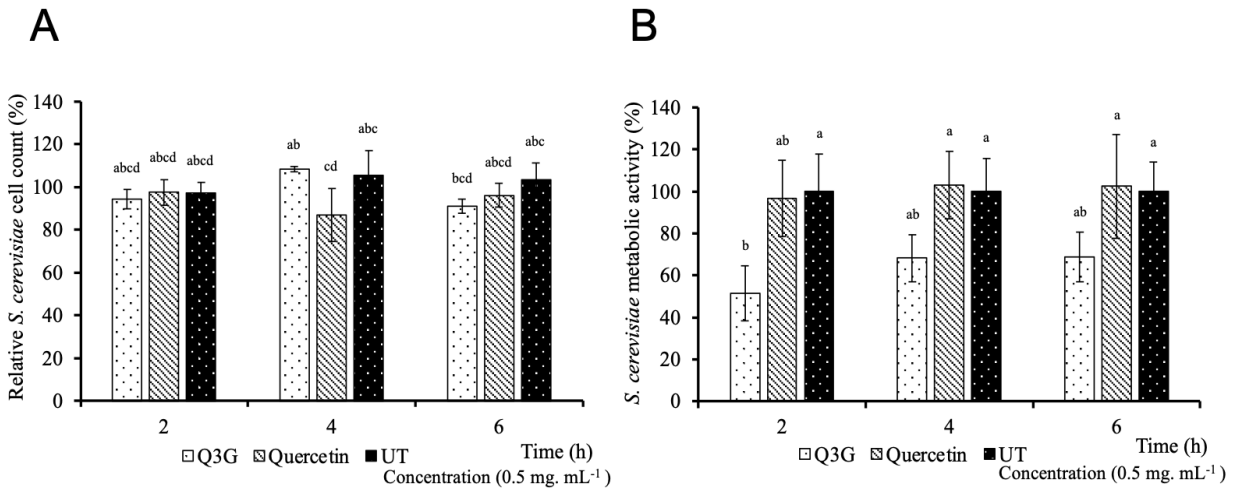


Figure 5. Cell viability (A) and metabolic activity (B) of *S. cerevisiae* treated or not with Q3G or quercetin at 2, 4, and 6 h – Viable cell numbers were determined using the Trypan blue exclusion method, and *S. cerevisiae* metabolic activity was measured using the WST-8 assay. Data are expressed as mean ± standard error of the mean (n = 3). Different letters (a, b, c, d) indicate statistically significant differences among groups (p < 0.05; ANOVA followed by Tukey tests). Groups sharing the same letter are not significantly different.

Discussion

Quercetin is a bioactive flavonol. In *S. cerevisiae*, it has been reported to impair mitochondrial respiratory function and inhibit growth (Carrillo-Garmendia et al. 2022), but also to act protectively under certain conditions (Vilaça et al. 2012), suggesting that its effects are context-dependent. Under the present experimental conditions, the aglycone quercetin did not show a clear inhibitory effect on *S. cerevisiae* metabolic activity at 0.5 mg. mL^{-1}. This may be explained by its extremely low aqueous solubility, which likely limited its interaction with cells. In contrast, the glycoside Q3G, which is substantially more soluble in water, did inhibit *S. cerevisiae* metabolic activity at 0.5 mg. mL^{-1}, likely because of its stronger interaction with the yeast cells. It should be noted that the metabolic activity assessed using the WST-8 in this study primarily reflects the reductive activity of intracellular dehydrogenases, not respiratory activity in the mitochondrial electron transport chain. Therefore, the association between the decrease in metabolic activity induced by Q3G and mitochondrial respiratory inhibition is based on a theoretical interpretation informed by previously reported mechanisms of quercetin action (Carrillo-Garmendia et al. 2022). Nevertheless, as NADH produced by dehydrogenases feeds electrons into the electron transport chain, it is plausible that the reduction in dehydrogenase activity caused by Q3G would suppress respiratory activity.

Similarly, K3G has been reported to strongly inhibit the growth of *S. cerevisiae* strains deficient in DNA repair function (Saito et al. 2012). In the present study, like Q3G, K3G suppressed the metabolic activity of *S. cerevisiae*. Since Q3G and K3G exhibited comparable potency, the number of hydroxyl groups on the B ring is unlikely to be responsible for the inhibitory activity. In contrast, the corresponding aglycones quercetin and kaempferol showed weaker inhibitory effects, demonstrating that glycosylation is essential for this inhibitory effect and constitutes a key structure–activity relationship (SAR).

Regarding the precise nature of the inhibitory effect, the WST-8 assay reflects cellular dehydrogenase activity; it does not directly equate to cell viability. Therefore, cell viability was assessed based on Trypan blue dye exclusion, which revealed no increase in cell death upon treatment with Q3G. This observation is a critical finding, clearly demonstrating that the reduced WST-8 signal reflects a specific physiological perturbation; the compound does not kill *S. cerevisiae* cells but rather reduces their metabolic activity while maintaining viability.

Fermentation by *S. cerevisiae* is influenced by various environmental factors, including salt and sugar concentrations (Bagum et al. 1999). However, to our knowledge, no previous studies have clearly demonstrated that Q3G and K3G derived from *M. oleifera* decrease the fermentative capacity of *S. cerevisiae*. This study provides the first evidence of fermentative metabolism inhibition by *M. oleifera* leaf extract and directly links it with specific active compounds.

Q3G and K3G have diverse biological activities, including antioxidant activity (Razavi et al. 2009) and antitumor effects (Amado et al. 2014), as well as anti-inflammatory and analgesic effects (Parveen et al. 2007). Therefore, they are of interest from a functional food perspective. At the same time, they may theoretically act as inhibitory factors during breadmaking by suppressing dough expansion, although this effect has not been directly tested in actual dough. However, this very property could be exploited to develop high-density breads or baked products with improved shelf stability. A recent study demonstrated that processing treatment (e.g., steam treatment) improved the expansion of Moringa-fortified bread (Koriyama et al. 2025), suggesting that other components present in Moringa leaves may also contribute to fermentation inhibition. While the present study successfully identified the major polar inhibitory compounds and elucidated a crucial SAR, the specific molecular target of these glycosides remain unknown, representing a limitation of this study. Furthermore, the preliminary activity observed in the non-polar fractions suggests that hydrophobic compounds also contribute to the overall inhibition of fermentative metabolism in the crude extract. Future studies focusing on the complete characterization of these secondary inhibitors and the precise mechanism of dehydrogenase suppression will be essential to advance the applied biotechnology of Moringa powder. These findings may contribute to optimizing fermentation processes and developing functional baked goods enriched with Moringa bioactive compounds.

Conclusions

This study successfully isolated and identified the primary yeast metabolism-inhibitory constituents in *M. oleifera* leaf extract as Q3G and K3G. These findings lead to the rejection of the null hypothesis, confirming that specific flavonoid glycosides are responsible for the reduced metabolic activity associated with fermentative processes of *S. cerevisiae*. Crucially, we established that Q3G and K3G suppress *S. cerevisiae* metabolic activity (dehydrogenase function) without compromising cell viability, thereby acquiring new fundamental knowledge regarding their mechanism of action. This work also revealed a critical SAR, demonstrating that glycosylation is essential for the inhibitory effect. Overall, the findings of this study are highly valuable for understanding the mechanism by which Moringa leaf powder suppresses bread expansion and for clarifying the specific impact of flavonoid glycosides on *S. cerevisiae* metabolism and fermentation. From the perspective of food processing and applied food science, these results highlight both the beneficial and limiting aspects of Q3G and K3G in designing quality attributes for breadmaking. A precise understanding of their activity will be essential for the application of Moringa as a novel food material, and the present work provides new insights into food science and applied biotechnology.

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Author Contributions

Y.K. and T.H. performed the assay design, analysis, and isolation and determination of compounds. T.K. contributed to the conceptualization and discussion of experimental design. T.H. supervised the experiments and manuscript preparation. All authors have read and approved the final manuscript.

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Institutional Review Board Statement

Ethical review and approval were not applicable to this study as it did not involve humans or animals.

Informed Consent Statement

Not applicable.

Data Availability Statement

The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding authors.

Conflicts of Interest

The authors declare no conflicts of interest.

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