Int.J.Curr.Res.Aca.Rev.2026; 14(6): 12-19

EXCELLENT PUBLISHERS

International Journal of Current Research and Academic Review

ISSN: 2347-3215 (Online) Volume 14 Number 6 (June-2026)

Journal homepage: http://www.ijcrar.com

doi: https://doi.org/10.20546/ijcrar.2026.1406.002

Decreased Mitochondrial Activity of *S. cerevisiae* by the Thymus Vulgaris Essential Oil

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Abstract

The increase in antimicrobial resistance has motivated the study and search for new substances to combat infectious diseases caused by bacteria, fungi, viruses or parasites. Various plant-based substances have shown antibacterial and antifungal properties. Essential oils are one example. Essential oils have been used for various purposes in both the food and pharmaceutical sectors. Previous studies have shown that *T. vulgaris* essential oil of is a potent inhibitor of bacterial and fungal growth. Its mode of activity is intriguing, as it effectively inhibits the growth of microorganisms. Therefore, this study aimed to investigate the action of *T. vulgaris* essential oil as a pore former in the cell membrane and its effect on mitochondrial activity in *S. cerevisiae*.

Article Info

Received: 05 April 2026
Accepted: 22 May 2026
Available Online: 20 June 2026

Keywords

Essential oil, Respiratory activity, Thymus vulgaris, Essential oil, Saccharomyces cerevisie

Introduction

The essential oils are substances obtained from plant materials as flowers, leaves, fruits, branches, seeds, bark by different methods. The essential oils are secondary metabolites produced by plants in order to provide a defense function or attraction. The defense mechanisms related to secondary metabolites include flavonoids, phenols, terpenes, oils, alkaloids, lectins and polypeptides (Burt, 2004; Butkiené *et al.,* 2015; Citarasu, 2010; Flores-Encarnación *et al.,* 2016; Rufa'i *et al.,* 2017; Solórzano-Santos and Miranda-Novales, 2012). In response to the growing interest in "natural" healing methods and the return to folk medicine, essential oils appear to be a promising source of a universal remedy for patients' basic ailments. Moreover, these findings could lead to the search for new antimicrobial, antiviral and anticancer drugs (Żukowska and Durczyńska, 2024).

Plant extracts and essential oils possess antifungal, antibacterial, and antiviral properties and have been screened on a global scale as potential sources of novel antimicrobial compounds, agents promoting food preservation, and alternatives to treat infectious diseases. Essential oils have been reported to possess significant antiseptic, antibacterial, antiviral, antioxidant, anti-parasitic, antifungal, and insecticidal activities. Essential oils can serve as a powerful tool to reduce the bacterial resistance (Astani *et al.,* 2010; Burt, 2004; Chouhan *et al.,* 2017; Safaei-Ghomi and Ahd, 2010; Stefanakis *et al.,* 2013). Signifcant attention focused on essential oils of oregano, clove, cinnamon and rosemary (composed primarily of aldehydes, terpenes and phenols) (Błaszczyk *et al.,* 2021; Cui *et al.,* 2018; El-Sakhawy *et al.,* 2026; Romero-Montero *et al.,* 2023). In recent years, some mechanisms of action of essential oils have been elucidated, especially at the antimicrobial level. The

common mechanisms include inhibition of cell wall synthesis and disruption of plasma membrane integrity (Eshboev *et al.,* 2024; Żukowska and Durczyńska, 2024). This work shows the effect of *T. vulgaris* essential oil on mitochondrial and respiratory activity of *S. cerevisiae*.

Material and Methods

Source of material

In this study, the commercial essential oil of thyme was used. It was obtained from a flavour and fragrance company at Puebla, México.

Biological material

The *Saccharomyces cerevisiae* strain was used. The strain of *S. cerevisiae* used was the yeast marketed for making bread. Yeast was stored in cryovials at -40°C in yeast peptone dextrose (YPD) broth with 20% glycerol until analysis.

Culture

S. cerevisiae strain were cultivated on yeast peptone dextrose broth containing amoxicillin (16µg/mL) and gentamicin (40 µg/mL) and the following components of medium (g/L): 10 yeast extract, 20 peptone and 20 dextrose pH 6.5. The stationary cultures were grown at 30°C for 24 hours in glass tubes containing 5 mL of yeast peptone dextrose broth and were used as precultures. The yeast peptone dextrose agar plates containing 20 mL of medium were prepared. Sterile Petri dishes (100 mm) were used. Plates were inoculated by crossstriation with a stationary 24-hour preculture of *S. cerevisiae* in yeast peptone dextrose broth (Ab_{560nm}= 5).

Antifungal activity of *T. vulgaris* essential oil

The antifungal activity of *T. vulgaris* essential oil was determined using the technique of diffusion in agar using paper discs. For it, yeast peptone dextrose agar plates (containing 20 mL of medium) were prepared. Sterile Petri dishes (100 mm) were used. Plates were inoculated by crossstriation with a stationary 24-hour preculture of *S. cerevisiae* in yeast peptone dextrose broth (Ab_{560nm}= 5.0). Then, sterile filter paper disks (5 mm diameter) were placed on the surface of yeast peptone dextrose agar plates. Different concentrations (0.13, 0.26, 0.52, 0.78 and 1.3 mg) of essential oil were used. The agar plates were incubated at 30°C for 24 h. The diameters of the inhibition halos formed were measured. The analyses were conducted in triplicate. As reference, yeast peptone dextrose agar plates were inoculated by crossstriation with *S. cerevisiae*. The agar plates were incubated at 30°C for 24 h.

Cell viability assay

The cell viability assay was performed using the trypan blue dye according to methodology described by Castillo *et al.,* (2009). For that, 1 mL of an active culture of *S. cerevisiae* (18-24 hours of culture, Ab_{560nm}= 5) was centrifuged at 3,000 r.p.m. for 10 min at 4 ºC. The supernatant was removed and 200 µL of fresh yeast peptone dextrose broth were added (cell suspension).

The cell viability assay was determined by mixing 10 µL of cell suspension and 10 µL of 0.1% trypan blue dye, and then placing 10 µL of the mix on a slide observing at 40X power. Dead cells were observed in a deep blue color. All determinations were made in triplicate. For negative control, non-viable cells of *S. cerevisiae* were used. This cells were obtained by heating at 100°C for 10 minutes.

Effect of *T. vulgaris* essential oil on cell viability

The effect of *T. vulgaris* essential oil on cell viability was determined as follows. The cell suspension was prepared and mixed with the trypan blue dye as described before. Then, 1.3 mg of *T. vulgaris* essential oil was added; this mixture was incubated at room temperature at 1 min and then placing 10 µL of the mix on a slide observing at 40X power. Dead cells were observed in a deep blue color. The preparations were observed at 40X power. All determinations were made in triplicate.

Mitochondrial activity

The mitochondrial activity assay was performed using the Janus green B dye according to methodology described by Ahmad *et al.,* (2018). For that, 5 mL of an active culture of *S. cerevisiae* (24-72 hours of culture at 30°C, Ab_{560nm}= 5.3) was centrifuged at 3,500 r.p.m. for 10 min at 4 ºC. The supernatant was removed and *S. cerevisiae* cells were washed once with phosphate-buffered saline buffer (PBS) pH 7. 200 µL of PBS pH 7 were added (cell suspension). Then mitochondrial activity assay was determined by mixing 10 µL of cell suspension and 10 µL of 0.1% Janus green B. The mixture was incubated for 15-20 minutes at room temperature in the dark, and placing 10 µL of the mix on

a slide observing at 63X power. Active mitochondria were observed in a green-blue color (oxidized form Janus green). All determinations were made in triplicate. For negative control, non-viable cells of *S. cerevisiae* were used. This cells were obtained by heating at 100°C for 5 minutes.

Effect of *T. vulgaris* essential oil on mitochondrial activity

The effect of *T. vulgaris* essential oil on mitochondrial activity was determined as follows. From the cell suspension described above, 10 µL were taken and mixed with 1.3 mg of *T. vulgaris* essential oil. The mixture was incubated for 5 min at room temperature and then 10 µL of 0.1% Janus green B were added.

The mixture was incubated for 15-20 minutes at room temperature in the dark, and placing 10 µL of the mix on a slide observing at 63X power. All determinations were made in triplicate.

Measurement of respiratory activity

The respiratory activity was measured polarographically with a Clark oxygen electrode according to the methodology established by Flores-Encarnación *et al.,* (2020). For it, cells of *S. cerevisiae* were used. The cells of *S. cerevisiae* were obtained from a culture in a glass tube containing 5 mL of fresh yeast peptone dextrose broth pH 6.5, which was inoculated with 125 µL (from stationary 24-hour preculture of *S. cerevisiae* in yeast peptone dextrose broth, Ab_{560nm}= 6) and then was incubated at 30 ºC for 18-48 hours.

In the end, the culture showed a Ab_{560nm}= 5.8. To determine the respiratory activity of *S. cerevisiae*, 5 mL of culture were used. *S. cerevisiae* cells was recovered centrifuging at 3,500 r.p.m. for 10 min at 4 ºC. The supernatant was removed and *S. cerevisiae* cells were washed once with 1 mL of 50 mM phosphate buffer pH 6. The pellet was resuspended using 500 µL of 50 mM phosphate buffer pH 6 (cell suspension).

The reaction mixture (final volumen= 10 mL) contained: 9 mL of buffer 50 mM phosphate pH 6 and 20 mM glucose. The reactions were initiated adding the cell suspensión. The oxygen consumption kinetics were recorded for 30 min. The temperature was kept constant at 30°C. In all tests, the respiratory activities of *S. cerevisiae* were reported as consumed nmol O_2 min^{-1}. The analyses were conducted in triplicate.

Effect of *T. vulgaris* on respiratory activity of *S. cerevisiae*

The effect of *T. vulgaris* essential oil on respiratory activity of *S. cerevisiae* was determinated. For this purpose, 5 mL of culture were used. *S. cerevisiae* cells was recovered centrifuging at 3,500 r.p.m. for 10 min at 4 ºC. The supernatant was removed and *S. cerevisiae* cells were washed once with 1 mL of 50 mM phosphate buffer pH 6. The pellet was resuspended using 200 µL of 50 mM phosphate buffer pH 6 (cell suspension) which 0.65 mg of *T. vulgaris* essential oil was added; the mixture was incubated for 15 min at room temperature. Then, reaction mixture was prepared and respiratory activity was measured as previously was indicated. The reactions were initiated adding the cell suspensión incubated with *T. vulgaris*. The oxygen consumption kinetics were recorded for 30 min. The temperature was kept constant at 30°C. In all tests, the respiratory activities of *S. cerevisiae* were reported as consumed nmol O_2 min^{-1}. The respiratory activity of *S. cerevisiae* cells was also determined by incubating them with 1.3, 3.25 and 6.5 mg of *T. vulgaris* essential oil. The analyses were conducted in triplicate.

Results and Discussion

In this study, the effect of *T. vulgaris* essential oil on the mitochondrial activity of *S. cerevisiae* was determined. Previous studies have shown that *T. vulgaris* has antibacterial properties, so its antifungal activity was tested first. For this, the technique of diffusion in agar using paper discs was used. So, different concentrations essential oil were used: 0.13, 0.26, 0.52, 0.78 and 1.3 mg. The results are shown in Fig. 1A. *S. cerevisiae* growth was not observed on the yeast peptone dextrose agar plates with all quantities of *T. vulgaris* tested. The essential oil had a strong antifungal effect. At a short time (1 min), it was observed that *T. vulgaris* essential oil caused the death of *S. cerevisiae* cells. The results are shown in Fig. 1C, where the *S. cerevisiae* cells were stained a deep blue color (vital staining with trypan blue). These results indicated that *T. vulgaris* essential oil acts immediately causing the death of *S. cerevisiae* cells. *S. cerevisiae* cells that were not treated with *T. vulgaris* essential oil and stained with trypan blue dye did not show blue color, indicating that the membranes of the *S. cerevisiae* cells were intact (membrane permeability was not affected) (Fig. 1F). As observed in Fig. 1C*, S. cerevisiae* cells are not destroyed (lysed), only the trypan blue dye penetrates them. Therefore, the *T. vulgaris* essential oil formed pores in the membranes

of *S. cerevisiae*. This is one mode of antifungal action of *T. vulgaris* essential oil against *S. cerevisiae*. Furthermore, it was found that effects observed, both in the plate diffusion assay and by direct contact assay, were fungicidal effects (data not shown). This property could explain why some essential oils do not promote antimicrobial resistance. In addition to the formation of pores in the cytoplasmic membrane of *S. cerevisiae*, it was proposed that *T. vulgaris* essential oil could affect mitochondrial activity. So, the mitochondrial activity assay was performed using the Janus green B dye as described in Materials and Methods. The results are shown in Fig. 1E. In this case, it was observed that mitochondrial activity was lost, meaning that active mitochondria were not detected because they could not oxidize the Janus green B dye and were not stained in green-blue color (oxidized form Janus green). Fig. 1D shows *S. cerevisiae* cells that were not treated with *T. vulgaris* essential oil and that were stained with Janus green B dye. This image shows the active mitochondria of *S. cerevisiae* stained in blue-green color. To provide further evidence of the loss of mitochondrial activity, the respiratory activity was measured in the presence and absence of *T. vulgaris* essential oil using a Clark oxygen electrode as described in Materials and Methods. The quantities of *T. vulgaris* essential oil were: 0.65, 1.3, 3.25 and 6.5 mg. The oxygen consumption kinetics were recorded for 30 min and temperature was kept constant at 30°C. The results are shown in Table 1. As can be seen in this table, the incubation of *S. cerevisiae* cells with the *T. vulgaris* essential oil produced a significant decrease in respiratory activity. Using 0.65 mg of the essential oil resulted in a decrease in respiratory activity of around 75%, while with 1.3 mg a decrease in respiratory activity of around 85% was recorded. At 6.5 mg of the *T. vulgaris* essential oil, *S. cerevisiae* cells completely lost respiratory activity. These results confirmed that *T. vulgaris* essential oil, in addition to forming pores in the cell membrane of *S. cerevisiae* cells, also affected mitochondrial function and, consequently, respiratory activity.

Antibiotics are potent medications that either kill or stop the growth of bacteria to treat infections. They fall into one of two categories: broad-spectrum or narrow-spectrum based on their effectiveness against different types of bacteria. Various antibiotics have different modes of action, interfering with important biochemical reactions in bacterial cells. For example, β-lactam antibiotics interact with penicillin-binding proteins and sensitive enzymes, preventing cell division and possibly resulting in lysis (Etebu and Arikekpar, 2016; Kundu *et al.,* 2025). However, antimicrobial resistance has emerged as one of the most pressing global public health threats of the 21st century. Antimicrobial resistance manifests when microorganisms, encompassing bacteria, fungi, parasites, and viruses, undergo evolutionary processes leading to their resistance against antimicrobial medications for treating infections (Ahmed *et al.,* 2024; Ferdinand *et al.,* 2024; Lim *et al.,* 2024; Prestinaci *et al.,* 2015; Ruckert *et al.,* 2024; Salam *et al.,* 2023). However, the development of novel antibiotics has slowed down significantly in recent years, and as a result, antimicrobial resistance has increased exponentially (Berger and Loewy. 2024; Martinez, 2014). With the rise of antimicrobial resistance and the difficulties associated with antibiotic discovery, the pursuit of alternatives has become an urgent medical need. Current research is focusing on investigating novel alternatives to antibiotics that may involve targeting unique mechanisms of action or will work synergistically with current antibiotics to enhance their effects (Berger and Loewy, 2024; Gupta and Sharma, 2022). Alternative strategies include the use of plant-based substances. Several plant-based products (plant extracts, essential oils) have been used to treat infections from ancient times. Essential oils have showed pharmacological activities, recognized for their antibacterial, antifungal, antioxidant, anti-inflammatory, and insecticidal properties and are widely used in medicine (Chauhan and Dahiya, 2016; Raikwar *et al.,* 2024).

Essential oils are highly concentrated hydrophobic combinations of volatile ingredients that can be produced in almost all parts of aromatic medicinal plants like flowers, fruits, leaves, stems, seeds, and are stored in epidermal cells, glandular trichomes, secretory cells, cavities, or canals. The tea tree, oregano, lavender and thyme essential oils have showed promising role in biomedicine. Due to their antimicrobial properties, they effectively combat various bacteria, fungi, and viruses (Aljaafari *et al.,* 2021; Raikwar *et al.,* 2024; Soni and Dahiya, 2014; Swamy *et al.,* 2016). As mentioned before, essential oils possess antimicrobial properties; however, their modes of action are not fully understood, especially in the case of *T. vulgaris* essential oil. In this study, the effect of *T. vulgaris* essential oil on the mitochondrial activity of *S. cerevisiae* was determined. By technique of diffusion in agar and using paper discs the antifungal activity was determined. The results indicated that the *T. vulgaris* essential oil produced a strong inhibitory effect on the growth of *S. cerevisiae*.

Fig.1 Effect of *T. vulgaris* essential oil on the growth and mitochondrial activity of *S. cerevisiae*. A. Powerful inhibitory effect of *T. vulgaris* on the growth of *S. cerevisiae*. Essential oil were placed in increasing amounts (0.13, 0.26, 0.52, 0.78 and 1.3 mg) in clockwise direction starting with the top. B. Growth of *S. cerevisiae* in yeast peptone dextrose agar (control). C. *S. cerevisiae* cells treated with *T. vulgaris* essential oil and stained with trypan blue. D. Mitochondrial activity assay using Janus green B dye. E. Loss of mitochondrial activity in S. *cerevisiae* cells treated with *T. vulgaris*. F. *S. cerevisiae* cells only stained with trypan blue dye.

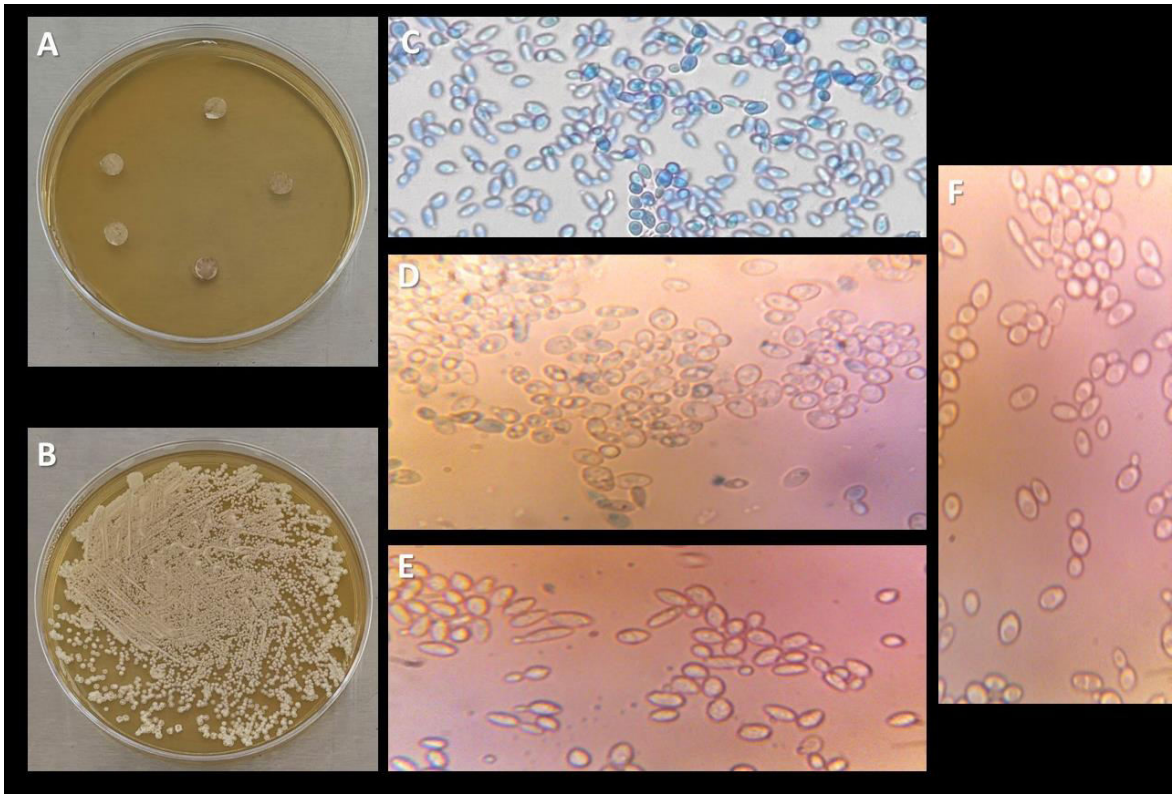

Table.1 Effect of *T. vulgaris* essential oil on respiratory activity of *S. cerevisiae* cells.

T. vulgaris Essential Oil (mg)	Respiratory Activity (nmol O_2 min^{-1})	Loss of Activity (%)
0.00	109.72	0.00
0.65	26.62	75.73
1.30	16.60	84.87
3.25	12.01	89.05
6.25	0.00	100.00

It was also observed that the growth inhibitory effect is very rapid because the essential oil can diffuse freely through the membranes of *S. cerevisiae* causing the death of the yeasts almost instantly and making it impossible for them to reproduce again once the essential oil is removed: fungicidal effect. This property could explain why some essential oils do not promote antimicrobial resistance. *T. vulgaris* essential oil formed pores in the membranes of *S. cerevisiae*. Boubrik *et al.,* (2025) demonstrate that *Cinnamomum cassia* essential oil could be used as a biological control agent (potential fungicidal agent) against the two primary fungal contaminants of fruit products, *Saccharomyces cerevisiae* and *Acremonium* sp. Food deterioration and intoxication caused by microbial pathogens are major issues, particularly in the industrial world, leading to substantial economic losses. The *S. cerevisiae* strains are among the microbial pathogens linked to foodborne illnesses and it is also a usual beverage contaminant. This yeast strain releases fermented products with undesirable tastes attributable to the release of CO_2, ethanol, and residues from other fermentation products (Lotmani *et al.,* 2024; Tajchakavit *et al.,* 1998). Lotmani *et al.,* (2024) reported that *T. vulgaris* essential oil showed a great antifungal

potential against *S. cerevisiae* and *Candida albicans* strains due mainly to its phenolic compounds including carvacrol and thymol. It has been reported that carvacrol is one of essential oil most effective compounds against fungal species due to its hydrophobic characteristics. These properties allow it to attach to the lipophilic region of the cell membrane and solubilise it, which is likely to result in fungal death. Likewise, the hydroxyl functional group in carvacrol may cause the production of free radicals in oxidative phosphorylation process, which can lead to microbial cell death (Kawhena *et al.,* 2021; Lotmani *et al.,* 2024; Yan *et al.,* 2021). In addition to the formation of pores in the cytoplasmic membrane of *S. cerevisiae*, in the present study, it was also proposed that *T. vulgaris* essential oil could affect mitochondrial activity. As described above, mitochondrial activity assay was performed using the Janus green B dye. The results indicated that mitochondrial activity decreased significantly when *S. cerevisiae* cells were treated with *T. vulgaris* essential oil. Helal *et al.,* (2006) reported that *T. vulgaris* essential oil phenolic monoterpenes affected fungal cells by altering the cellular organelles, including the mitochondria, and the plasma membrane. Those authors found that *T. vulgaris* essential oil caused plasma membrane disruption and mitochondrial structure disorganization. Moreover, Ca^{+2}, K^{+} and Mg^{+2} leakages increased from the fumigated mycelium and its total lipid content decreased, while the saturated fatty acids decreased and unsaturated fatty acids increased. On the other hand, in the present study the respiratory activity was also measured. The results indicated that *T. vulgaris* essential oil produced a significant decrease in respiratory activity which explained why active mitochondria were not detected in *S. cerevisiae* cells after treatment with the essential oil. The results confirmed that *T. vulgaris* essential oil, in addition to forming pores in the cell membrane of *S. cerevisiae* cells, also affected mitochondrial function and consequently respiratory activity. Several authors have reported that essential oils can produce depolarisation of the mitochondrial membranes by decreasing the membrane potential, affect ionic Ca^{2+} cycling and other ionic channels and reducing the pH gradient, affecting (as in bacteria) the proton pump and the ATP pool. Essential oils change the fluidity of membranes, which become abnormally permeable resulting in leakage of radicals, cytochrome C, calcium ions and proteins. Permeabilization of outer and inner mitochondrial membranes leads to cell death by apoptosis and necrosis (Armstrong, 2006; Bakkali *et al.,* 2008; Fukumoto and Mazza, 2000). Finally, further studies are needed to better understand the mode of action of essential oils, especially those of *T. vulgaris* and their potent antimicrobial properties.

Conflict of interest

The authors declare that they have no conflict of interest.

Declaration of competing interest

The authors declare that they have no potential competing financial interests.

Conclusion

Several mechanisms of action of essential oils are known for their antimicrobial properties. The most common of these involves the formation of pores in cell membranes, causing the release of cytoplasmic contents. *T. vulgaris* essential oil has potent antifungal properties, which led to the proposal that it must perform its action through different modes of action that operate simultaneously. In this work it was found that in addition to forming pores in the cell membrane of *S. cerevisiae*, the *T. vulgaris* essential oil affected mitochondrial function significantly decreasing respiratory activity.

Acknowledgements

We appreciate the enthusiastic collaboration and technical support of Morales-Cortés M.I. from Biomedicina- BUAP. Thank to Facultad de Medicina-BUAP and Grupo de Académicos de Puebla SC for the facilities provided for the development of this work.

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How to cite this article:

Flores-Encarnación M., Ocaña-Lozano D. and Cabrera-Maldonado C. 2026. Decreased Mitochondrial Activity of *S. cerevisiae* By the Thymus Vulgaris Essential Oil. *Int.J.Curr.Res.Aca.Rev.* 14(6), 12-19. doi: https://doi.org/10.20546/ijcrar.2026.1406.002