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Effect of gamma irradiation, high sugar content and antimicrobials on survival of *Escherichia coli*: A review

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Abstract: Dried fruits are popular ready-to-eat snacks. However, due to cross-contamination or contact with infected persons, *Escherichia coli* could be present, of which some strains are pathogenic, thus, the consumption of contaminated dried fruits could pose a public health risk. Microbial cells subjected to stress factors such as osmotic shock, radiation and antimicrobials could induce complex stress response systems and adaptation. Radiation and antimicrobials have been shown to cause an SOS response in *E. coli*, which affects cellular metabolism, such as the enhanced ability to repair DNA and mutagenesis. Studies have shown that glucose plays a critical role in the down- or upregulation of locus for enterocyte effacement (LEE)-encoded virulence of *E. coli*. Gamma radiation could also cause the formation of viable but nonculturable (VBNC) cells. If these cells are present in a sample, the number of viable cells will be underestimated by the plate count method leading to the false conclusion that the product is germ-free. We have reviewed in this article how stressors such as high sugar content, gamma radiation, and antimicrobials affect the survival of *E. coli* in dried fruits.

Keywords: antimicrobial agents; dried fruits; *E. coli*; food processing; osmotic stress; radiation

Considerable numbers of foodborne illnesses have been associated with consuming fresh fruits and juices (Burnett and Beuchat 2001; Beuchat 2002; Scallan et al. 2011). Due to the emergence of healthy lifestyle recommendations (WHO 2020), more and more people worldwide choose dried fruits daily. Since these products are primarily raw, they are considered high-risk foods. The microbiota consists of spoilage bacteria, yeasts, and moulds, but in some cases, pathogenic bacteria, viruses and even parasites can also be found on raw fruits and vegetables (Predmore and Li 2011; Leff and Fierer 2013; Turtoi 2013; Li et al. 2020). Due to this, several outbreaks occur each year around the world. These outbreaks put the spotlight on food safety issues. Goods travelling thousands of miles increase the risk of getting contaminated at any point in the food chain. Other factors, such as changes in agronomic and processing practices and increased immunocompromised consumers, also contribute to the increasing number of foodborne diseases (Beuchat 2002).

Most fruits are not available all year round, so to prolong their shelf-life, various techniques are used, e.g. the production of dried fruits. These are concentrated fresh fruits from which the original water content has been removed. Dried fruits retain the flavour of the original fruit, as well as most of the vitamins (e.g. vi-

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tamins A and C, niacin, thiamine, riboflavin, beta-carotene) and minerals (e.g. potassium, iron, copper). Due to their concentrated sugar content, they satisfy our sweet tooth and be an excellent substitute for the sugar component in some desserts. Their best-known representatives are prunes, apples, pears, apricots, raisins, figs, and dates (Bennett et al. 2010; Gyurova and Enikova 2014; Chang et al. 2016).

Dried fruits have been linked to several food-borne pathogens. Sheng and Wang (2023) state that Shiga-toxin-producing *Escherichia coli* (STEC), *Salmonella* spp., and *Listeria monocytogenes* can survive on dried produce such as apricots, cranberries, dates, plums, raisins, strawberries, and tomatoes for an extended period. As published by Canakapalli et al. (2022), the survival of *Salmonella, E. coli* O157:H7, and *L. monocytogenes* on dried fruits was impacted by multiple factors, including types of fruits, inoculation methods, storage temperatures, and bacterial species. Bacteria died faster when the fruits were stored at room temperature. Beuchat and Mann (2014) showed that *Salmonella* could survive 182 days on dried strawberries and 242 days on dried cranberries and raisins when the products were stored at 4 °C. Ntuli et al. (2017) have isolated pathogens of the genera *Salmonella*, *Shigella*, *Bacillus* and other *Enterobacteriaceae* from home-dried samples. Faecal coliforms were detected in 55% of the investigated products. These studies prove that common food-borne pathogens can survive on dried fruits for extended periods, which could lead to food safety issues and even health problems.

We must learn to prevent infections. Nowadays, there are a number of gentle food processing techniques that neither alter the product's consistency, shape, taste, or smell nor apply heat -such as gamma irradiation- which can be used to sterilise and prolong the product's shelf life. However, the different processing techniques could act as stressors, enhancing *E. coli* or other bacteria's survivability. Due to this phenomenon, foodstuffs thought to be bacterium-free could still contain enough microbial cells to cause spoilage or food-borne diseases.

MATERIAL AND METHODS

E. coli associated with food-borne outbreaks

E. coli is known to be a human commensal bacteria and is a harmless food contaminant to some extent. Still, some strains could also be pathogenic (e.g. Shiga toxin-producing *E. coli*, Enterohemorrhagic *E. coli*), causing severe diseases.

Low-moisture food products such as dried fruits, spices, and seasonings have generally been accepted as safe because they do not support the growth of pathogenic bacteria. This belief seems to be disproved, as there have been several food-borne outbreaks after consuming low-water-activity products in recent years. Pathogenic bacteria can enter these products via contaminated ingredients or cross-contamination, where they can survive for long periods. This could pose a potential health risk as dried fruits are usually consumed without further cooking or heat treatment (Canadian Food Inspection Agency 2018). Table 1 pre-

Table 1. Food-borne outbreaks associated with food-borne pathogens in low water-activity products

Low water-activity products	Pathogenic microorganism	Disease	Reference
Raw cake batter	*E. coli*	*E. coli* infection	CDC 2021
Flour	Shiga toxin-producing *E. coli* (STEC)	*E. coli* infection	CDC 2016
Flour	*E. coli*	*E. coli* infection	CDC 2019
Flour (wheat, spelt, and rye)	Shiga toxin-producing *Escherichia coli* (STEC)	*E. coli* infection	Food Safety News 2020
In-shell hazelnuts	*E. coli* O157:H7	*E. coli* infection	CDC 2011
Raw refrigerated, pre-packaged cookie dough	*E. coli* O157:H7	*E. coli* infection	CDC 2009
Exotic dried fruits	*Salmonella* Agbeni	Salmonellosis	Johansen et al. 2021
Dried fruit or ice cream served in open containers	Hepatitis A virus (HAV)	Hepatitis	Howitz et al. 2005
Powdered milk formula	*Enterobacter sakazakii*	Necrotising enterocolitis	Van Acker et al. 2001
Chocolate products	*Salmonella Typhimurium*	Salmonellosis	WHO 2022

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sents a few examples of outbreaks associated with low water-activity products. *E. coli* was responsible for numerous hospitalisations, and many people have developed haemolytic uremic syndrome (HUS) (CDC 2009; CDC 2011; CDC 2016; CDC 2019; CDC 2021). Apart from HUS, *E. coli* has been linked to cause several illnesses that are sometimes severe, such as diarrhoea, urinary tract infections, respiratory illness, and bloodstream infections. The types of *E. coli* responsible for diarrhoea are usually spread through contaminated food or water or may have come into contact with infected animals and humans (CDC 2022).

One of the most common pathogenic *E. coli* is the Shiga toxin-producing *Escherichia coli* (STEC), of which *E. coli* O157:H7 is the most well-known. It has several virulence factors, such as the production of Shiga toxins, although the toxin production is insufficient to cause disease.

Approximately 265 000 STEC infections occur in the United States annually, ranging in severity from mild diarrhoea to ischemic colitis and HUS (Tack et al. 2021). In Germany and France in 2011, an outbreak of Shiga toxin-producing *E. coli* O104:H4 from sprouted seeds occurred. This has been ever since one of Europe's biggest, most extensive *E. coli* outbreaks, infecting nearly 4 000 persons, mainly in Germany, producing more than 900 cases of HUS and resulting in 54 deaths (Karch et al. 2012).

Adaptation to stress factors

Microbial cells subjected to stress factors (such as osmotic shock, radiation, lack of nutrients, high temperature, and low pH) can generate mutations by mechanisms different from those found in growing cells. These mechanisms might increase mutation rates that alter evolution rates (Lombardo et al. 2004).

Gene expression. Gene expression involves a series of chemical changes in which an RNA molecule is formed, and the cell synthesises protein. Gene expression is an on-off switch which controls where and when RNA molecules and proteins are produced. It is also a volume control, determining how many of these products are formed (Alberts et al. 2002; Science Daily 2016).

Studies (Kato et al. 2012; Atsumi et al. 2014) have shown that certain enzymes and molecular processes in prokaryotes remain functional in cells that have lost their ability to reproduce after being irradiated with DNA damage-inducing ionising radiation. Kato and Futenma (2014) examined the ability of *E. coli* cells to continue transcription and translation processes after irradiation with cell death-inducing gamma irradiation. For this experiment, they examined the expression of the *lacZ* gene in *E. coli* irradiated with gamma rays. This gene is important because the expression of l*acZ* is induced by lactose and isopropyl β-d-thiogalactoside, which binds to the lac repressor, thus promoting transcription of the lac promoter. Hence, the expression of this gene means that the processes required for transcription and translation are still active even after lethal levels of irradiation. They discovered that cells irradiated with 6 and 8 kGy gamma rays had lost their ability to grow on nutrient agar plates – this raises food safety concerns as the plating technique is the most common technique to isolate and count viable microorganisms, and if cells cannot grow on agar plates, the total bacterial count will be underestimated- but maintained their ability to induce *lacZ* gene expression so leading to the conclusion that gene expression was still induced after lethal doses of gamma irradiation. This data proves that irradiated cells may present new vehicles for transporting protein or DNA.

DNA damaging treatments such as irradiation induce the SOS system, which is a complex response (SOS response) to DNA damage in *E. coli* that manifests in the expression of SOS genes. Two proteins (a repressor and an inducer) are important in regulating the SOS response: LexA is the repressor, while RecA is the inducer. During normal environmental conditions, the LexA binds to the SOS box in the promoter region of SOS genes and limits or prevents their expression. SOS genes are repressed to a certain degree under normal growth conditions. However, suppose there is increased DNA damage in the cells. In that case, RecA proteins are formed at the sites of damage and activate the autocleavage of the LexA repressor, allowing SOS gene expression, and leading to DNA repair mechanisms. SOS induction is reversed once the damages are repaired (Michael 2005).

Bolsunovsky et al. (2016) studied the effects of low doses of gamma radiation. They have observed that the induction of SOS response and mutation frequencies have increased in samples irradiated with low doses of gamma radiation compared to the non-irradiated control cells. This data suggests that low doses of gamma irradiation elicit an adaptive response in *E. coli,* raising public health issues as bacteria thought to be eliminated could still be present in the sample as a potentially infectious agent.

The prokaryotic single strand binding (SSB) proteins are indispensable for the normal functioning of bacteria. Their role is to bind single-stranded DNA and

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thereby regulate its metabolism, which is necessary for replication, transcription, and repair mechanisms. Although the promoters of the *ssb* gene contain an SOS box, whether gene expression is SOS-dependent has not yet been clarified. Feliciello et al. (2022) have determined the *ssb* gene (encodes the SSB protein in *E. coli*) expression kinetics in gamma-irradiated *E. coli* using quantitative real-time PCR and concluded that the *ssb* gene expression in the treated cells is SOS-dependent, but during normal bacterial growth, it is unlinked to SOS induction.

However, gamma irradiation is not the only radiation that changes gene expression in *E. coli*. In a study by Said-Salman et al. (2019b), the effect of Wi-Fi radiofrequency radiation of 2.4 GHz on global gene expression was investigated in *E. coli* K-12 DH5α. High-throughput RNA-sequencing of 2.4 GHz-exposed and non-exposed bacteria revealed that 101 genes were differentially expressed (DEGs) due to the radiation. 52 genes were up-regulated, and 49 were down-regulated genes. Among the differentially expressed genes, 7% were involved in the cellular component organisation, 6% in response to stress stimulus, 6% in biological regulation, 6% in localisation, 5% in locomotion, and 3% in cell adhesion. Their analysis also showed that the up-regulated DEGs were involved in metabolic pathways, transposition, response to stimuli, motility, chemotaxis, and cell adhesion, while the down-regulated DEGs were associated with metabolic pathways and localisation of ions and organic molecules. In conclusion, the 2.4 GHz wireless fidelity radiation affected several bacterial cellular and metabolic processes in *E. coli* K-12 DH5α.

Antibiotics are also able to influence the bacterial SOS response, as it was proven by Kimmit et al. (2000). The SOS-inducing antimicrobials are especially the quinolones (ofloxacin, nalidixic acid, cinoxacin, ciprofloxacin etc.), trimethoprim and furazolidone. In the Shiga toxin-producing *E. coli* (STEC) strain, the Shigella toxin (stx) genes are encoded on bacteriophage genomes integrated into the bacterial chromosome. Bacteriophage production is linked to the induction of the bacterial SOS response, a ubiquitous response to DNA damage. The study states that the SOS-inducing antimicrobials can increase the amount of stx2 synthesised by the STEC strain.

Nalidixic acid has also been shown to induce an SOS response in *E. coli*, affecting cellular metabolism, such as inhibition of DNA synthesis, enhanced ability to DNA repair and mutagenesis, and inhibition of cell death and damage (Little and Mount 1982).

RpoS (general stress response regulator) – the sigma subunit of RNA polymerase – is up-regulated when the bacterium is exposed to environmental stress factors (Huang et al. 2009).

Biofilm formation. Surfaces in contact with water provide a living space for many microorganisms. The living community created by these organisms, called biofilm, can form on any surface that comes in contact with water: it can be on solid and liquid surfaces, as long as nutrients and sufficient moisture are available.

The layer gradually grows as nutrients and other substances accumulate in it. This multi-species community is held together and protected by a gelatinous coating (adherent matrix) formed from their metabolic products, extracellular polymers (EPS), and water. This makes killing organisms in the biofilm much more complex than floating microorganisms. It is much more complicated for disinfectants to penetrate the biofilm through this gelatinous layer, so they are only temporarily effective on top of the biofilm. Therefore, biofilms are significant hazards when they form in a food processing environment because they are a potential source of contamination and can cause food spoilage or even diseases. It is estimated that 95% of bacteria in water systems are found in biofilms (Flemming et al. 2002).

Different factors affect biofilm formation, such as nutrient availability, the presence of specific ions, osmotic pressure, temperature, pH, and O_2 levels (Goller and Romeo 2008).

Kawarai et al. (2009) tested whether *E. coli* can form biofilm in a hyperosmotic environment. They investigated the effect of sucrose, mannose, sodium chloride, manganese chloride and potassium chloride on the biofilm formation of *E. coli* K-12. They explored that this strain could form biofilms only in a sucrose-containing medium if tested under the high osmotic pressure at 1 M of each solute. Surprisingly, the biofilm-forming cells in a 1 M sucrose environment took a fat and filamentous morphology. The conclusion was that 1 M sucrose in food environments (as a common osmotic food preservative) is not sufficient to prevent the biofilm formation of *E. coli*.

Zhang et al. (2007) investigated the relationship between stress response and biofilm formation of *E. coli*. They concluded that *ycfR* is a multiple stress resistance protein and is responsible for biofilm formations in *E. coli*. The deletion of *ycfR* increased biofilm formation fivefold in the presence of glucose. Dried fruits are rich in sugar, and if the consumers are not careful

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with storing these products, biofilms could form on the surface of the fruits and the packaging material leading to potential health risks.

Radiation as a type of stressor can also induce biofilm formation. Said-Salman et al. (2019a) concluded that the exposure of *E. coli* O157:H7 to wi-fi radiation enhanced its metabolic activity and biofilm formation. This could be interesting from a food safety point of view. If dried fruits are stored near (30 cm, according to this study) the Wi-Fi router for 2 days under the right conditions, biofilm could form due to the electromagnetic fields leading to potential diseases.

VBNC state. In 1982 *E. coli* was discovered to enter the 'viable but non-culturable' (VBNC) state, which has been unknown so far (Xu et al. 1982). The characteristic of these cells is that they are living cells but have lost the ability to grow on routine media (on which they usually grow), which impairs their detection by conventional plate count techniques. Yet, VBNC cells maintain intact cytoplasmic membranes ($MEMB^+$) and functional electron transport system (CTC^+), while dead cells have damaged membrane that is unable to retain chromosomal and plasmid DNA (Muela et al. 2008; Li et al. 2014). If the bacterium has plasmids, they are also included in VBNC cells (Oliver 2010). This could pose a great challenge to public health since all the accepted methods for detecting and enumerating *E. coli* rely on culturing. This means that if VBNC cells are present in a sample, the plate count method will underestimate the number of viable cells. If all the cells presents are in the VBNC state, we could draw the false conclusion that the sample is germ-free since not a single viable microbe could be detected. Some VBNC cells can even stay virulent. For example, the VBNC cells of *Vibrio fluvialis* are still viable after 6 years of starvation (Amel et al. 2008). Those VBNC cells that are still virulent can cause fatal infections, which may be due to rapid resuscitation into culturable cells in suitable hosts (Highmore et al. 2018).

Although VBNC cells share many common characteristics as a type of viable cell, there are many physiological and molecular differences from viable, culturable cells. These differences include cell morphology, cell wall and membrane composition, metabolism, gene expression, physical and chemical resistance, adhesion properties, and virulence potential. In terms of cell morphology, a decrease in cell size, and thus an increase in the surface/volume ratio, is usually observed in VBNC cells. These cells show significant cell wall and membrane composition differences, including proteins, fatty acids, and peptidoglycan (Li et al. 2014).

The viable but non-culturable state may be an adaptive strategy for the bacteria to endure long-term unfavourable environmental conditions. These conditions are stressors such as lack of nutrients, high or low temperatures, osmotic pressure, low pH, radiation etc. However, many strains have the ability to leave this VBNC state and become culturable again when the stress is removed (Pinto et al. 2013).

Since VBNC cells cannot be cultured on normal growth media, detecting these cells is more complex. According to a general rule, if the number of culturable cells drops to an undetectable level while the number of viable cells remains high, the population in the sample has become VBNC cells (Li et al. 2014). So, the first step is estimating the remaining culturable cells in the sample using the traditional plate count method. Next comes the detection of viable cells. For this purpose, one of the most commonly used assays is the LIVE/DEAD® BacLight™ assay. The detection of gene expression by reverse transcription polymerase chain reaction (RT-PCR) is also a well-known method for detecting the VBNC state (Casasola-Rodríguez et al. 2018).

Zhang et al. (2015) have investigated the potential of UV treatment to induce a VBNC state in *E. coli* and *Pseudomonas aeruginosa*. They have concluded that following UV radiation, copy numbers for the high transcriptional levels of 16S rRNA genes varied non-significantly in both strains, confirming results from plate count assays indicating that VBNC states were induced in both strains. Propidium monoazide qPCR results showed that cell membranes remained intact even at a UV dose of 300 $mJ \cdot cm^{-2}$. Their results revealed that UV disinfection is not enough to kill bacteria completely. Therefore, combined disinfection procedures must be used, especially in food production environments.

A study by Sheng and Wang (2023) states that the stressful environment of dried fruits may induce, *Salmonella*'s VBNC state, which is closely related to *E. coli*. Se et al. (2021) studied the VBNC state of *E. coli* O157:H7 during desiccation. They concluded that the cells reduced their cultivability, protein synthesis and DNA replication during this process and changed their morphology. After adding water to the samples, *E. coli* could be resuscitated thus, it regained its cultivability, and the protein synthesis was restored. Since dried fruits can be added to confectionery and bakery goods, the ability to resuscitate bacteria may pose public health risks.

Virulence factors. Virulence factors are specific to the pathogenic strains, but in general, they are cellular components, molecules and regulatory systems

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that allow the bacterium to survive, colonise and invade the host. Over 100 Shiga are toxin-producing *E. coli* strains, but *E. coli* O157:H7 is the most well-known serotype (Nataro and Kaper 1998). The Shiga toxin family consists of three members: Shiga toxin produced by *Shigella dysenteriae* type1 is the prototype Shiga toxin, while the other two types (stx1, stx2) are produced by the enterohaemorrhagic *E. coli* strains. *E. coli* O157:H7 strains can produce stx1, stx2, or toxins (Mead and Griffin 1998). Shiga toxin and stx1 differ only by a single amino acid, however, stx2 is antigenically distinct and unrelated. The cellular receptors for the Shiga toxins are the neutral glycolipids globotriosylceramide (Gb3) and globotetraosylceramide (Gb4).

Shiga toxin causes cell death through the following steps: *i*) the toxin binds to the cell membrane by its receptors; *ii*) incubation leads to aggregation of toxin-receptor complexes in clathrin-coated pits; *iii*) the A fragment is endocytosed; *iv*) the toxin is then transported to the trans-Golgi network; *v*) there, the enzyme furin cleaves the toxin into A_1 and A_2 subunits; *vi*) now the toxin is transported to the endoplasmic reticulum, where it is translocated to the cytosol; *vii*) the A_1 subunit is a 28S rRNA N-glycosidase. The toxin cleaves an adenine residue from a specific nucleotide of the 28S rRNA component of the 60S ribosomal subunit. This blocks tRNA binding to the large subunit. Peptide elongation is prevented, and protein synthesis is disrupted (Rahal et al. 2012).

Apart from the Shiga toxin, *E. coli* can produce pO157 toxin. This protein shows strong similarities in the first 700 residues with the N-terminal domain of a toxin family known as the large clostridial toxins (LCT). It includes toxins A and B of *Clostridium difficile* (Law 2000). Descriptions of the pathology of *E. coli* O157 infections show similarities to toxin-mediated *Cl. difficile*-associated colitis, raising the possibility that the pO157 toxin may be involved in intestinal damage (Nataro and Kaper 1998).

Another important characteristic of STEC O157 and some other STEC is the ability to produce attaching and effacing (A/E) lesions on a variety of cell types. The binding of EPEC to epithelial cells induces several signalling pathways in the eukaryotic cells. These signals are responsible for A/E lesion formation, ion secretion, and bacterial invasion (Law 2000). The locus of enterocyte effacement (LEE) contains all the genes necessary for inducing the A/E lesions typical to *E. coli* O157:H7 infection (Rahal et al. 2012).

Acidic resistance is also a crucial virulence factor of *E. coli*, as it has to pass through the stomach to cause diseases. An acid-induced oxidative system, an acid-induced arginine-dependent system and a glutamate-dependent system are mechanisms that help *E. coli* endure an acidic environment (Law 2000).

A study by Chung et al. (2006) states that unfavourable conditions may enhance the expression of EHEC virulence factors. Se et al. (2021) investigated the proteomic changes of *E. coli* that had entered the VBNC state due to low moisture. They concluded that proteins involved in virulence (e.g. pathogenicity, flagellar movement) are upregulated in VBNC cells, implying that *E. coli* could still pose a huge risk of severe diseases even in a viable but non-culturable state. A study (Zhang et al. 2015) aiming to investigate whether UV treatment causes *E. coli* to enter the VBNC state concluded that the virulence genes (*gadA* and *oprL*) in VBNC-state cells remained highly expressed, suggesting that the VBNC bacteria still displayed pathogenicity. This emphasises open-air sun-dried products since UV rays could induce a VBNC state in which bacteria might remain virulent and cause serious diseases.

Gaougaou et al. (2020) determined that *E. coli* O157:H7 has a complex stress response triggered by gamma irradiation leading to changed virulence. They found several virulence genes, including stx2A/stx2B (responsible for producing Shiga toxins), were upregulated 60 min after gamma irradiation at a non-lethal dose of 0.4 kGy. Further studies would need to be conducted to find the correct doses that neither induce virulence genes nor change product quality. Apart from UV and gamma radiation, exposure to 2.4 GHz Wi-Fi also increased the virulence of *E. coli* O157:H7 by increasing its motility (Said-Salman et al. 2019b). According to their result, bacteria on dried fruits stored near the Wi-Fi router could pose health risks.

Effect of different stress factors on *E. coli*

Microorganisms encounter many compounds and agents in nature and foodstuffs as well. We could think these agents are potentially growth-compromising but on the contrary. These stresses could elicit protective and/or even adaptive responses, enhancing bacterial survivability.

Drying is a traditional food-preserving method which goes back thousands of years. By reducing the water content of a fruit, its relative energy and nutrient content are increased and concentrated. Dried fruits contain essential nutrients such as vitamins (vitamins A, D, B6, K1, and E), minerals (potassium, magnesium, calcium, zinc, and phosphor) and bioac-

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tive compounds such as polyphenols, carotenoids, and phytoestrogens (Chang et al. 2016).

In dried fruit, bacteria encounter many stressors, such as osmotic pressure, naturally occurring antimicrobials, UV radiation (open-air, sun-dried products) and sometimes even gamma irradiation (during processing).

Gamma irradiation

Sterilisation is a process that kills and destroys almost all kinds of living ,microorganisms, such as bacteria, viruses, and fungi. There are different methods of sterilisation depending on the type of food needing to be sterilised and the purpose of the sterilisation. Some of these methods are the following: vaporised hydrogen peroxide sterilisation (VHP), gaseous chlorine dioxide sterilization, ozone sterilisation, dry-heat sterilisers, infrared radiation, e-beam sterilisation, and ionising radiation (CDC 2008).

Gamma radiation is mainly used for a number of medical products (e.g. pharmaceuticals, medical devices, tissue for transplantation), but in some cases, it can be used for food as well. Depending on the country, meat, poultry, seafood (live oysters), fruits, vegetables and spices can be irradiated using gamma rays (Eustice 2018).

In the late 1980s, only a few irradiated products could be found in supermarkets, labelling was not required, and most of the foods were speciality items (e.g. frog leg in France). Nowadays, people have become more open-minded about irradiated food, although consumer acceptance of irradiated products varies worldwide. Some people still strongly dislike unusual food processing technologies such as food irradiation. Furthermore, consumers with negative feelings about nuclear energy perceive irradiated food as being of poorer quality and higher risk (Bearth and Siegrist 2019; D'Souza et al. 2021). Other consumers are more concerned about food additives, growth hormones, bacteria, and other microbiological contamination (Bruhn 1995). A study suggests that the increase in consumer acceptance of irradiated food products depends on providing helpful information for them (Shahbaz et al. 2016). Those who trust the irradiation technology are more likely to pay a premium price for irradiated food (Nayga 2003).

The irradiation of dried aromatic herbs, spices, and vegetable seasonings is authorised at the EU level by Directive 1999/3/EC of the European Parliament and of the Council on the establishment of a Community list of food and food ingredients treated with ionising radiation (European Commission 2001). According to the directive 1999/2/EC on the irradiation of foods and food ingredients, the words 'irradiated' or 'treated with ionising radiation' must appear on the label or packaging or on the documents which accompany irradiated foodstuffs or foodstuffs containing irradiated ingredients (European Commission 1999).

Approximately 60 countries permit irradiation of different foodstuffs (Castell-Perez and Moreira 2021). There are 14 member states within the European Union with approved food irradiation facilities. The total quantity of irradiated foods was 9 264 tons in 2010 and 5 690 tons in 2015. Compared to 2010, in 2015, there was a decreasing trend in food irradiation: France reduced the number of irradiated foods by 64%, The Netherlands by 60%, and Belgium by 33%. Only three countries have managed to increase the number of irradiated foodstuffs: Croatia, Estonia, and Germany (Eustice 2018). The decline in the volume of irradiated foodstuffs might be because consumer acceptance is still not fully developed. Another factor could be its high fixed cost (Ferrier 2010; Bearth and Siegrist 2019; D'Souza et al. 2021).

According to the CODEX General Standard for Irradiation Foods, only radiation from high-energy gamma rays, x-rays and accelerated electrons can be used to sterilise foods and medical and pharmaceutical devices (FAO 2003).

Gamma rays are part of the electromagnetic spectrum (in the short wavelength, high-energy region). The ionising radiation originates from different sources: gamma rays which are produced by radioisotopes; cobalt 60 (the most common) and caesium 137. Gamma rays can penetrate foods to a depth of several centimetres. The energies from the radiation source are too low, so neither the food nor any other material becomes radioactive (Farkas and Mohácsi-Farkas 2011).

In biology, a model called target theory states that inside an organism, there are target locations (each of them is considered a unit of biological function), and the inactivation of these locations by radiation results in the organism's death (Nomiya 2013). Bacterial cells are more sensitive to irradiation than viruses or enzymes because the correlation of radiation sensitivity is inversely proportional to the size of the targets. There is a value that describes the sensitivity of an organism to radiation. The D-value describes the time required for the number of viable microorganisms to decrease to 10% of its original number. The type of microbe, the temperature, and the used radiation dose rate influence its value. Gamma rays damage the

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cells by disrupting the DNA. The disruption can happen directly (energy deposition in the critical target) or indirectly (the interaction of radiation with other atoms or molecules within or surrounding the cell). Radiation interacts with water, creating free radicals, which are any kind of molecular species containing an unpaired electron in their atomic orbital (making them highly reactive) and can exist independently. The most important radical is OH; it is responsible for 90% of DNA damage. In a living cell, the indirect effect is more significant. It is estimated that the irradiation of a living cell at one Gray induces 1 000 single-strand breaks, 40 double-strand breaks, 150 cross-links between DNA and proteins, and 250 oxidations of thymine (Borrely et al. 1998). The most important factors that affect the microorganism's radiation resistance are: *i*) water content: microorganisms are more resistant when irradiated in dry conditions; *ii*) oxygen: oxygen increases the lethal effect on microorganisms; *iii*) temperature: irradiating at higher temperatures enhances the bactericidal effects on vegetative cells; *iv*) the medium in which bacteria are irradiated: decimal reduction values (D-values) can differ significantly according to the medium; *v*) post-irradiation conditions: microorganisms that survive irradiation will possibly be more sensitive to environmental conditions such as temperature, pH, nutrients, inhibitors etc.; *vi*) size and structural arrangement of the DNA in the microbial cell; *vii*) compounds associated with the DNA in the cell, such as peptides, nucleoproteins, RNA, and lipids (Silva Aquino 2012).

The various types of microorganisms have adapted differently on how to repair the loss of genetic information due to DNA damage. Since the spatial configuration is altered, the DNA damage is recognisable, and thus, the cell can detect and try to repair it. If the radiation causes a single strand break, the damaged DNA strand gets excised, and the complementary DNA strand is used as a template to restore the information. Radiosensitivity greatly depends on the bacterium's ability to repair single-strand breaks. Those microorganisms that do not have this ability are more sensitive to the effect of irradiation than others. Double-strand breaks can cause genome rearrangements. The non-homologous end joining and recombination repair is two mechanisms that can repair double-strand breaks (Broomfield et al. 2001).

Byrne and others (2014) have investigated *E. coli* genes and pathways involved in surviving extreme exposure to ionising radiation. For this, they have screened nonessential *E. coli* genes involved in ionising radiation resistance by using transposon-directed insertion sequencing (TraDIS). They identified forty-six genes required for cells to recover from ionising radiation exposure. Twenty genes are responsible for DNA repair functions: several genes, particularly *recF*, *recN*, and *recG*, contribute substantially to survival. Other genes affect the cellular response to oxidative damage, cell division, and intermediary metabolites. They concluded that survival after high irradiation doses depends not on a single mechanism but is multifaceted.

The outer membrane of Gram-negative bacteria acts as a permeability barrier to certain antibiotics, dyes, and detergents, thus protecting the bacteria from their inhibitory effects. The different food preserving methods, such as heating, freezing, drying and even gamma radiation, damage the outer membrane leading to the underestimation of viable bacteria in foods (Nikaido and Nakae 1980). According to a study by Mackey (1983), gamma radiation could change antibiotic sensitivity and cell surface hydrophobicity in *E. coli*. The irradiated samples were sensitised to vancomycin, novobiocin and bacitracin. This means the damaged cells increased their sensitivity to hydrophobic antibiotics due to increased cell surface hydrophobicity. This may suggest that gamma radiation might decrease hydrophobic antibiotic resistance in *E. coli*.

In another study, gamma radiation affected the resistance of *E. coli* to chloramphenicol, gentamycin, and streptomycin. Before irradiation, the bacterium was sensitive to the previously mentioned antibiotics. After exposure to 2, 3, and 4 Gy, the organism was not inhibited by the antibiotics, which means an increase in resistance. Although, a small inhibition zone was observed in the case of samples exposed to 5 Gy, suggesting they were sensitised to antibiotics at a higher dose (Oguanniran et al. 2019). It is unknown whether these changes are permanent; thus, more thorough experiments should be carried out to gather greater knowledge on the subject and to determine the correct irradiation doses that neither affect the product quality nor increase antibiotic resistance.

There are various types of food processing and preservation methods. Nowadays, there is a huge emphasis on gentle preservation methods such as irradiation. If irradiation is combined with other preservation methods (e.g. the addition of spices, herbal extracts), the overall effect could be synergistic at the correct dose and concentration. In this way, the irradiation dose could be reduced, thus, food quality is not affected, and it is more environmentally friendly. Suppose the dose or concentration applied is insufficient,

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or there are other stressors in the food environment (e.g. acid, sugar). In that case, bacterial cells may adapt, leading to enhanced survivability in harsh conditions (e.g. dried fruit), which pose a potential risk for diseases (Chung et al. 2006; Lim and Ha 2020). Cross-protection is also important in stress adaptation since stress-adapted bacteria can resist similar and different stresses. One stress condition protects against other stresses (Chung et al. 2006).

Various studies have shown that oregano oil is one of the most effective oils against *E. coli* (Rhayour et al. 2003; Bhargava et al. 2015). Due to the essential oils' antimicrobial properties, the bacterial cell wall is damaged, and the intracellular ATP is released, leading to cell death. Caillet et al. (2005) have evaluated that gamma irradiation affects the murein (peptidoglycan) composition of *E. coli* O157:H7. The peptidoglycan wall gives most bacteria their shape and is responsible for their stability. If it is disrupted, the bacteria cannot reproduce (Höltje 1998). Different radiation doses influenced the number of muropeptides detected by HPLC. The bacterial strain was treated with three radiation doses: 0.4 kGy to induce cell damage, 1.1 kGy to obtain a viable but nonculturable state (VBNC), and 1.3 kGy to cause cell death. In samples irradiated with 0.4 kGy, the number of muropeptides was 22. They found 24 muropeptides in samples irradiated with 1.1 kGy, and 21 in samples irradiated with 1.3 kGy. There were peaks only detectable in samples after irradiation at 0.4 kGy, and peaks only noticeable in the VBNC group. With the lethal dose, the concentration of high molecular weight muropeptides decreased. Gamma radiation may cause lesions in the DNA of *E. coli* and alters protein expressions resulting in changes in enzyme activity and peptidoglycan biosynthesis. This study shows that oregano oil, combined with irradiation, is an efficient preservation method, as the relative percentages of various muropeptides were severely affected by gamma irradiation.

Bolsunovsky and co-workers (2016) have observed the genotoxicity of gamma radiation at low doses in *E. coli*. The most considerable increase in the induction of SOS response and mutation frequencies was observed in the first 24 h of exposure to gamma radiation.

Presence of antimicrobials

Like gamma irradiation, antimicrobials are also stressors to which protective stress responses have evolved. Antimicrobials are agents that kill microorganisms or stop their growth, and the type of antimicrobial to be used depends on the target microorganism. Antibacterials are used for treating bacterial infections, antivirals can be applied in the case of virus-causing illnesses, while antifungals kill or prevent the growth of fungi. The emergence of antibiotic-resistant bacteria is still a major challenge for the medicine industry. Over the past decade, more resistance genes have been discovered in *E. coli*, often acquired through horizontal gene transfer. Another issue is that *E. coli* could act as both a donor and a recipient of resistance genes, which means it can receive resistance genes from other bacteria and tran its resistance genes to other bacteria (Poirel et al. 2018). Extended-spectrum β-lactamase (ESBL)-producing organisms such as *E. coli* have been responsible for numerous outbreaks of infections worldwide. They produce antibiotic-degrading enzymes (Iroha et al.5), which is why these resistant bacteria pose a considerable risk worldwide.

Sun drying is one of the most common ways to preserve apricot protection, reducing the moisture content and increasing the shelf life (Wei et al. 2014). During this process, the fruit (and thus the contaminating bacteria) is exposed to ultraviolet rays from the Sun. UV light has germicidal properties and can kill bacteria, fungi yeasts, moulds, and viruses. In a study (Pang et al. 2015), the effect of UV radiation on the change in the resistance of ampicillin-resistant *E. coli* was investigated. It was observed that the ampicillin-resistant *E. coli* CGMCC 1.1595 strain showed greater resistance to low doses of UV irradiation than other *E. coli* strains analysed previously. This could be a problem from a food safety point of view because if the product becomes contaminated with this or other similar strains during the drying process, the UV light applied would not kill the bacteria but would increase its resistance.

During the drying process, another important stressor could be the heat. Ahmadi et al. (2007) investigated whether heat stress affects the antibacterial resistance and plasmid profile in *E. coli* isolates. It was concluded that there was no difference amongst the plasmid profiles of the isolates at 37 °C (no stress) and 43 °C (stress). The conclusion was that antibacterial resistance is not affected as long as the duration of the stress is short. In another study (Moro et al. 2000), the effect of heat stress on the antimicrobial drug resistance of *E. coli* in the intestinal tract of swine was investigated. This study could be significant from a food safety point of view because if the open-air sun-drying process occurs near a swine farm and the bacteria are carried by wind and rain to the fruit, it could pose a disease risk. For the experiment, ten finisher hogs were heat-stressed for 24 h. The antimicrobial resistance levels

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were compared before and after heat stress for amikacin, ampicillin, cephalothin, neomycin and tetracycline from faecal samples. It was concluded that the antimicrobial resistance levels were significantly higher after the heat stress for the mentioned antibiotics. Moreover, the high resistance level persisted for 10 days (slaughter day). This suggests that the increase in antimicrobial resistance could be permanent, although more studies would need to be conducted to gain more knowledge on this topic.

Antimicrobials, such as phytochemicals, can naturally be found in food. The mechanism of action is the same as antibiotics: they prevent growth and/or kill microorganisms. Essential oils have proven to be effective against several food-borne pathogens such as *E. coli* O157:H7, *Salmonella Typhimurium, Staphylococcus aureus, Listeria monocytogenes, Campylobacter* sp. and others (Callaway et al. 2011). Essential oils are a group of metabolic products found in fruits, flowers, and seeds of different plants. The phenolic compounds in the essential oils might be responsible for the antimicrobial effect (Elegir et al. 2008). According to a study by Nychas (1995), phenols either weaken or destroy the permeability barrier of the cell membrane, resulting in the release of cellular constituents, thus killing bacteria. Another way of affecting the microorganism is the alteration of the physiological status of the cells by changing the fatty acid composition and phospholipid content of bacteria, interfering with energy metabolism, disrupting electron transport or nutrient uptake, and affecting nucleic acid synthesis.

Anthocyanins which are water-soluble pigments can be found in flowers and fruits. The action of the mechanism is the inhibition of bacterial enzymes leading to the inhibition of bacterial growth.

Organic oils have proven effective against food-borne pathogens such as *E. coli* (Lopez-Romero et al. 2015). Herb extracts also have antimicrobial properties, although they are not widely used in the food industry. In an experiment in 1999 (Cutter 2000) *E. coli* O157:H7 was inoculated onto beef meat. It was subjected to surface spray treatments with a herb extract dispersed in sodium citrate or another herb extract dispersed in sodium chloride. After 7 days *E. coli* O157:H7 was reduced by > 1.3 $\log_{10}$ CFU·cm^{-2} by the latter herb extract. In another experiment, surface spray treatments of beef with solutions of the different herb extracts reduced the number of *E. coli* O157:H7. These studies might lead to the broader use of herb extracts to enhance certain food products' safety.

A study by Fisher and Phillips (2006) aimed to investigate the effectiveness of oils and vapours of lemon, sweet orange, and bergamot against common food-borne pathogenic bacteria (*E. coli* O157, *Listeria monocytogenes, Staphylococcus aureus, Bacillus cereus* and *Campylobacter jejuni*). They discovered that bergamot was the most effective oil and linalool the most effective antibacterial component. *E. coli* O157 was inhibited by bergamot, linalool oils, and linalool vapour.

Liu and others (2020) have investigated the survival of common food-borne pathogens on dried apricots. Sun-dried apricots (with and without sulphur dioxide treatment) were inoculated using dry and wet carriers to mimic different contamination scenarios during production and processing. The survival of STEC, *Salmonella* spp. And *L. monocytogenes* on inoculated dried apricots were monitored for three months during the ambient temperature storage. They concluded that STEC survived with higher culturable numbers for longer than the other two pathogens on apricots treated without sulphur dioxide, indicating the antimicrobial properties of free SO_2 contained in sulphur dioxide. This means that the presence of phenolic and other natural antimicrobial compounds may also impact the survival of the pathogens (Byrne et al. 2014).

According to a study in 2016 (Sheng et al. 2016), cinnamon oil inhibited Shiga toxin type 2 phage induction and Shiga toxin type 2 production in *E. coli* O157:H7. The importance of this study was to prove that cinnamon oil can be used to control *E. coli* O157: H7 infection through the inhibition of bacterial growth and virulence factors.

Cationic peptide antimicrobials (for example, polymyxin and cecropin) induce selective transcription of *micF* in *E. coli* (Oh et al. 2000). The *micF* gene is a stress response gene – found in *E. coli*, *Salmonella* spp., *Klebsiella pneumoniae*, and *Serratia marcescens* – that post-transcriptionally controls the outer membrane porin protein F (*OmpF*) expression under stress conditions. *OmpF* and *OmpC* (another outer membrane protein) form pores in the membrane through which small hydrophilic molecules passively diffuse. The ability to control the permeability of molecules through the outer membrane is a key factor in the survival of stressed cells. The decrease in permeability may lead to antibiotic resistance in originally antibiotic-susceptible species. If the conditions are not favourable for the bacteria, *MicF* synthesis is increased, which causes a decrease in *OmpF* production which results in multiple antibiotic resistance (Nikaido 1994; Delihas and Forst 2001). Thus, the harsh environment of dried

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foodstuffs can increase *micF* levels, decreasing OmpF levels and leading to antibiotic resistance. This is a public health issue as treating diseases caused by potentially pathogenic microorganisms digested with food becomes more difficult with known antibiotics.

High sugar content

Properly storing dried fruits retains their taste, texture, and nutritional value for a long time, even without additives. However, we can still find varieties containing chemical substances (e.g. sulphur dioxide, sorbic acid) in stores. Their advantage is that they preserve the bright colour and durability of the product (protects from fungi), but their disadvantage is the allergic reactions they can cause (Santos et al. 2011; Scheman et al. 2012; Hao et al. 2020).

In general, raisins, prunes and apricots are the most well-known and liked dried fruits, but a wider range of other dried fruit products can also be found on the shelves of the supermarkets, such as dates, figs, apples, cherries, cranberries, pears, mangoes, and pineapples.

Dried fruits contain high amounts of natural sugars, including glucose, fructose, and sucrose. Table 2 shows the diverse amount of sugars found in 100 g of different dried fruits (FoodData Central 2014).

A study by Bae et al. (2021) investigated the effects of combinations of acetic or malic acid and various solutes (salt, glucose, glycine, or sucrose) on the survival of *E. coli* O157:H7 in laboratory broth. A protective effect of combinations of acid and salt or sugar (sucrose and glucose) on *E. coli* O157:H7 survival was observed. It was concluded in another study by Casey and Condon (2002) that NaCl decreased the water activity (due to water loss from the cytoplasm), which caused the *E. coli* cell volume to shrink. Because of this, the pH of the cells has increased. This may explain the protection of STEC cells in acidic conditions by sugar alone and the combination of salt and sugar. Also, the induction of the adaptive tolerance response (ATR) to stress increases the survival of *E. coli* O157:H7 under stress and may also confer cross-protection against other stresses (Wang and Doyle 1998). Hyperosmotic salt or sucrose gradient induces selective transcription of both *micF* and *osmY* genes (Oh et al. 2000). These studies are important from a food safety point of view since the use of salt and sugar is one of the most commonly used traditional food preservative methods (Pittia and Antonello 2016).

Another important virulence factor is the locus of enterocyte effacement (LEE) (Rahal et al. 2012). LEE gene expression is influenced by quorum sensing through the *luxS* system. In a study from 2012, the effect of glucose on the expression of several genes from LEE, e.g. Shiga toxin genes and *luxS*, was assessed with real-time reverse transcription PCR. The results showed that glucose down-regulates LEE1 expression in a luminescent strain of *E. coli* O157:H7. The down-regulation was evident even with the lowest concentration of glucose (0.1%). A slight down-regulation of genes involved in the expression of Shiga toxin was also observed, but it was only significant at low glucose doses (0.1–0.5%). A significant increase in *luxS* expression was detected in the case of 1% glucose. This means that glucose plays a critical role in the down- or upregulation of LEE-encoded virulence genes of this bacterium. In conclusion, the presence of glucose can have an important effect on the virulence of *E. coli* O157:H7 (Delcenserie et al. 2012).

Buchanan and Edelson (1996) evaluated the effect of glucose (a source of fermentable carbohydrates) on the acid tolerance of seven enterohaemorrhagic and one non-enterohemorrhagic strain of *E. coli* in tryptic soy broth (TSB). They have concluded that all enterohemorrhagic strains were acid resistant when initially cultured in TSB with glucose, but significant differences were observed in acid tolerance among strains

Table 2. Diverse amounts of sugars found in dried fruits (100 g) (FoodData Central 2014)

Dried fruit	Total sugars (g)	Glucose (g)	Fructose (g)	Sucrose (g)
Dried apricots	53.4	33.1	12.5	7.89
Dried prunes	38.1	25.5	12.4	0.15
Dried figs	47.9	24.8	22.9	0.07
Dried peaches	41.7	12.8	13.5	15.4
Dried pears	62.2	NA	NA	NA
Dried goji berries	45.6	NA	NA	NA
Dried apple	57.2	NA	NA	NA

NA – no data available

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when initially cultured in TSB without glucose. An important virulence factor of *E. coli* is its acid tolerance, as it has to pass through the acidic conditions of the stomach to cause diseases. The results of this study show that glucose (as a fermentable carbohydrate) plays an important role in the acid tolerance of *E. coli*.

It was presented in a study that the sublethal food preservation stresses (such as osmotic stress) altered the antibiotic resistance in *E. coli*. Under high salt-salt concentrations, the MICs of the tested antibiotics (amikacin, ceftriaxone, nalidixic acid) were higher than the MICs for the non-stressed samples. Interestingly, *E. coli* continued to express higher levels of antibiotic resistance even after the stress was removed. Post NaCl-stressed *E. coli* suspensions had higher MICs for all three antibiotics tested than the not stressed *E. coli* suspensions. In some cases, more than a four-fold increase in the MIC values was observed. This suggests that in some cases, the sublethal stressors induced the sublethal stressors caused a stable increase of antibiotic resistance a stable increase of antibiotic resistance(McMahon et al. 2007).

CONCLUSION

A healthy lifestyle has led to increased consumption of vegetables, fruits, and dried fruits. If there is a break anywhere in the food chain or inadequate conditions in a food production plant, it can lead to bacterial growth on food during storage, transport, or home storage. On the one hand, this could cause the spoilage of food, on the other hand, it could lead to serious health problems and even food-borne outbreaks if any pathogenic cells remain viable. Non-coliform and some coliform bacteria, and even *E. coli* were detected on dried fruits (Torres 2007). *E. coli* as a member of the normal intestinal microbiota, plays an important role in preventing the colonisation of pathogenic bacteria. Temporarily, *E. coli* strains can be found on the skin, in the mucous membrane of the pharynx, and on the external female genital organs, however, it also has the pathogenic capacity to cause enteric- and extraintestinal diseases, urinary tract infections (UTIs) and sepsis/meningitis (Smith et al. 2007; Nielsen et al. 2014; Kim 2016).

Dried fruits are the dehydrated forms of fresh fruits. They are valuable sources of vitamins, minerals, and bioactive compounds (e.g. polyphenols, carotenoids, and phytoestrogens), have longer shelf-life than fresh fruits, and can be used in various ways while cooking. Dried fruits are also great sources of fibres which lower cholesterol and better regulate blood sugar levels and normal bowel movement, thus shortening the transit time of food through the intestines (Nsor-Atindana et al. 2012). The unsweetened dried fruits contain naturally occurring fructose, glucose, and sucrose. The total sugar content may vary depending on the fruit but is generally around 35–60% (FoodData Central 2014; Chang et al. 2016).

The types of stresses to which *E. coli* is exposed in dried fruits, such as high sugar content, antimicrobials, and gamma irradiation, affect its survival ability. If pathogenic *E. coli* survives in dried fruits, it could pose serious public health risks.

The use of sugar is a traditional food-preserving technique. sugar content can affect the acid tolerance of bacteria and alter the antibiotic resistance in *E. coli* (Buchanan and Edelson 1996; Mcmahon et al. 2007). Antibiotics can influence the bacterial SOS response (Kimmit et al. 2000). The SOS-inducing antimicrobials are especially the quinolones (ofloxacin, nalidixic acid, cinoxacin, ciprofloxacin etc.), trimethoprim and furazolidone. SOS genes are repressed to a certain degree under normal growth conditions, but when the cell senses increased DNA damage due to stress factors, DNA repair and mutagenesis are induced (McKenzie et al. 2000; Michael 2005).

Gamma irradiation disrupts the DNA, leading to cell death. Although gamma radiation is lethal to the cell at the right dose, it may also affect *E. coli*'s antibiotic resistance (Oguanniran et al. 2019). According to a study by Mackey, gamma radiation could change antibiotic sensitivity and cell surface hydrophobicity in *E. coli*. The irradiated samples were sensitised to vancomycin, novobiocin and bacitracin. Due to their increased cell surface hydrophobicity, the damaged cells had increased sensitivity to hydrophobic antibiotics (Mackey 1983).

Irradiation can also induce the viable but non-culturable (VBNC) state of *E. coli* (Caillet et al. 2005). In this state, the cells are alive but have lost the ability to be cultured on normal media. They have intact membranes and functional electron transport systems (Li et al. 2014). VBNC cells could pose great risks in the food industry because if these cells are present in a sample, the number of viable cells will be underestimated, hence false conclusions on the microbiological status of the food can lead to food-borne diseases.

Irradiation and the presence of antimicrobials can also up or down-regulate different genes in *E. coli* that can contribute to food-borne outbreaks via increasement in toxin production (Kimmit et al. 2000; Feliciello et al. 2022).

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By investigating the combined effects of gamma radiation, antimicrobials, and high sugar content, a more accurate picture of the microorganisms found on dried fruits (containing high amounts of sugars and natural antimicrobials) and their behaviour under these stress conditions could be obtained.

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