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Growth and Development in Plants and Their Medicinal and Environmental Impact

Edited by Marcos Soto-Hernández, Mariana Palma-Tenango and Eva Aguirre-Hernández

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Contributors
A. Anandkumar, Adeyanmola Oluwaseyi Faturoti, Azra Đulović, Clement Olusola Ogidi, Eva Aguirre-Hernández, Franko Burčul, Ivana Generalić Mekinić, Ivica Blažević, Josip Tomaš, Marcos Soto-Hernández, Mariana Palma-Tenango, N. Malligarjunan, Olivera Politeo, Petra Brzović, Sanja Radman, Shivanand Koti, Vijay R. Zala, Yatinkumar N. Tandel

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Physiology

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Aims and Scope of the Series

Modern physiology requires a comprehensive understanding of the integration of tissues and organs throughout the mammalian body, including the cooperation between structure and function at the cellular and molecular levels governed by gene and protein expression. While a daunting task, learning is facilitated by identifying common and effective signaling pathways mediated by a variety of factors employed by nature to preserve and sustain homeostatic life. As a leading example, the cellular interaction between intracellular concentration of Ca+2 increases, and changes in plasma membrane potential is integral for coordinating blood flow, governing the exocytosis of neurotransmitters, and modulating gene expression and cell effector secretory functions. Furthermore, in this manner, understanding the systemic interaction between the cardiovascular and nervous systems has become more important than ever as human populations' life prolongation, aging and mechanisms of cellular oxidative signaling are utilised for sustaining life. Altogether, physiological research enables our identification of distinct and precise points of transition from health to the development of multimorbidity throughout the inevitable aging disorders (e.g., diabetes, hypertension, chronic kidney disease, heart failure, peptic ulcer, inflammatory bowel disease, age-related macular degeneration, cancer). With consideration of all organ systems (e.g., brain, heart, lung, gut, skeletal and smooth muscle, liver, pancreas, kidney, eye) and the interactions thereof, this Physiology Series will address the goals of resolving (1) Aging physiology and chronic disease progression (2) Examination of key cellular pathways as they relate to calcium, oxidative stress, and electrical signaling, and (3) How changes in plasma membrane produced by lipid peroxidation products can affect aging physiology, covering new research in the area of cell, human, plant and animal physiology.

Meet the Series Editor

Prof. Dr. Thomas Brzozowski works as a professor of Human Physiology and is currently a Chairman at the Department of Physiology and is V-Dean of the Medical Faculty at Jagiellonian University Medical College, Cracow, Poland. His primary area of interest is physiology and pathophysiology of the gastrointestinal (GI) tract, with a major focus on the mechanism of GI mucosal defense, protection, and ulcer healing. He was a postdoctoral NIH fellow at the University of California and the Gastroenterology VA Medical Center, Irvine, Long Beach, CA, USA, and at the Gastroenterology Clinics Erlangen-Nuremberg and Munster in Germany. He has published 290 original articles in some of the most prestigious scientific journals and seven book chapters on the pathophysiology of the GI tract, gastroprotection, ulcer healing, drug therapy of peptic ulcers, hormonal regulation of the gut, and inflammatory bowel disease.

Meet the Volume Editors

Dr. Marcos Soto Hernández is a pharmacist from the National University of Mexico, where he completed his Ph.D. at the University of Wales, Cardiff, UK. He is now a full Professor at Colegio de Postgraduados, where he conducts research in phytochemistry and the bioactivity of natural products. He has established collaborations with research groups in the UK, the Netherlands, Spain, and other groups in Mexico and has received several awards locally and abroad. Currently, his primary research focus is on the guided isolation of secondary metabolites with significant importance in medicine and agriculture. Additionally, the potential of local aromatic plants is part of his recent research.

Dr. Mariana Palma Tenango is an Agricultural Engineer from the Autonomous University of Chapingo and a Doctor in Plant Physiology from the Postgraduate College of Mexico. She is a teacher and researcher at the Science Faculty in the National Autonomous University of Mexico (UNAM), a reviewer for several journals and an editor. She has participated in organizing congresses and symposiums in Mexico and serves as a supervisor for master's and doctoral students. Her line of research is phytochemistry, aromatic and medicinal plants, and metabolomics.

Dr. Eva Aguirre Hernández obtained her Bachelor's degree in Biology at the UNAM Faculty of Sciences. She received her Master's and Doctorate Degrees in Science at the Graduate College, Montecillo campus, Texcoco, State of Mexico. She teaches subjects such as Organic Chemistry and Plant Biology II, as well as workshops in Phytochemistry and Pharmacology. Her research line is related to natural products. She is a supervisor of social service, the thesis advisor for undergraduate and postgraduate students, as well as a member of the tutorial committee for Master's and Doctorate Postgraduate Programs in Biological Sciences. She has also reviewed several scientific journals and has contributed to the dissemination of research at national and international conferences and is responsible for the Laboratory of Natural Products at the Faculty of Sciences of the National Autonomous University of Mexico (UNAM).

Contents

Preface

The study of medicinal and aromatic plants has long been of interdisciplinary interest, ranging from their traditional herbal uses to modern pharmacology. In recent decades, interest in these species has grown significantly due to the recognition of the complex relationship between their physiological development and the biosynthesis of secondary metabolites, which are key compounds produced by plants for defense, communication, and adaptation to their environment.

This book arises in response to the need to understand, from an integrated perspective, the factors that determine the production, accumulation, and variability of these bioactive compounds. Structured around three thematic axes, plant growth dynamics and the influence of biotic and abiotic factors, this work aims to provide readers with a holistic view that connects plant physiology with phytochemistry, functional ecology, and practical applications.

Throughout the chapters of this volume, key topics are explored, including plant responses to environmental stress and the role of interactions with microorganisms and other organisms in triggering defensive mechanisms that lead to the increased production of valuable compounds. Emerging approaches and cultivation strategies that aim to optimize phytochemical yield without compromising sustainability are also discussed.

This book is intended for students, researchers, and professionals in the biological, pharmaceutical, and agricultural sciences who are interested in deepening their understanding of medicinal plants from a physiological perspective. We hope this work will inspire new lines of research.

Dr. Marcos Soto-Hernández
Full Professor,
Department of Botany,
Postgraduate College,
Montecillo Campus,
Texcoco, Mexico

Dr. Mariana Palma-Tenango
Researcher,
Department of Plant Physiology,
Postgraduate College,
Montecillo Campus,
Texcoco, Mexico

Dr. Eva Aguirre-Hernández
Full Professor,
Faculty of Sciences,
The National Autonomous University of Mexico,
Coyoacán, Mexico

Chapter 1

Introductory Chapter: Relationship between the Growth and Development of Medicinal and Aromatic Plants and the Biosynthesis of Secondary Metabolites

Mariana Palma-Tenango, Eva Aguirre-Hernández and Marcos Soto-Hernández

1. Introduction

Scientific research is increasingly interested in the relationship between the development and growth of medicinal and aromatic plants and the biosynthesis of secondary metabolites. Understanding this interaction requires considering a wide range of biotic, abiotic, genetic, and molecular factors that significantly influence both processes.

During plant development and growth, there is a close association with the response of various secondary metabolites. These compounds play essential roles in plant physiology and ecology and represent a valuable source of pharmaceutical products, food additives, aromatic compounds, and biochemicals of industrial importance [1]. Numerous studies have shown that environmental factors such as temperature, humidity, light intensity, water supply, mineral availability, and CO_2 levels, as well as stress conditions such as drought, high salinity, and low temperatures, affect both plant growth and the production of secondary metabolites [1, 2]. In addition, internal factors such as developmental genetic circuits, gene expression, and transcriptional regulation play a crucial role in the synthesis and accumulation of these compounds [3].

Due to this multifaceted potential, analyzing the mechanisms that regulate plant growth and the accumulation of secondary metabolites in medicinal and aromatic plants is essential not only to optimize cultivation and improve quality but also to promote sustainable production strategies, biotechnological innovation, and the rational use of natural resources. Integrating this knowledge will help improve the quality of products derived from medicinal plants and enhance their clinical, agricultural, and industrial applications [4].

2. Growth and development dynamics in medicinal plant species

The growth and development of medicinal plants are dynamic and complex processes involving genetic, physiological, and environmental interactions. These dynamics determine the plant's biomass and the quality and quantity of the secondary metabolites produced, which are essential for their medicinal properties [3]. Plant growth consists of organized stages, each regulated by internal hormonal mechanisms and modulated by external signals [5]. In medicinal species, certain developmental phases, such as flowering or controlled water stress, can be associated with increased production of bioactive compounds. This reflects a close relationship between development and the biosynthesis of secondary metabolites [4]. For example, in *Catharanthus roseus*, the production of alkaloids such as vinblastine and vincristine peaks at specific stages of the life cycle, coinciding with particular hormonal profiles and cell growth rates [6].

Furthermore, growth dynamics can be influenced by environmental conditions such as nutrient availability, light intensity, or abiotic stress. These factors not only affect morphological parameters such as leaf number, plant height, or root biomass, but also trigger metabolic responses that promote the accumulation of secondary compounds of therapeutic interest [1]. For instance, in *Artemisia annua*, artemisinin concentrations are higher when plants are exposed to moderate water stress during the vegetative phase. Detailed knowledge of growth dynamics and their relationship with the synthesis of secondary metabolites has led to the development of agronomic strategies to enhance the quality of medicinal plants [7, 8].

3. Influence of biotic and abiotic factors on the accumulation of secondary metabolites

Changes in climatic conditions are causing an increase in both biotic and abiotic stress in living organisms. This stress significantly affects the productivity of medicinal and aromatic plants worldwide. Various environmental factors lead to changes in agroecological conditions and impact plant growth and development, sometimes resulting in total crop loss [9, 10]. Different parts of the plant such as roots, stems, leaves, flowers, fruits, and seeds are used because they are an essential source of secondary metabolites, valued for their medicinal and nutraceutical properties, as well as a source of essential oils used in the production of perfumes, soaps, cosmetics, and more. These metabolites are also crucial as food additives due to their aromatic and pigment properties [11].

Ecological stress factors such as light intensity, UV radiation, ozone, drought, salinity, extremely high or low temperatures, exposure to heavy metals, soil fertility, and attacks by herbivores, fungi, bacteria, and viruses significantly influence the physiological and biochemical responses of plants, restricting their growth and productivity [12–14]. In response to stress, plants activate the synthesis of various groups of secondary metabolites, including terpenoids, phenolic compounds, and alkaloids, as an adaptive defense mechanism for survival [10, 12, 15]. These chemical constituents also facilitate pollination, seed dispersal, and symbiotic relationships with bacteria and fungi [13–16].

The type and concentration of metabolites depend on the plant species, the organ, the phenological stage, and the biotic and abiotic factors of the environment in which the plant grows [12–14]. For instance, phenolic acids and flavonoids protect

plants from diseases caused by pathogenic microorganisms and provide resistance to UV radiation [10]. Most alkaloids have antiviral properties, while terpenes and carotenoids help plants develop complex defense systems against numerous pathogens. Overall, secondary metabolites are key in enhancing plant resistance to various abiotic factors and diseases, thus increasing their survival. However, stressors such as temperature, light, and humidity influence plant growth and the production of secondary metabolites. In some species, drought increases the content of phenolic acids and flavonoids. On the other hand, elevated CO_2 levels reduce the concentration of monoterpenes, while increasing that of phenolic acids [10]. In *Salvia officinalis* L., temperature has been found to correlate positively with the amount of sesquiterpenes and negatively with that of monoterpenes [17].

Studies on the cultivation of *Salvia miltiorrhiza* Bunge in different regions of China have shown that soil physicochemical properties and genotype influence the quantity of active components such as diterpenoids and phenolic acids [18, 19]. Currently, climate change is affecting abiotic environmental factors such as irregular rainfall, temperature fluctuations, and variations in humidity. These changes cause both biotic and abiotic stress, which impact the development of plant species and the production of secondary metabolites, compounds that are useful for evaluating the quality of medicinal and aromatic plants. As a result, recent research has focused on improving the growth environment through the use of non-pathogenic endophytes [14]. Endophytes improve various conditions of biotic and abiotic stress in plants. They contribute to the production of phytohormones, enzymes, and secondary metabolites that are vital for plant growth and stress mitigation. Moreover, these bacteria and fungi enhance nutrient availability for plants [20]. In this regard, a recent study demonstrated that the combined application of rhizobacteria and arbuscular mycorrhizal fungi to *Codonopsis pilosula* (Franch) Nannf., a plant widely used in traditional Chinese medicine for its healing and nutritional properties, increased plant height and leaf area and significantly enhanced the content of bioactive secondary metabolites [21].

4. Conclusions and perspectives

The study of the growth and development of medicinal plants, as well as the biotic and abiotic factors that influence the production of secondary metabolites, is essential for optimizing their use in fields such as medicine, agriculture, and industry. It has been shown that these factors not only affect plant physiology but also significantly modulate the quality and quantity of bioactive compounds produced by these species.

Understanding these dynamics enables the development of more efficient and environmentally friendly agronomic practices, with a focus on sustainable production. It also facilitates the selection of optimal cultivation conditions to maximize the concentration of target metabolites. This, in turn, contributes to the standardization and valorization of products derived from medicinal plants.

Looking ahead, there is a growing need to continue research that integrates multidisciplinary approaches, including biotechnology, genetics, metabolomics, and environmental studies. These efforts will help deepen our understanding of the molecular mechanisms that regulate the synthesis of these compounds. Furthermore, it is crucial to explore sustainable production models that support the rational cultivation and use of medicinal plants while also promoting the conservation of biodiversity, particularly in regions where medicinal and aromatic species are part of the cultural, medicinal, and traditional heritage.

Author details

Mariana Palma-Tenango[1,2], Eva Aguirre-Hernández[3] and Marcos Soto-Hernández[4*]

1 Posgrado en Fisiología Vegetal, Recursos Genéticos y Productividad, Colegio de Postgraduados-Campus Montecillo, Texcoco, Mexico

2 Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, Mexico

3 Laboratorio de Productos Naturales, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, Mexico

4 Posgrado en Botánica, Colegio de Postgraduados-Campus Montecillo, Texcoco, Mexico

*Address all correspondence to: msoto@colpos.mx

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Chapter 2

Adaptation of the Chasmophyte *Crithmum maritimum* to High-Salinity Conditions

Ivica Blažević, Azra Đulović, Franko Burčul, Josip Tomaš, Petra Brzović, Sanja Radman, Olivera Politeo and Ivana Generalić Mekinić

Abstract

Salt tolerance in plants is essential for sustainable agriculture on saline soils, a growing concern as climate change intensifies soil salinization globally. Halophytes, naturally salt-tolerant plants, possess unique characteristics that allow them to thrive in high-salinity environments. This review examines the salt tolerance mechanisms in *Crithmum maritimum* L. (sea fennel). This plant employs various strategies to manage osmotic, ionic, and oxidative stress, key among them being the accumulation of osmolytes, such as proline and glycine betaine, which help maintain balance and protect cellular structures under saline conditions. Proline accumulation, for example, aids osmotic adjustment across salt gradients. Additionally, halophytes bolster antioxidant enzyme activities—including superoxide dismutase, catalase, and peroxidase—to neutralize reactive oxygen species, thus minimizing oxidative damage. Secondary metabolites, such as phenolic acids and flavonoids, enhance antioxidative defenses, while compounds such as carotenoids help maintain osmotic and cellular stability. Salinity also induces shifts in fatty acid composition, with increased linoleic acid enhancing membrane stability. The variability of essential oil produced by *C. maritimum* under salt stress suggests nutraceutical and agricultural potential. These findings highlight sea fennel as sustainable option for saline agriculture, offering resilience and productivity in salt-affected soils and bolstering future food security.

Keywords: *Crithmum maritimum* L., sea fennel, Apiaceae, halophytes, salinity stress, osmolytes, secondary metabolites

1. Introduction

Traditional agriculture is facing increasing water shortages. Freshwater makes up only 2% of all water on Earth, and there is no access to most of this small percentage as it is trapped in glaciers. Additionally, water pollution is a significant issue in many regions. Salinity is among the most widespread constraints in irrigated agriculture, affecting up to 7% of the world's total land area and about one-third of irrigated lands [1].

Climate change, rising sea levels, and growing drought are predicted to make matters worse and increase soil salinization in many regions of the world. This poses a threat to conventional crops, which cannot withstand significant salinization. Due to their ability to provide sustainable yields in saline environments, salt-tolerant plants are gaining agronomic importance as the world's population continues to rise and water supplies become more scarce and unaffordable.

Halophytes exhibit a high degree of variability, which has led to controversy in their classification and even their definition. Over time, different definitions of halophytes have emerged, classifying halophytes based on their salt tolerance levels, physiological and anatomical traits, and their mechanisms for coping with drought. Salt stress mainly induces osmotic, oxidative, and ionic stresses in plants. In response, plants detect these stresses and activate complex signaling pathways, allowing them to accumulate compounds that aid in osmotic adjustment while preserving ionic and redox balance, ultimately leading to salt tolerance [2]. Regarding tolerance to salinity stress, plants can be categorized into two groups: glycophytes and halophytes. Glycophytes, such as those discussed by Haro et al., exhibit sensitivity to salt, even at relatively low concentrations like 25–50 mM NaCl [3]. In contrast, halophytes demonstrate significantly higher tolerance to NaCl. As highlighted by Zhu and Flowers and Colmer, approximately 2% of all plant species are halophytes, capable of withstanding much higher concentrations of NaCl ranging from 200 to 1000 mM [1, 4]. Among others, their survival in such extreme environments is attributed to their capacity for osmotic adjustment, achieved through the accumulation of both inorganic ions, such as Na^+ and Cl^-, and a diverse array of low-molecular-weight organic compounds collectively referred to as osmolytes (**Figure 1**) [5]. These organic compounds, which include compounds such as proline, glycine betaine, sucrose, sorbitol, myo-inositol,

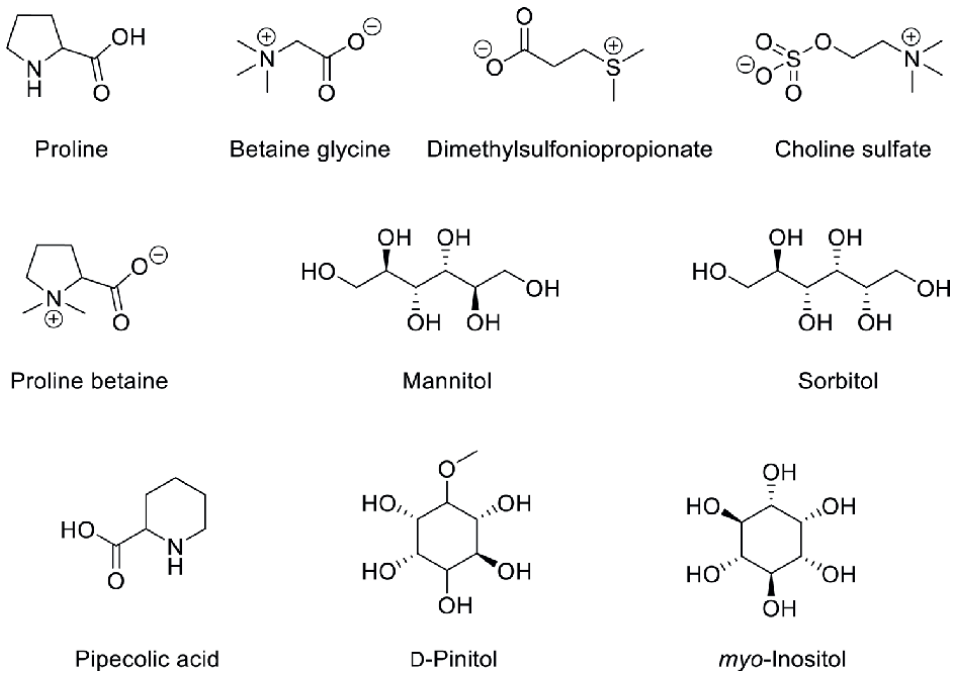


Figure 1.
Structures of common osmolytes identified in halophytes [5].

are accumulated in high amounts in the cytoplasm. This accumulation counterbalances the osmotic pressure exerted by the high concentrations of Na^+ and Cl^- sequestered in the vacuole, preventing cellular dehydration and maintaining turgor pressure [5]. Interestingly, different halophyte families tend to specialize in the synthesis and accumulation of particular osmolytes, reflecting their evolutionary adaptations to specific stress conditions. This family-specific osmolyte production not only facilitates effective osmotic regulation but also underscores the diversity of mechanisms employed by halophytes to thrive in saline environments, as highlighted by Slama et al. [5]. These adaptations make halophytes a critical subject of study for understanding plant resilience to abiotic stresses and for developing strategies to enhance crop tolerance in salt-affected soils.

In addition to osmolytes, studies have shown that primary plant metabolism undergoes significant adjustments in saline conditions. Specifically, the levels of sugars and free amino acids, as well as the synthesis of lipophilic carotenoids and sterols, are heightened in saline environments compared to non-saline conditions [6, 7]. Globally, more than 2500 plant species have been identified as halophytes, distributed across a wide range of plant families. These include Aizoaceae, Apiaceae, Asteraceae, Brassicaceae, Chenopodiaceae, Combretaceae, Elaeagnaceae, Fabaceae, Lamiaceae, Liliaceae, Malvaceae, Moraceae, Palmae, Plantaginaceae, Plumbaginaceae, Poaceae, Rubiaceae, Tamaricaceae, Verbenaceae, and Zygophyllaceae [8]. Among these, Apiaceae, also known as Umbelliferae, is a family of aromatic flowering plants, named after the genus *Apium*. It is commonly referred to as the celery, carrot, or parsley family, or simply as umbellifers. As one of the largest plant families, it ranks 16th among flowering plants, encompassing about 446 genera, and over 3800 species. Beach silvertop (*Glehnia littoralis*), carrot (*Daucus carota*), celery (*Apium graveolens*), coastal hog fennel (*Peucedanum japonicum*), fennel (*Foeniculum vulgare*), sea fennel (*Crithmum maritimum*), and sea holly (*Eryngium maritimum*) are some of the well-known and economically and medicinally important halophytes of this family.

Research on halophytes is important for understanding salt tolerance mechanisms in plants. This knowledge will be vital as climate change and population growth challenge our ability to sustain agricultural productivity in the future. This review focuses on *Crithmum maritimum*, one of the most commonly studied halophytic species of the Apiaceae family, and discusses physiological and biochemical changes under stress conditions.

2. *Crithmum maritimum*

C. maritimum (**Figure 2**) is a perennial halophyte classified as a chasmophyte. It is the only species within the genus *Crithmum* and is commonly found in coastal regions, rocky slopes, and sandy terrain [9]. This facultative halophyte is widespread across various European countries, and its resilience to saline and harsh environments has sparked interest for its potential in sustainable agriculture [10, 11].

In many parts of the world, sea fennel is used as an important food ingredient, adding flavor and nutrition to various dishes. Its leaves are consumed fresh in salads or pickled, while dried leaves are used as a spice and coloring agent. Additionally, the flower tops are popular as the components of herbal teas [12]. The aerial parts can be also used in beverages, making it a versatile addition to the culinary scene [10]. Historically, its high vitamin C content made it a popular choice among seafarers as an effective means of preventing scurvy. Nowadays, it has been rediscovered as a

Figure 2.
*Sea fennel (*Crithmum maritimum *L., photo by Ivana Generalić Mekinić).*

versatile ingredient in modern culinary creations. Its aromatic leaves are featured in a variety of Mediterranean dishes, offering unique flavors and enriching contemporary recipes. Products such as preserved sea fennel in extra virgin olive oil and pesto-like sauces blend its traditional heritage with innovative uses, highlighting its growing appeal in both home kitchens and gourmet cuisine [13].

In addition to its culinary applications, sea fennel is also valued for its health beneficial properties, including diuretic, digestive, laxative, and purgative effects, underscoring its potential in traditional medicine [14]. Despite its benefits and adaptability to saline and water-deficit soils, *C. maritimum* remains underutilized in commercial cultivation. Given its ability to thrive in diverse habitats, it is a promising alternative food crop that can contribute to food security in arid regions.

The dispersal of *C. maritimum* is facilitated by hydrochory, which is attributed to its spongy fruits that can float in sea water for extended periods, possibly up to a year [15, 16]. This floating characteristic allows the seeds to be carried out by sea currents enabling the plant to colonize new coastal areas. After several days of floating, the dispersal units have the potential to be deposited onto another cliff by waves, establishing themselves in micro-niches with saline conditions, thus ensuring the plant's persistence and spread across suitable habitats.

2.1 Physiological changes due to salt stress

2.1.1 Effects of salinity on growth and biomass distribution

Studies have shown that *C. maritimum* exhibits notable physiological adaptations when exposed to different concentrations of salt. Okusanya studied the dry matter distribution in leaves, stems, and roots of seedlings cultivated in sand and watered

with different concentrations of sea water [17]. The findings showed a significant increase in growth when exposed to 10% sea water (ca. 90 mM NaCl) and a substantial reduction at 30%. Generally, the results showed a decrease in leaf weight ratio, and an increase in root and stem weight ratios, particularly at the 10% sea water concentration, indicating an adaptation to optimize water and nutrient absorption.

Further research by Ben Amor et al. showed that root and shoot biomass, root length, and leaf number reached their maximum at 50 mM NaCl, with a marked decrease observed at 200 mM NaCl [18]. This aligns with the findings from Ben Hamed, who classified *C. maritimum* as a facultative halophyte due to its reduced growth at higher salinity [19]. Significant reductions, including 50% decrease in shoot dry weight, leaf surface area, and leaf number, were noted at 150 mM NaCl. The physiological response of *C. maritimum* to salinity involves a range of adjustments, including ion regulation and biomass distribution. Ben Hamed et al. noted that under saline conditions (100 and 300 mM NaCl), roots biomass and growth were more susceptible to NaCl than leaves, which suggested a prioritization of resources to maintain above-ground function under stress. This ability to manage water and ion uptake efficiently is crucial for the plant's survival in saline environments [20].

Plaza et al. conducted a 60-day pots experiment using a peat: perlite mixture (80:20, v/v) and nutrient solutions with different salt concentrations (100, 200, and 300 mM) [21]. The study found that *C. maritimum* responded well to the increasing salinity levels with no differences observed in stem dry weight, leaf fresh and dry weight, or total biomass. This indicates a level of resilience to varying saline conditions.

Similarly, Boestfleisch and Papenbrock [22] observed changes in biomass under mild salinity stress, expressed in Practical Salinity Units (PSU, 1 g of salt per 1000 g of H2O), ranging from 0 to 15 PSU over 3 weeks. While salinity did not significantly inhibit biomass production during the first week, a trend of reduced biomass was seen in plants grown at 10 and 15 PSU, suggesting that prolonged exposure to mild salt stress can negatively affect plant growth [22].

Jiménez-Becker et al. further evaluated the effects of different salinity treatments (100, 200, and 300 mM NaCl) on *C. maritimum* [23]. The study found that fresh and dry weight of the plant material remained largely unaffected by tested salt levels. However, a 41% decrease in water content was observed in plants exposed to the highest salt concentration (300 mM NaCl), compared to those treated with 100 mM NaCl. Interestingly, the highest salt concentrations did not lead to oxidative damage in the leaves, nor were there changes in the root-to-shoot dry weight ratio, indicating a robust plant physiological adaptability.

2.1.2 Salinity thresholds and survival rates

Salinity thresholds for survival have also been studied. Hamdani et al. investigated the effects of elevated concentrations of NaCl on young seedlings over a 6-week period, ranging from 0 to 512 mM [24]. It was observed that at NaCl concentrations exceeding 85 mM, plant survival began to decline, while growth was significantly impacted at concentrations surpassing 341 mM. At the highest tested concentration (512 mM NaCl), survival decreased to 58%. Additionally, there was a significant reduction in shoot height observed at concentrations exceeding 341 mM, reaching a maximum reduction of 18% compared to the control group after 6 weeks. Similarly, Castillo et al. observed substantial decreases in both above-ground and below-ground biomass at 500 mM NaCl, with reductions of 77 and

68%, respectively, and a 33% decrease in plant height, indicating a critical threshold for salinity tolerance in *C. maritimum* [25].

2.1.3 Germination and seedling performance

Seed germination and early growth are critical stages for plant establishment. Nimac et al. [26] studied the effect of seed priming on germination under different salt concentrations. Results showed that higher levels of NaCl had negative effect on both the percentage of germination and early seedling growth. However, primed seeds exhibited better performance compared to non-primed seeds, especially at lower salinity levels [26]. These findings suggest that seed priming, using 50 mM NaCl and distilled water, could be employed to accelerate sea fennel seed germination and enhance early seedling growth. Additionally, Strumia et al. found that seedling roots of *C. maritimum* develop strong adhesion to rocky substrates, preventing them from rolling off the cliff, highlighting an essential trait for survival in its natural habitat [27].

2.2 Biochemical changes due to salt stress

The biochemical response of *C. maritimum* to salt stress involves producing specific organic compounds, such as osmolytes and secondary metabolites, which stabilizes cells under stress conditions. These compounds help mitigate the effects of salinity by maintaining cellular function and protecting against oxidative damage. Additionally, to counteract oxidative stress, which is another consequence of salinity, plants generate antioxidants [28]. These antioxidants can be categorized into two types: antioxidant enzyme systems and non-enzymatic compounds such as ascorbate, glutathione, carotenoids, and phenolic compounds.

2.2.1 Osmolyte accumulation for osmotic balance

Salinity induces both hyperosmotic and hyperionic stresses in plants, prompting the production of osmolytes. These compounds aid in osmotic balance, protein stabilization, and membrane protection.

Boestfleisch and Papenbrock highlighted that proline accumulation is a crucial biochemical adaptation in *C. maritimum* under saline stress, acting as an osmoprotectant to help the plant manage increased salinity [22]. Proline is synthesized primarily through the glutamate pathway (**Figure 3**); glutamate is first converted to glutamate semialdehyde by the enzyme pyrroline-5-carboxylate synthetase (P5CS), which then spontaneously forms pyrroline-5-carboxylate (P5C) and is reduced to proline by P5C reductase (P5CR) [29, 30]. Proline breakdown occurs in the mitochondria, where proline dehydrogenase (ProDH) and P5C dehydrogenase (P5CDH) convert proline back to glutamate [30, 31]. Additionally, ornithine contributes as a precursor to proline synthesis *via* transamination to P5C by ornithine δ-aminotransferase (OAT) [32, 33]. Proline plays an essential role in relieving cytoplasmic acidosis, maintaining $NADP^+$/NADPH balance, and acting as a sink for excess reductants, thus supporting respiration and photosynthesis during stress [34]. Thus, proline is crucial for plants to manage abiotic stress by maintaining cellular function and metabolism.

The study by Boestfleisch and Papenbrock revealed that *C. maritimum* had a significant rise in proline levels, especially at a salinity of 15 PSU (ca. 250 mM NaCl), with noticeable proline accumulation beginning at 48 hours of exposure

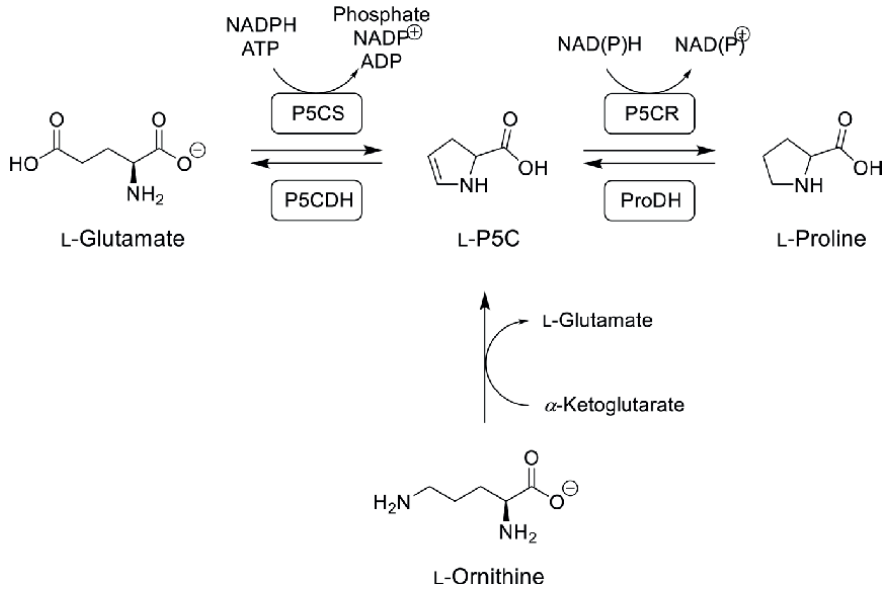


Figure 3.
The metabolic pathway of L-proline through glutamate and ornithine; pyrroline-5-carboxylate synthase (P5CS); pyrroline-5-carboxylate (P5C); ornithine aminotransferase (OAT); pyrroline-5-carboxylate reductase (P5CR); proline dehydrogenase (ProDH); P5C dehydrogenase (P5CDH) [29].

and continuing over various time intervals (96, 168, 336, and 504 hours) [22]. After 504 hours, proline levels at 15 PSU had increased ca. 5-fold, that is, from 30.96 to 150.23 μmol g^{-1} fresh plant material (FW). This sustained elevation in proline concentration is essential for counteracting osmotic stress, as it aids in water retention within cells. This mechanism allows *C. maritimum* to maintain cellular stability and function, ensuring its survival in saline environments. Although higher salinity levels can generally reduce biomass, the significant increase in proline helps mitigate stress, reflecting an effective strategy that the plant employs to endure adverse conditions. This adaptive response allows the plant to survive and continue functioning despite environmental challenges. *C. maritimum*'s capacity to accumulate proline highlights its potential for saline agriculture, where its salt tolerance could support sustainable farming practices.

Hamdani et al. revealed that when exposed to increasing salt concentrations, *C. maritimum* seedlings activated several physiological responses, notably the accumulation of key osmolytes such as proline, glycine betaine, and soluble sugars [24]. These compounds were crucial in maintaining cellular water balance and protecting cellular structures from the damaging effects. At the beginning, proline concentration was low in both leaves and roots (ca. 40 μmol g^{-1} FW). Proline concentration in leaves peaked at 427 mM NaCl after 2 and 6 weeks, reaching 162 μmol g^{-1} FW, but decreased at 512 mM. This indicated a threshold at 427 mM where proline accumulation is maximized. In contrast to leaves, proline continued to accumulate in roots across increasing NaCl levels, even at the highest concentration of 512 mM, suggesting its consistent protective role in roots under extreme salinity. The study observed a marked rise in root proline between 256 and 341 mM NaCl after 6 weeks, unlike in leaves where the increase peaked earlier.

Glycine betaine also showed a threshold accumulation pattern, similar to that of proline. This quaternary ammonium compound is synthesized mainly from

choline (**Figure 4**), which undergoes conversion to betaine aldehyde and then to glycine betaine *via* the sequential action enzymes choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH), respectively [35, 36].

Hamdani et al. observed that glycine betaine significantly increased with rising salinity, particularly between 256 and 341 mM NaCl, but declined at 512 mM [24]. This drop at high concentrations implies a stress limit for glycine betaine synthesis or stability in leaves. Contrarily, glycine betaine concentrations in roots remained high even at 512 mM NaCl, showing two distinct rises: one between 85 and 171 mM, and another between 256 and 341 mM NaCl. These findings revealed that both proline and glycine betaine significantly increased with salinity, particularly after prolonged exposure, although accumulation patterns and limits varied between leaves and roots at high salinity levels. The study showed that proline and soluble sugars accumulated significantly, especially in leaves, as salinity increased, while roots displayed higher glycine betaine concentrations, suggesting a tissue-specific adaptive strategy. Osmolyte levels peaked at salinity levels of 256–341 mM NaCl, enabling the plants to maintain cellular stability and minimize damage. This pattern of accumulation suggests that roots rely heavily on these osmolytes to maintain functionality under prolonged and high salinity stress, while leaves reach a synthesis limit.

The study revealed that soluble sugars, along with proline and glycine betaine, significantly contributed to *C. maritimum*'s response to elevated salinity, especially in its leaves. As salinity levels increased, soluble sugars accumulated markedly, helping to maintain osmotic balance and protect cells under saline stress. Their concentration in the leaves rose substantially with increasing NaCl levels, reaching a maximum between 256 and 341 mM NaCl, followed by a slight decline at the highest concentration of 512 mM. This threshold (256–341 mM) represents a crucial range for osmotic adjustment in leaves, supporting cellular stability and helping to offset stress effects on growth. Unlike in leaves, the accumulation of soluble sugars in roots did not display a sharp decrease at 512 mM NaCl, although peak levels were also reached at similar salinity thresholds. Together, these osmolytes allow *C. maritimum* to balance osmotic pressure effectively, with each playing distinct roles: Proline and glycine betaine enhance cellular protection in roots and leaves, while soluble sugars provide immediate osmotic stability in leaves. This coordinated response across tissues enables the plant to withstand high salinity levels by maintaining water balance and minimizing salt-induced damage.

In the study by Jiménez-Becker et al., *C. maritimum* responded to salinity stress by accumulating osmoprotectants, specifically proline and soluble sugars, in its tissues [23]. Proline content in the leaves increased by approximately 65% at 300 mM NaCl compared to 100 mM NaCl, contributing to the osmotic adjustment. Additionally, soluble sugars were found to accumulate variably across plant organs, aiding in osmoprotection and providing carbon storage. Under elevated salinity conditions, the roots

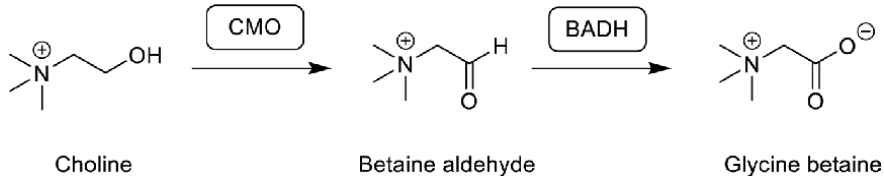


Figure 4.
Biosynthesis of glycine betaine in higher plants (CMO—choline monooxygenase, BADH—betaine aldehyde dehydrogenase).

showed decrease of soluble sugar concentrations, while their concentration increased in the leaves, supporting *C. maritimum*'s resilience by maintaining cellular stability and countering osmotic stress.

Colak Esetlili et al. also reported specific data on osmolyte accumulation in *C. maritimum* under varying salinity levels [37]. The study found that at 100 mM NaCl, proline content in the leaves decreased by 58.82% compared to control plants, suggesting limited osmotic stress response at this concentration. However, as salinity increased, proline levels surged: At 200 mM NaCl, proline content increased by 316.12%, and at 300 mM NaCl, it rose by 214.25% relative to control plants. This sharp rise at higher salinity levels highlights proline's role in counteracting severe osmotic stress. Glycine betaine content also showed substantial increases under higher salinity. At 200 mM NaCl, glycine betaine content in the leaves rose by 101.41% relative to plants at 100 mM NaCl, while at 300 mM NaCl, it increased by 123.64%. These values indicate that glycine betaine serves as a secondary osmolyte, providing osmotic adjustment and supporting antioxidant defenses as salinity stress intensifies. The data suggest that 200 mM NaCl is a critical threshold where osmolyte accumulation becomes vital for maintaining osmotic balance and cellular stability in *C. maritimum*, enabling it to withstand high saline conditions.

2.2.2 Role of antioxidant systems and secondary metabolites

The antioxidant system is crucial in plants for mitigating the damaging effects of reactive oxygen species (ROS), which accumulates under stress conditions such as salinity, drought, extreme temperatures, and herbivore attack. ROS, including hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet-}$), and hydroxyl radicals (•OH), is highly reactive species that can cause oxidative damage to cellular structures, proteins, lipids, and nucleic acids. Under salt stress, plants experience osmotic and ionic imbalances that lead to excessive ROS production, particularly in chloroplasts and mitochondria, where active photosynthesis and respiration occur. Plants have evolved a complex antioxidant defense system to scavenge and neutralize ROS, thereby preventing cellular damage and ensuring survival under stress. This system includes both enzymatic and non-enzymatic antioxidants. The enzymatic antioxidant system includes superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase. Research has demonstrated that salt-tolerant plants enhance their salt resilience by strengthening these antioxidant defenses [38, 39]. Additionally, non-enzymatic antioxidants such as glutathione, ascorbic acid, carotenoids, and phenolics play a crucial role in neutralizing ROS within plants [40]. Together, these antioxidants form an integrated system that not only controls ROS levels, but also supports signaling pathways essential for stress responses and adaptation. In halophytes, which are naturally salt-tolerant plants, robust antioxidant defenses are particularly vital, as they allow these plants to thrive in environments, such as saline soils.

2.2.2.1 Antioxidant systems

Studies by Ben Amor highlighted that the tolerance of *C. maritimum* was linked with maintaining tissue hydration, selective K^+ versus Na^+ accumulation, and enhanced antioxidant enzyme activity including superoxide dismutase (SOD: EC 1.15.1.1), catalase (CAT: EC 1.111.1.6), and peroxidase (POD: EC 1.111.1.7) [18]. These enzymes limit the buildup of ROS, thus preventing oxidative damage. At the highest salinity level tested (200 mM NaCl), *C. maritimum* experienced disruptions

in mineral nutrition within its shoots, as concentrations of Ca^{2+}, Mg^{2+}, and K^{+} significantly decreased, while the roots were less impacted. Measurements of lipid peroxidation indicated that malonyldialdehyde (MDA) levels, a marker of oxidative stress, were lower in both roots and shoots of plants grown at an optimal salinity of 50 mM NaCl compared to control plants. This reduction was attributed to the enhanced activity of antioxidant enzymes, including SOD, CAT, and POD, particularly in the shoots. At 200 mM NaCl, the reduced plant growth was linked to a decrease in the efficiency of these protective enzymes. However, MDA levels in both roots and shoots remained comparable to those in the control group, suggesting that the radicals generated in response to stress did not primarily damage cell membrane lipids at this salt concentration. This contrasts with findings from Ben Hamed et al. who studied increase of H_2O_2 and MDA in *C. maritimum* roots and leaves under varying salinity conditions (0, 100, and 300 mM) [20]. Significant oxidative stress was observed by marked increase of MDA at higher salt levels (300 mM), particularly in roots. The antioxidant enzyme activities also varied between roots and leaves, while SOD activity decreased in both roots and leaves at high salinity, and ascorbate peroxidase (APX) increased in roots, but remained unaffected in leaves at 100 mM NaCl.

Additionally, CAT and glutathione reductase activities declined significantly in leaves at 300 mM NaCl, but CAT activity was not affected in roots. The concentrations of non-enzymatic antioxidants, like ascorbic acid, were markedly higher in leaves compared to roots under control conditions and decreased with increasing salinity, particularly in leaves. These findings suggest that *C. maritimum* relies on different antioxidant mechanisms in roots and leaves to mitigate the effects of salt-induced oxidative stress, with roots showing a pronounced response in APX activity and leaves relying more on high constitutive antioxidant defense levels.

Hamdani et al. examined the antioxidant responses of *C. maritimum* to salinity stress, identifying key mechanisms that help the plant counter oxidative damage induced by ROS [24]. As salinity levels rose, *C. maritimum* demonstrated a notable decrease in H_2O_2 levels in leaves, suggesting an efficient reduction of ROS to prevent cellular damage. The study also observed a significant increase in ascorbic acid, a primary non-enzymatic antioxidant, which reached its highest concentration at 512 mM NaCl, underscoring its vital role in ROS scavenging and redox balance. Additionally, CAT activity rose with salinity increase from 256 to 427 mM NaCl, decomposing H_2O_2 into water and oxygen, and further protecting the plant's cells from oxidative stress. However, a slight reduction in CAT activity at 512 mM NaCl indicated a possible threshold where antioxidant defenses may begin to decline. These antioxidant activities, particularly in the leaves, work alongside osmolyte accumulation to support *C. maritimum's* cellular stability and function under high salinity, highlighting the synergistic role of the antioxidant system in enhancing salt tolerance in this halophyte.

In a separate study, Gil et al. examined the antioxidant defense activity in *C. maritimum* leaves from two different environments: a coastal region exposed to high salinity due to marine influence and an inland area without such salinity influence [41]. The findings revealed that plants growing in the coastal, salt-affected zone, exhibited markedly higher activities of key antioxidant enzymes (SOD, CAT, and glutathione peroxidase). Additionally, these plants had increased levels of polyphenols and reduced glutathione compared to those from the inland region. These findings suggest that *C. maritimum* has adapted its antioxidant defense system to mitigate salinity-induced oxidative stress, thereby enabling it to thrive in environments with varying degrees of salinity.

Colak Esetlili et al. also observed that *C. maritimum* employs a dynamic antioxidant system to combat the oxidative stress associated with salinity [37]. The primary antioxidant enzymes analyzed were SOD, CAT, and peroxidase (POX), each of which plays a distinct role in neutralizing ROS. At salinity of 100 mM NaCl, there was a slight reduction in POX activity, while SOD and CAT levels remained stable, suggesting minimal oxidative stress at this level. However, as salinity increased, the plant's antioxidant response shifted significantly.

At 200 mM NaCl, enzyme activity levels of SOD, CAT, and POX dropped by 28.95, 45.45, and 54.37%, respectively, indicating that the antioxidant system may reach a limit. In contrast, exposure to 300 mM NaCl triggered a notable surge in enzyme activity, where SOD, CAT, and POX were increased by 112.91, 63.64, and 69.97%, respectively. This heightened response suggests that *C. maritimum* activates a robust antioxidant defense at high salinity to manage excessive ROS production effectively.

The study also reported increased antiradical activity at elevated NaCl concentrations, with the antiradical potential of leaves increasing by approximately 73.43% at 200 mM NaCl and 101.41% at 300 mM NaCl. This response likely involves other antioxidant compounds, such as phenolics, which complements enzymatic defenses and provides additional ROS-scavenging capacity. Together, these findings indicate that *C. maritimum* relies on a threshold-dependent activation of its antioxidant system, with significant upregulation at high salinity levels to maintain redox balance, protect cellular structures, and ensure survival in saline environments [37].

In conclusion, *C. maritimum* demonstrates strong salt tolerance through mechanisms such as selective K^+ retention over Na^+, maintaining cellular hydration, and boosting antioxidant defenses to counteract oxidative stress. Studies show that at salinity levels from 50 to 256 mM NaCl, the plant enhances antioxidant enzymes (SOD, CAT, APX) and non-enzymatic antioxidants (like ascorbic acid), which effectively limits ROS and oxidative damage. However, at higher salinity levels (300–512 mM NaCl), antioxidant activity and mineral balance begin to decline, resulting in reduced growth. These adaptations illustrate *C. maritimum*'s resilience and efficiency in managing oxidative stress across varying saline conditions.

2.2.2.2 Secondary metabolites

C. maritimum produces a range of secondary metabolites that contribute to its biological and stress-resistance properties (**Figure 5**). Recent studies have provided in-depth chemical profiles, highlighting the diversity of bioactive compounds influenced by geographic location along the Croatian coast. For instance, recently Generalic Mekinic et al. reported the chemical profile of *C. maritimum* from several Croatian coastal populations, highlighting a diverse range of bioactive compounds influenced by location [42]. Essential oil yields ranged from 0.04 to 0.88%, with limonene, sabinene, γ-terpinene, and terpinen-4-ol as primary components, varying significantly with environmental factors. In Radman et al., essential oil content in *C. maritimum* flowers varied even more substantially from 0.19 (Cavtat) to 1.87% (Pag), where limonene dominated (up to 96.78% in Cavtat) [43]. Sabinene and γ-terpinene were also notable in some regions, reaching up to 31.43% in Pag.

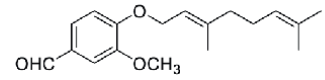
Both studies highlighted abundant phenolic compounds, particularly chlorogenic acid and its derivatives, with significant location-based and plant part-based differences. For example, chlorogenic acid reached 248.44 mg/g in Korčula leaf samples [42] and 13.27 mg/g in Cavtat flower samples [43].

Carotenoids such as lutein and β-carotene also varied, with lutein concentrations peaking at 435.4 mg/kg in Pelješac sea fennel leaf sample, also demonstrating the influence of environmental factors [42].

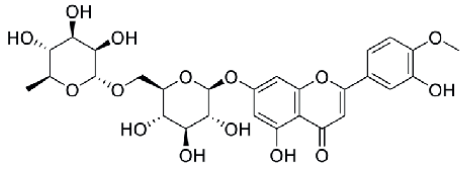
Essential fatty acids, particularly linoleic and linolenic acids, were prominent and key to the plant's saline stress resilience. Additionally, α-tocopherol was the most abundant tocopherol, with its highest concentration (73.62 mg/kg) recorded in Pag flower sample, which again suggests biological potential driven by geographical diversity [43].

Additionally, *C. maritimum* contains polyacetylenes, such as falcarinol and falcarindiol, that have been recognized for their antimicrobial and anti-inflammatory properties, suggesting a protective role against pathogens and environmental

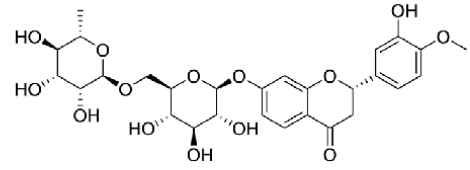
Falcarinol (R=H)
Falcarindiol (R=OH)



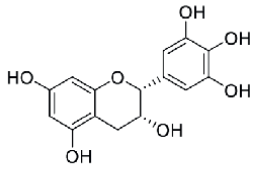
O-Geranylvanillin



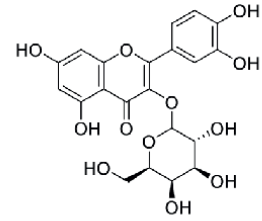
Diosmin



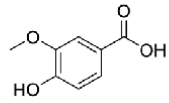
Hesperidin



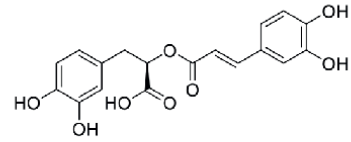
Epigallocatechin



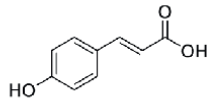
Quercetin-3-galactoside



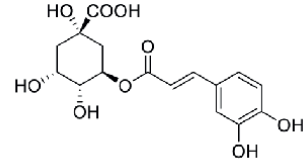
Vanillic acid



Rosmarinic acid



p-Coumaric acid



Chlorogenic acid

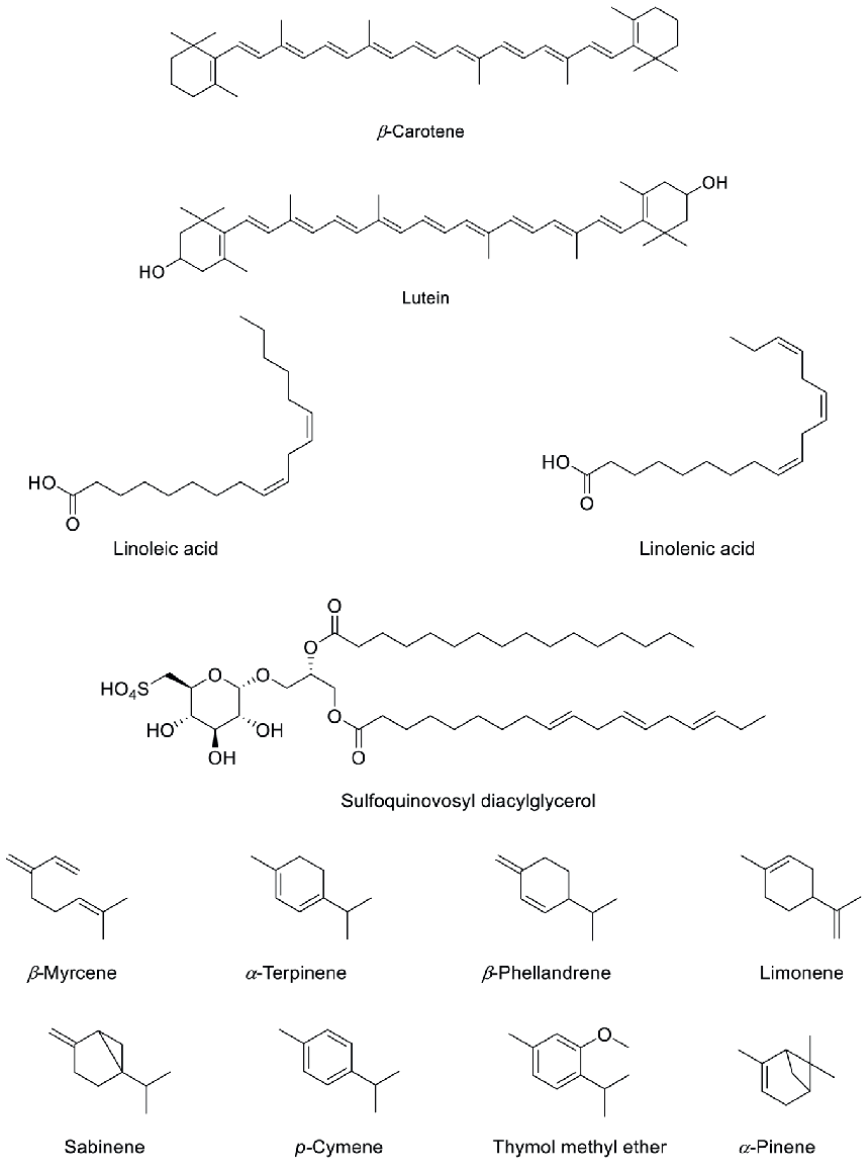


Figure 5.
Chemical structures of compounds found in Crithmum maritimum.

stressors [44, 45]. Many edible Apiaceae plants, such as carrots, celery, and parsley, are known to contain health-promoting aliphatic C17-polyacetylenes [46]. However, detailed research on polyacetylenes specifically in *C. maritimum*, or on similar compounds within related species, remains limited. The potential role of these compounds in enhancing cellular stability in saline conditions through ROS modulation and antioxidant support has not been extensively studied, making this an area with promising research potential. Additionally, the plant produces a rare aromatic compound, *O*-geranylvanillin, which was initially identified as a synthetic product, highlighting the plant's unique chemical profile [45]. This rich profile, encompassing high levels of limonene, chlorogenic acid, lutein, α-tocopherol, and

other health-beneficial constituents with positive properties, positions *C. maritimum* as a valuable source of antioxidants and bioactive compounds for applications in food technology, pharmacology, and cosmetic industry.

The study by Cornara et al. focused on the micromorphological and chemical analysis of the leaves of *C. maritimum* and detected significant amounts (0.6% w/w) of flavonoids hesperidin and diosmin [47]. These compounds are known for their antioxidant and anti-inflammatory properties, which help protect the plant from oxidative stress. Using scanning electron microscopy (SEM) and energy-dispersive X-ray (EDX), the study detected needle-like crystals of hesperidin and diosmin concentrated around the vascular bundles. Such deposits are similar to those observed in other plants that also endure stressful environments, suggesting that these flavonoids may be part of a defensive strategy to counteract the effects of salinity. Additionally, high-performance liquid chromatography (HPLC) confirmed that these flavonoids are present in significant and comparable concentrations, enhancing the plant's resilience.

The study by Meot-Duros and Magné focused on the antioxidant properties and phenolic content of *C. maritimum*, particularly under saline conditions [44]. The research identified chlorogenic acid as a prominent phenolic compound in the leaves, contributing significantly to the plant's antioxidant activity. The study highlighted that *C. maritimum* accumulates higher levels of chlorogenic acid when exposed to more stressful conditions, such as those found in sandy, nutrient-poor, and saline environments. For instance, plants in sand hills, where salinity stress was intensified by sea sprays and nutrient scarcity, showed chlorogenic acid levels 18.8–27.9 mg/g DW, in contrast to the lower concentrations of 3–10 mg/g DW found in cliff plants. This suggests that the production of chlorogenic acid is part of the plant's adaptive response to salinity stress. The study also assessed the plant's antioxidant activity using DPPH and ABTS assays, demonstrating that the leaves of *C. maritimum* exhibit strong radical-scavenging abilities. The antioxidant activity was closely correlated with the levels of phenolic compounds, particularly chlorogenic acid, which helps neutralize ROS generated under stress conditions. These findings underscore the plant's potential as a natural source of antioxidants and suggest that its secondary metabolites play a crucial role in protecting it from the damaging effects of salinity stress.

The study by Jallali et al. examined the phenolic composition and antioxidant activity of *C. maritimum*, particularly in the context of how these properties help the plant adapt to salinity stress [11]. The research identified a range of phenolic compounds, with major being epigallocatechin, vanillic acid, rosmarinic acid, quercetin-3-galactoside, and *p*-coumaric acid, which are known for their strong antioxidant effects. These compounds play a crucial role in helping the plant manage oxidative stress, a common challenge in saline environments. The study found that the production of these antioxidants varied across different plant growth stages (phenophases), with higher concentrations observed during the flowering period. This suggests that *C. maritimum* enhances the synthesis of these protective compounds as a defense mechanism against stressors, such as salinity and increased exposure to UV radiation. For example, during the flowering stage, the total phenolic content was 8.27 mg GAE/g DW in conventional maceration extracts and 4.33 mg GAE/g DW in Soxhlet extracts, both prepared using 80% aqueous acetone. In contrast, lower phenolic levels were observed during the vegetative stage, with 7.16 mg GAE/g DW in maceration extracts and 3.68 mg GAE/g DW in Soxhlet extracts. This seasonal increase suggests that *C. maritimum* enhances the synthesis of these protective compounds as a defense

mechanism against environmental stressors. The antioxidant activity, assessed by DPPH radical scavenging and iron-reducing assays, mirrored these changes in phenolic levels. Soxhlet extracts from the flowering stage showed the highest antioxidant activity, with a notably low IC_{50} value of 7.68 μg/mL, indicating superior radical-scavenging ability compared to vegetative stage extracts, which had an IC_{50} of 43.17 μg/mL. Similarly, reducing power in the flowering stage Soxhlet extracts were higher, with an EC_{50} of 245 μg/mL, compared to 556.67 μg/mL during the vegetative stage. Overall, these findings highlight the increased production of phenolic compounds and enhanced antioxidant activity in *C. maritimum* in response to salinity and environmental stress factors during the flowering stage.

In the study by Castillo et al., *C. maritimum*, tested under four different NaCl concentrations (at 0.5 mM (control), 50, 200, and 500 mM), displayed increased levels of several key phenolic acids in response to salinity and nutrient stress [25]. Hydroxycinnamic acid levels, notably, 3-caffeoylquinic acid rose by approximately 64% under high salinity, highlighting its role in osmotic stress adaptation. Under nutrient-deficient conditions, concentrations of 5-caffeoylquinic acid, feruloyl quinic acid, 3,5-di-caffeoylquinic acid, and 4,5-di-caffeoylquinic acid were also elevated. These compounds help in mitigation of oxidative damage from ROS under stress, indicating *C. maritimum*'s resilience and potential as a source of natural antioxidants.

The study by Ben Hamed et al. investigated how *C. maritimum* responds to salt stress by analyzing changes in its lipid content, particularly focusing on sulfolipids [18]. The research revealed that under increased salinity, there was a notable rise in the content of sulfoquinovosyldiacylglycerol (SQDG), a specific type of sulfolipid, within the leaves of the plant. This increase was associated with the plant's ability to adapt to and tolerate high-salt levels. In control conditions, SQDG accounted for 2.8% of total lipids, whereas, at 200 mM NaCl, its content rose to 8.3%, indicating SQDG's role in the plant's ability to tolerate high-salt levels. Interestingly, the study found that, although the overall fatty acid composition of the sulfolipids remained relatively stable during salt treatment, specific changes were observed. The proportion of linolenic acid (C18:3), a polyunsaturated fatty acid prone to oxidation, decreased significantly (sixfold), while the proportion of linoleic acid (C18:2) increased (two-fold) leading to a shift in the C18:2/C18:3 ratio from 0.63 under no salt to 7.3 at 200 mM NaCl. This adjustment likely aids membrane stabilization, making it less vulnerable to oxidative stress caused by salinity. The increase in linoleic acid, along with higher levels of SQDG, suggests that *C. maritimum* utilizes these biochemical adjustments to maintain membrane integrity and proper photosynthetic function under salt stress. Moreover, the results imply that SQDG plays a critical role in stabilizing the photosynthetic complexes within chloroplasts, particularly the ATP synthase and light-harvesting complex II. This stabilization helps *C. maritimum* maintain its photosynthetic efficiency, even in high-salt environments. This adaptive mechanism supports the plant's growth and survival on coastal and saline habitats, indicating that sulfolipids and their associated fatty acids are the crucial components of the plant's strategy to cope with saline stress.

The study by Ventura et al. found that salinity significantly influenced the accumulation of secondary metabolites in *C. maritimum*, with notable variations across genotypes [48]. Antioxidants such as ascorbic acid and phenols increased in response to salinity in specific genotypes, indicating a potential protective mechanism against oxidative stress. For example, in the French genotype, ascorbate levels rose with salinity, reaching 15 mg/g DW at 100 mM NaCl, and phenolic content peaked at 4.2 mg GAE/g DW at 50 mM NaCl. These antioxidants likely help neutralize ROS generated under stress, thus protecting cellular structures.

Additionally, total fatty acid content, including omega-3 fatty acids such as linolenic acid (18,3$\Delta^{9,12,15}$), increased with salinity in the Israeli and French genotypes, peaking at 2.7% of DW at 100 mM NaCl. These fatty acids may aid in stabilizing cell membranes under osmotic stress. The Portuguese genotype also showed an increase in ureides, such as allantoin and allantoic acid, reaching up to 0.3 mg/g DW, which could support nitrogen transport and stress response.

In the study by Castillo et al., *C. maritimum* exhibited specific changes in fatty acid composition in response to varying salinity levels and nutrient availability [25]. Total lipid content decreased by approximately 30% as salinity increased, especially under nutrient-limited conditions (5% Hoagland's solution) from 1.68 mg/g at 0.5 mM NaCl to 1.11 mg/g at 500 mM NaCl. Among the unsaturated fatty acids, palmitolinolenic acid (16:3$\Delta^{7,10,13}$) was the lowest at 50 mM NaCl, indicating a particular response to mid-level salinity stress. Saturated fatty acids, including palmitic acid (16:0), stearic acid (18:0), arachidic acid (20:0), and behenic acid (22:0), concentrations significantly increased at higher salinities (200–500 mM NaCl). For example, palmitic acid increased from 19.05% at 0.5 mM NaCl to 26.01% at 500 mM NaCl. Similarly, stearic acid rose from 4.29% at low salinity to 5.96% at 500 mM NaCl. This shift toward saturation likely supports membrane stability against osmotic stress. Nutrient deficiency led to an approximate 20% decrease in total lipid content and specific unsaturated fatty acids, like 16:3 and petroselinic acid (18:1Δ^{6}), compared to nutrient-sufficient plants. Conversely, vaccenic acid (18:1Δ^{11}) increased by about 29% under low nutrient conditions, potentially facilitating stress signaling and protection through oxylipin production. An interaction between salinity and nutrient deficiency further influenced fatty acid composition. In nutrient-limited plants at higher salinities, concentrations of certain saturated and monounsaturated fatty acids, such as 16:0, palmitoleic acid (16:1Δ^{9}), and oleic acid (18,1Δ^{9}), increased by around 30%, a change not observed in the freshwater conditions. This increase suggests an adaptive mechanism by which *C. maritimum* adjusts its membrane composition, enhancing rigidity and resistance to osmotic stress when facing both salinity and nutrient stress simultaneously.

The study by Colak et al. examined *C. maritimum*'s carotenoid response to salinity, finding a notable decrease in total carotenoid content under increased salinity levels [37]. Specifically, exposure to 200 and 300 mM NaCl reduced carotenoid levels by 67.9 and 73.2%, respectively, compared to control plants. This reduction paralleled declines in chlorophyll content, suggesting that elevated salinity might impair photosynthetic and antioxidant defenses. Carotenoids are fundamental in mitigating photooxidative stress within chloroplasts; thus, their decline under high salinity indicates a potential vulnerability in the plant's stress response mechanisms.

In the study by Castillo et al., *C. maritimum* was analyzed for its essential oil components in response to varying levels of salinity and nutrient availability [25]. Sabinene and thymol methyl ether emerged as the primary constituents. A notable decrease in terpene levels was observed, with concentrations of α-terpinene, *p*-cymene, limonene, β-phellandrene, and α-pinene dropping by 50–76% at 500 mM NaCl in comparison with freshwater conditions. Furthermore, under nutrient-limited conditions (5% Hoagland's solution), these terpenes, along with β-myrcene and thymol methyl ether, were found to be 30–50% lower than those in nutrient-rich (20% Hoagland's solution) settings. This trend indicates that terpene production may be suppressed due to stress, likely resulting from reduced antioxidant defenses in the face of combined salinity and nutrient deficiencies.

3. Conclusions

The studies on *Crithmum maritimum* provide comprehensive insights into how this halophyte adapts to environmental stress through its rich primary and secondary metabolite profiles, making it a promising candidate for applications in saline agriculture, as a source of natural antioxidants and bioactives. The plant's flavonoid content, particularly hesperidin and diosmin, plays a critical role in managing oxidative stress under salinity. Similarly, chlorogenic acid and their derivatives, which accumulate under stressful conditions, further underscore *C. maritimum*'s antioxidant capabilities. High salinity and nutrient deficiency stimulate the accumulation of hydroxycinnamic acids, which are likely to contribute to osmotic stress adaptation. Various other phenolics, such as epigallocatechin and rosmarinic acid, peak during the flowering stage, enhancing stress resilience through increased radical-scavenging activity. Additionally, the increase in sulfolipids and adjustments in fatty acid composition under high salinity highlights *C. maritimum*'s ability to stabilize membranes and maintain photosynthetic efficiency in saline environments.

The research also emphasizes the importance of carotenoids such as lutein and β-carotene in protecting against photooxidative damage, enhancing *C. maritimum*'s value for culinary and medicinal uses. A study identified sabinene and thymol methyl ether as one of the major components in essential oil, noting that their levels decreased under conditions of extreme salinity and nutrient limitation. This highlights the need for further research into the various chemotypes of *C. maritimum* essential oils. The plant's adaptive biochemical responses, including increased tocopherol levels and selective accumulation of bioactive terpenes, phenolics, and lipids, demonstrate a multifaceted approach to managing oxidative and osmotic stress. Collectively, these findings highlight *C. maritimum*'s potential as a sustainable crop in saline environments and a valuable source of nutrients, natural antioxidants, and bioactive compounds, offering promising applications in food, nutraceutical, pharmaceutical, and agricultural sectors.

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Conflict of interest

The authors declare no conflict of interest.

Author details

Ivica Blažević[1*], Azra Đulović[1], Franko Burčul[2], Josip Tomaš[3], Petra Brzović[3], Sanja Radman[3], Olivera Politeo[4] and Ivana Generalić Mekinić[3]

1 Faculty of Chemistry and Technology, Department of Organic Chemistry, University of Split, Split, Croatia

2 Faculty of Chemistry and Technology, Department of Analytical Chemistry and Environmental Chemistry, University of Split, Split, Croatia

3 Faculty of Chemistry and Technology, Department of Food Technology and Biotechnology, University of Split, Split, Croatia

4 Department of Biochemistry, Faculty of Chemistry and Technology, University of Split, Split, Croatia

*Address all correspondence to: blazevic@ktf-split.hr

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Chapter 3

Impact of High-Temperature on Growth and Development of Fruit Crops

Yatinkumar N. Tandel, Vijay R. Zala and Shivanand Koti

Abstract

Heat stress significantly threatens fruit crop productivity and quality, resulting in substantial economic losses. High temperatures induce morphological, anatomical, physiological, and biochemical changes in plants. A lack of understanding regarding the impact of heat stress during critical developmental stages hinders efforts to mitigate its effects. Therefore, enhancing heat stress tolerance in fruit crops through traditional breeding and transgenic approaches is crucial. This chapter discusses the effects of heat stress and explores various management techniques to alleviate its impact. These techniques include selecting appropriate fruit crops, cultivars, and rootstocks, implementing effective canopy management, optimizing irrigation and nutrient management, utilizing mulching, applying growth regulators, and employing bagging and film sprays.

Keywords: heat stress, fruit crops, hormonal signaling, heat stress management, productivity

1. Introduction

Plant growth and development rate depend on various factors surrounding the plant and the temperature is one of the important among those. Each species has a specific temperature range represented by a minimum, maximum, and optimum. These values were summarized by Hatfield et al. [1] for several different species typical of grain and fruit production. The rise in global temperatures has emerged as a significant environmental stressor with profound implications for plant life. According to the Goddard Institute for Space Studies (GISS), global temperatures are projected to increase by approximately 0.15–0.20°C per decade, potentially leading to a total rise of 1.8–4.0°C by the end of the century. This anticipated warming presents a serious challenge for plants, which, as immobile organisms, cannot migrate to more favorable environments. As a result, elevated temperatures often disrupt plant growth and developmental processes and in extreme cases, can prove critical. Understanding and mitigating the impacts of high-temperature stress are critical for sustaining plant health and productivity in a rapidly warming world.

Heat stress, defined as a temperature rise beyond a certain threshold for a sustained period, negatively impacts plant growth and development. This stress is influenced

by factors such as temperature intensity, duration, and rate of increase. In tropical climates, high temperatures and excessive radiation often limit plant growth and yield. In temperate regions, heat stress is a major cause of reduced yield and dry matter production in various crops. High temperatures can cause significant pre- and post-harvest damage, including scorching of leaves and twigs, sunburns on leaves, branches, and stems, leaf senescence and abscission, inhibited shoot and root growth, and fruit discoloration, all these factors ultimately lead to a reduction in the yield [2–4]. Similarly, in temperate regions, heat stress has been reported as one of the most important causes of reduced yield and dry matter production in many crops (**Figure 1**) [6].

Each fruit species has a specific temperature range that supports optimal growth (**Table 1**). Higher temperatures tend to promote vegetative growth within this range, characterized by increased leaf expansion, stem elongation, and thickening. Nevertheless, temperatures above the optimal threshold can inhibit growth.

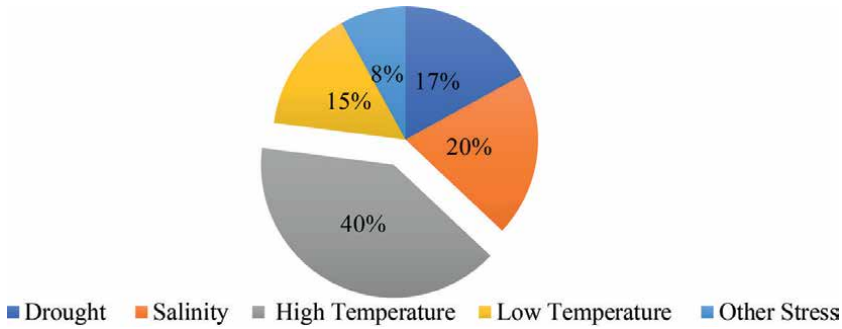

Figure 1.
Estimated yield losses due to abiotic stresses [5].

Fruits	Optimum temperature(°C)	References
Mango	24–30	[8]
Guava	23–28	[9]
Mangosteen	25–35	[10]
Litchi	25–35	[11]
Citrus	16–27	[9]
Rambutan	24–32	[9, 11]
Jackfruit	16–28	[12, 13]
Ber	22–36	—
Papaya	18–27	—
Apple	21–24 (during active growth period)	[14]
Pear	26–35 (in summer), 2 (in winter)	[15]
Peach	23–26	[16]
Strawberry	22–25 day and 7–13 night temperature	[17, 18]
Walnut	10–25	[19, 20]
Pecannut	24–30	[21, 22]

Table 1.
The optimum temperature requirement of some fruit [7].

2. Impact of high temperature on cell anatomy

2.1 Cell structure

Heat stress induces several physiological changes that can damage cell membranes. Exposure to high temperatures leads to the denaturation of membrane proteins and the inactivation of enzymes, resulting in increased membrane permeability and compromised integrity. This process disrupts ion flux, causes electrolyte leakage, alters relative water content, generates toxic compounds, and interrupts homeostasis, ultimately reducing cell viability. Decreased cell viability halts plant growth and triggers symptoms such as leaf wilting, abscission, and reduced leaf area [23]. High-temperature stress in strawberries, especially a 1.5–6°C increase in optimum growth temperature, causes inhibition of photosynthesis, cell membrane damage, and senescence-related changes that limit plant growth and development [24, 25].

2.2 Changes in leaf gas exchange

Transpiration, a vital physiological process in plants, converts net radiation energy into heat, controlled by stomatal aperture adjustments. The ability of plants to sustain CO_2 assimilation and gas exchange under high temperatures is linked to heat tolerance. High temperatures affect leaf water status, stomatal conductance, and intercellular CO_2 concentrations [26]. Stomatal closure under heat stress impairs photosynthesis by reducing intercellular CO_2. In many species, mild heat stress decreases stomatal conductance and the net photosynthetic rate due to reduced Rubisco activation. Additionally, high temperatures influence vapor pressure density, potentially altering hydraulic conductance and water delivery to leaves [27]. In mango, CO_2 exchange characteristics indicated that the changes in the temperature regime from 30/25 to 40/25 (°C) affected the net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular carbon dioxide concentration.

2.3 Chlorophyll pigment

High temperatures adversely affect chlorophyll biosynthesis, critical for light harvesting in plastids, by impairing and degrading chlorophyll pigments. Heat stress inhibits chlorophyll biosynthesis by disrupting the enzymes involved in its production, such as 5-aminolevulinate dehydratase (ALAD).

The maximum photochemical efficiency (Fv/Fm) of Photosystem II (PSII) reflects plant health. Decreases in Fv/Fm signal stress (temperature, light, water). In tropical fruit trees like pineapple, sugar apple, guava, and papaya, chlorophyll fluorescence (especially Fv/Fm) helps assess temperature stress. Early detection allows for timely interventions to protect the plants. Studies on crops show that heat stress reduces protochlorophyllide synthesis and impacts related enzymes. As a result, high temperatures decrease chlorophyll a, total chlorophyll content, and sucrose levels while increasing reducing sugars and soluble sugars in leaves, as observed in the work of Ashraf and Harris [28]. In citruses, high temperatures cause a decrease in chlorophyll, an accumulation of carotenoids, and delayed coloration. However, chlorophyll decomposition is delayed in tropical regions under high temperatures (above 25°C), and there is no characteristic increase in carotenoids.

2.4 Heat shock proteins (HSPs)

Heat shock proteins (HSPs) are produced in response to stress and help protect plant cells. Absent in non-stressed plants [29], HSPs are classified into high molecular weight (68–110 kDa) and low molecular weight (15–27 kDa) proteins. While low molecular weight HSPs are specific to higher plants, high molecular weight ones are universal. Some HSPs act as molecular chaperones, stabilizing denatured or unfolded proteins and preventing thermal aggregation [30]. These proteins maintain cellular homeostasis by eliminating harmful aggregates. In transgenic, HSPs reduce thermo-aggregation and thylakoid membrane damage, enhancing photosynthesis. Chloroplast-localized HSPs protect photosynthetic components such as PS-II from heat-induced oxidative stress, particularly in tomato leaves. Gradual temperature increases and heat shock proteins enhance heat tolerance in strawberry cultivars like Redlands Hope [31].

2.5 Impact on photosynthesis

High temperatures directly affect light intensity, damage photosystems, disrupt respiration and photosynthesis, shortening life cycles and reducing yields. Heat stress modifies chloroplast protein complexes and impairs enzymes involved in light-dependent reactions in the thylakoid membrane and carbon metabolism in the stroma. High leaf temperatures disrupt PS-II, causing imbalances in electron flow and reducing oxygen evolution. Enzyme activities critical for sucrose and starch synthesis are also negatively affected. Photosynthetic rates decline due to reduced Rubisco activation, chlorophyll damage, and hindrances in electron flow and PS-II photochemistry [32].

Despite the vulnerability of PS-II to heat stress, PS-I is more stable. Under mild heat stress, PS-I enhances proton conductance and cyclic electron flow, facilitating ATP production. Heat stress also stimulates the dark reduction of plastoquinone and the thylakoid proton gradient, activating cyclic electron flow around PS-I [30]. Increased ATP production supports active CO_2 fixation, even as NADPH/ATP ratios adapt to maintain energy balance and enhance photorespiration efficiency. High-temperature stress can also lead to physiological changes in strawberry plants, including decreased photosynthesis rates, increased respiration rates, and changes in carbohydrate metabolism [33].

3. Temperature-driven changes in plant hormonal signaling

Temperature plays a crucial role in regulating hormonal pathways in plants, influencing their growth, development, and ability to adapt to changing environmental conditions. Different phytohormones mediate these responses, enabling plants to optimize their metabolic processes under varying temperature regimes. Here is an overview of how temperature influences the major hormonal pathways in plants:

3.1 Auxin

Auxin is a key hormone in regulating growth, including thermomorphogenesis (growth patterns influenced by temperature). At higher temperatures. Auxin biosynthesis is often regulated, particularly through the action of PIF4 (Phytochrome

Interacting Factor 4), which activates the expression of YUCCA genes, involved in auxin biosynthesis. Auxin promotes elongation of cells and hypocotyl growth in warm conditions, a process known as thermomorphogenesis. This helps the plant adjust its structure to optimize exposure to light and temperature. Auxin signaling interacts with other pathways to control heat tolerance, with auxin-responsive genes helping plants adapt to temperature stress by modulating growth patterns (**Figure 2**). In Strawberry, elevated temperatures also inhibit auxin biosynthesis, transport, and signaling which negatively impacts strawberry plant growth, fruit initiation, and ripening [38] and high temperature inhibits lateral root development by reducing auxin levels and altering auxin distribution [39].

3.2 Gibberellins (GA)

Gibberellins are hormones that promote stem elongation, seed germination, and flowering. Temperature changes can affect GA biosynthesis and signaling, influencing seed germination and flowering time. Warmer temperatures often promote earlier flowering, partly through changes in GA signaling. However, high temperatures can also lead to reduced GA biosynthesis, especially under prolonged heat stress, which may suppress growth and lead to reduced seedling vigor. In strawberry, high temperatures additionally alter endogenous hormones like abscisic acid and gibberellins that regulate growth and development [40].

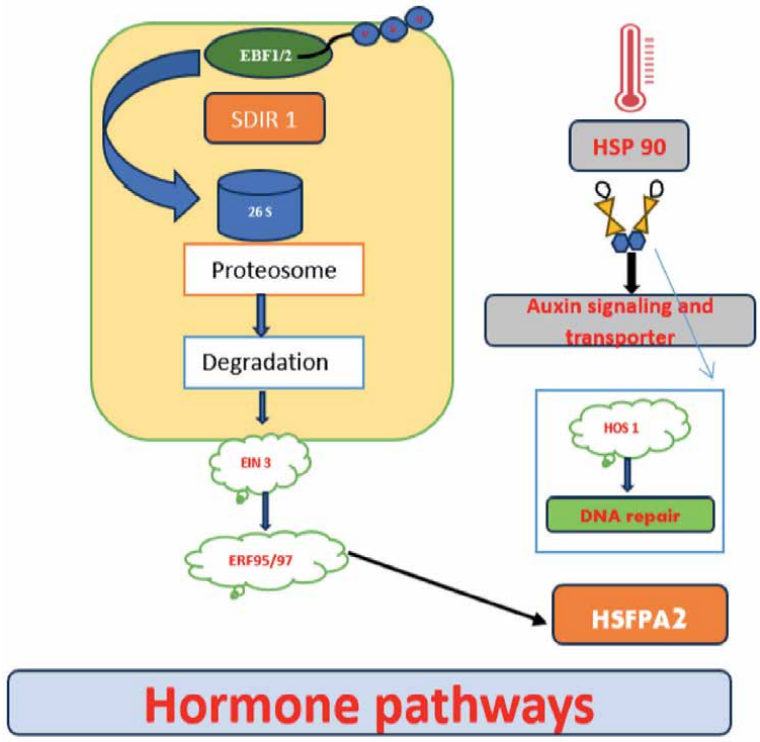

Figure 2.
Temperature influences several hormonal pathways, including auxin signaling and transport via HSP90 [34, 35] and ethylene signaling pathways [36]. HSP90 is also involved in thermostabilizing HOS1 which induces thermotolerance by activating DNA repair mechanisms [37].

3.3 Cytokinins

Cytokinins are involved in cell division, differentiation, and various developmental processes. High temperatures often lead to altered cytokinin levels, influencing plant growth and development. Cytokinin helps mitigate heat-induced damage by promoting cellular repair and protecting against oxidative stress. Cytokinin signaling interacts with auxin and ethylene to balance growth and stress responses, ensuring proper development even under thermal stress.

3.4 Abscisic acid (ABA)

Abscisic acid is essential for managing water stress and maintaining plant homeostasis under temperature extremes. High temperatures can induce ABA biosynthesis, which helps plants cope with heat stress by modulating stomatal closure and reducing water loss through transpiration. ABA also influences gene expression to enhance heat tolerance by activating the production of heat shock proteins (HSPs) and other protective molecules. In addition, ABA works in conjunction with other hormones, such as auxin, to modulate growth responses under stress conditions, balancing growth and stress tolerance.

3.5 Ethylene

Ethylene is a gas hormone involved in various developmental processes, including stress responses. Heat stress stimulates ethylene production in many plants and it is thought to mediate heat stress responses, including activating protective mechanisms. Ethylene plays a role in thermotolerance by regulating stress-responsive genes, such as those involved in antioxidant defense, which helps mitigate cellular damage from heat. The ethylene signaling pathway also contributes to flowering time regulation, with elevated temperatures often accelerating flowering through ethylene-mediated activation of key floral genes. Heat stress alters the expression of genes involved in ethylene biosynthesis, fruit ripening, and carbohydrate metabolism, affecting fruit flavor and nutritional quality [41].

3.6 Brassinosteroids

Brassinosteroids (BRs) are plant hormones that play a major role in regulating growth and stress responses. Elevated temperatures often trigger the BR signaling pathway, leading to enhanced cell elongation and thermotolerance. BRs are known to work synergistically with auxin in regulating thermomorphogenesis, especially in warm conditions. They promote cell expansion and vascular development, contributing to heat-induced growth changes. The BRs also help plants maintain structural integrity under stress, improving heat tolerance by regulating genes that protect against oxidative damage.

3.7 Jasmonic acid (JA)

Jasmonic acid is a hormone primarily associated with stress responses, including wounding and pathogen defense. Heat stress can trigger the production of jasmonic acid, which enhances the expression of genes involved in stress tolerance, such as those encoding heat shock proteins (HSPs) and antioxidant enzymes. JA signaling

also interacts with other stress-related hormones, such as ABA and ethylene, to coordinate the plant's response to high temperatures.

3.8 Salicylic acid (SA)

Salicylic acid is involved in plant defense, particularly against pathogens, but it also has a role in heat stress responses. In response to high temperatures, salicylic acid can promote thermotolerance by enhancing the plant's heat shock protein (HSP) expression and activating protective antioxidant systems.SA interacts with other hormones like ethylene and JA to regulate the plant's stress response and balance growth and defense mechanisms.

High-temperature stress profoundly impacts major plant growth-regulating hormones in strawberries. Phytohormones like auxins, cytokinins, gibberellins, abscisic acid (ABA), ethylene, salicylic acid, jasmonic acid, and brassinosteroids have all demonstrated altered levels and distribution under elevated temperatures [39, 42].

4. ROS in heat stress

Plants possess intricate mechanisms to cope with temperature stress. Reactive oxygen species (ROS), while potentially damaging at excessive levels, play a crucial role as signaling molecules in stress acclimation. Upon encountering temperature stress, plants activate stress-response pathways, including the upregulation of ROS-scavenging systems to maintain ROS levels within a tolerable range. This delicate balance is essential, as both insufficient and excessive ROS can negatively impact plant growth and survival. Temperature sensing involves various cellular components, including calcium channels, histone sensors, and the detection of denatured proteins in the endoplasmic reticulum and cytosol. The ability of plants to withstand sudden temperature increases is termed basal thermotolerance [43].

Plant hormone signaling pathways are pivotal in orchestrating responses to temperature fluctuations. These hormones regulate complex stress-adaptive cascades, inducing both heat and cold stress responses [44]. A key mechanism by which hormones contribute to thermotolerance involves the modulation of ROS production. This can occur by activating NADPH oxidases and/or influencing redox signaling pathways that regulate various cellular and physiological processes in response to temperature changes [45].

Extensive crosstalk between ROS and hormone signaling pathways facilitates plant development and acclimation responses [46]. Optimal ROS levels act as signaling molecules, generated in response to stress perception by cellular sensors. Heat stress disrupts membrane fluidity, simultaneously triggering hormone signaling pathways. This leads to increased cytosolic calcium and ROS production, which in turn modulate the activity of heat shock factors (e.g., HSFA1), ultimately influencing the plant's response to the stress condition [47].

Elevated temperatures induce excessive ROS production in plants, triggering the activation of heat stress (HS)-responsive pathways. Concurrently, plants upregulate the expression of genes encoding stress-related and antioxidant proteins. This leads to increased activity of antioxidant enzymes such as ascorbate peroxidase (APX), catalase (CAT), and superoxide dismutase (SOD), thereby mitigating the detrimental effects of oxidative damage caused by ROS [47, 48]. Studies have shown that subjecting plants to mild heat stress (heat priming) enhances their thermotolerance. This improved

tolerance is attributed to several key mechanisms. Firstly, heat priming strengthens the plant's antioxidant defense system, leading to lower levels of reactive oxygen species (ROS) and delaying ROS-induced cell death. Secondly, it enhances photosynthetic efficiency by increasing stomatal conductance and facilitating gas exchange. Finally, heat priming stimulates the synthesis of secondary metabolites with antioxidant properties, such as flavonoids and carotenoids, which help maintain the integrity of leaf membranes under subsequent heat stress. These findings highlight the importance of heat priming as a crucial strategy for enhancing plant resilience to high-temperature stress [49]. High temperatures stimulate the accumulation of toxic reactive oxygen species, overwhelming strawberry's antioxidant defenses and causing oxidative damage to cells [50].

5. High temperature-induced epigenetic changes

Temperature-induced epigenetic changes in fruit crops are crucial for how these plants adapt to varying environmental conditions. Epigenetic modifications, including DNA methylation, histone modifications, and small RNA regulation, allow plants to respond to temperature fluctuations without altering their genetic code. These changes influence gene expression, which in turn affects key traits like growth, development, and fruit quality. This is highlights the impact of temperature-driven epigenetic modifications on fruit crops, their role in stress adaptation, and their potential for crop improvement.

5.1 Epigenetic mechanisms in high temperature response

1. *DNA methylation*: DNA methylation is one of the most common epigenetic modifications. In response to temperature stress, DNA methylation patterns in fruit crops can change, altering the expression of genes involved in stress responses. For example, DNA methylation may regulate the expression of heat shock proteins (HSPs) that help protect plants from heat stress.

2. *Histone modifications*: Histones, the proteins around which DNA is wrapped, can undergo various modifications, such as acetylation, methylation, and phosphorylation. These changes can either activate or repress gene expression. For instance, in response to elevated temperatures, the histone variant H2A.Z may be removed from certain genomic regions, allowing transcription factors like PIF4 to bind and activate genes related to thermomorphogenesis (growth responses to temperature).

3. *Small RNAs*: Small RNAs, including micro RNAs (miRNAs) and small interfering RNAs (siRNAs), play a role in regulating gene expression at the post-transcriptional level. Temperature changes can influence the production of these small RNAs, which can modulate the expression of genes involved in temperature stress responses, such as those controlling flowering time or fruit ripening.

6. Influence of high temperature on seed germination and seedling development

Heat stress significantly threatens fruit crop production, particularly impacting seed germination. Elevated temperatures can disrupt crucial metabolic processes

within the seed, damage cellular structures, and ultimately reduce germination rates and seedling vigor.

6.1 Apples (*Malus domestica*)

- *Seed germination*: Apple seeds require a period of cold stratification (chilling) to break dormancy and germinate. However, excessively high temperatures *after* this chilling period can inhibit germination. Temperatures above 30–35°C can reduce germination percentage and delay the process [51].

- *Seedling development*: High temperatures following germination can have several detrimental effects on seedlings. Reduced growth rate and biomass accumulation are common consequences, hindering overall plant development. Furthermore, elevated temperatures increase seedling susceptibility to heat stress, leading to symptoms such as wilting and leaf damage. Additionally, high temperatures can create an environment more conducive to developing and spreading seedling diseases, further jeopardizing their survival and establishment.

6.2 Grapes (*Vitis vinifera*)

- *Seed germination*: Grape seeds require stratification for optimal germination. High temperatures can negatively impact this process by inducing secondary dormancy, reducing both the germination percentage and rate, and increasing the incidence of abnormal seedlings.

- *Seedling development*: High temperatures can hinder seedling growth by reducing root and shoot growth, decreasing photosynthetic efficiency, and increasing susceptibility to fungal diseases.

6.3 Citrus (*Citrus* spp.)

- *Seed germination*: Citrus seeds are generally more tolerant to high temperatures than some temperate fruit crops. However, very high temperatures (>40°C) can still reduce germination percentage and delay the process [52].

- *Seedling development*: High temperatures can negatively affect seedling growth by reducing leaf area and dry weight, increasing respiration rates and water loss and making seedlings more vulnerable to root rot and other diseases.

6.4 Mango (*Mangifera indica*)

- *Seed germination*: Mango seeds are recalcitrant, meaning they lose viability quickly if dried. High temperatures exacerbate this issue and can drastically reduce germination rates. Optimum temperatures for mango seed germination are generally between 25 and 30°C [53].

- *Seedling development*: High temperatures can cause stunted seedling growth, leaf scorching and damage, and increased susceptibility to fungal pathogens.

7. Impact of heat stress on fruit tree floral development

High temperatures during flowering significantly impact fruit tree development, disrupting crucial metabolic processes like transpiration, photosynthesis, and respiration. This disruption leads to reduced energy and carbohydrate accumulation, potentially causing flower malformation or abortion. Research on peach trees (*Prunus persica* L.) demonstrates that while warmer temperatures can induce earlier flowering, excessively high temperatures inhibit normal flower bud development, resulting in deformed flowers or complete failure to bloom a phenomenon known as flower bud shedding. Furthermore, temperature effects vary depending on the plant's sex. In cherry trees (*Prunus* spp.), where optimal growth occurs around 20°C, exposure to day/night temperatures of 35°C/10°C leads to substantial flower bud shedding due to impaired blooming. This high-temperature regime also significantly inhibits corolla and stamen growth. Studies on sweet cherry pollen mother cells exposed to high temperatures at different developmental stages (meiosis, mononuclear pollen, and mitosis) reveal that earlier heat exposure more strongly inhibits stamen development, particularly filament growth. Conversely, later heat exposure has a more pronounced inhibitory effect on pistil development.

8. Impact of high temperature on insect pests

Climate change significantly influences insect pests and diseases by impacting their development, reproduction, survival, and the dynamics of their natural enemies. As ectotherms, insects are highly sensitive to temperature, which directly affects their behavior, development, and reproduction. Potential consequences include altered phenology, shifts in habitat range, and changes in geographic distribution. Research has demonstrated that rising temperatures can profoundly affect insect survival, development, geographic range, and population size [54]. Temperature can also indirectly influence insect populations by impacting host physiology and availability.

Common observed responses to climate change include earlier adult emergence and extended flight periods. For example, Roy and Sparks [55] reported that butterfly flight periods in Europe have advanced by 2–10 days per 1°C increase in temperature. Furthermore, species diversity in insect communities generally decreases with increasing latitude and altitude. Therefore, rising temperatures could lead to an increase in the number of insect species attacking a wider range of hosts in temperate regions [54].

In Himachal Pradesh, India, the emergence of the European red mite (*Panonychusulmi*) as a significant pest in apple orchards exemplifies the impact of climate change. Kakar [56] attributed the initial infestation in Kullu during 1992 to prevailing high temperatures (25–30°C) and low humidity (62%) resulting from delayed monsoon rains. Subsequently, this pest spread to other districts. The Guava fruit fly (*Bactroceracorrecta*) provides another example. Liu and Ye [57] found that optimal survival for this species occurs within a temperature range of 24–33°C, with significantly reduced survival rates outside this range.

Tejashri and Kranti [58] investigated the impact of climate change on grape production in Tasgaon tehsil, India. Their study, conducted between 2008 and 2017,

revealed a significant increase in temperature and alterations in precipitation patterns. These climatic shifts resulted in a substantial decline in grape yield, primarily attributed to a surge in fungal diseases facilitated by warmer temperatures and altered precipitation regimes. Their study estimated yield losses within 40–50%.

9. Breeding strategies to combat high-temperature tolerance in fruit crops

Heat stress tolerance in plants can be improved through breeding programs that utilize conventional and advanced genetic tools.

9.1 Hybridization

Hybridization is a crucial conventional breeding strategy to enhance heat stress tolerance in fruit crops. The mandarin daisy variety was developed by inter-varietal hybridization between Fortune mandarin and Fremont mandarin and it is highly tolerant under heat stress. In custard apple, Arka Sahan variety is developed by inter-specific hybridization between Island gem (*Annona atemoya* Hort.) and Mammoth (*A. squamosa* L.). This variety is also suitable for high-temperature stress regions.

High-tech breeding approaches for heat tolerance in fruits include genome editing, marker-assisted selection, and quantitative trait locus (QTL) mapping. These approaches help identify genes that make plants more tolerant to heat stress.

9.2 Overexpression of genes

Apple transcription factor MdWRKY75 positively regulates heat tolerance in apple by enhancing basal thermotolerance. Overexpression of MdWRKY75 increased heat tolerance, while silencing MdWRKY75 decreased it [59]. In Ziziphus, overexpression of different transcriptomic responses gene (HSP17, HSP18, HSP21, HSP 22, HSP 23, HSP26, HSP70, HSP83, HSP90, HSF30, and HSC-2) helps the Protein stability and refolding [60].

9.3 Downregulation of genes

In bananas, downregulation of the miR159 transcriptomic responses gene helps hormone regulation under heat stress and the miR396 transcriptomic responses gene helps leaf development [61].

9.4 Transgenic breeding

Transgenic breeding is produced through genetic engineering techniques that modify the genetic makeup of the fruit. These techniques can improve quality, taste, nutrition, and stress resistance. Overexpression of MdATG18a in apples enhances antioxidant activity, boosts photosynthesis, and reduces chloroplast damage under heat stress, suggesting a crucial role for autophagy in basal thermotolerance (**Table 2**) [82].

Fruit crop	Effect of high temperature(°C) on fruit crops	References
Strawberry	High temperatures of 30°C and above adversely affect reproductive growth and development, fruit quality, and plant growth at different levels depending on the varieties and had negative effects on fruit yield and physical characteristics (weight, size, color, and shape) of strawberry	[62]
	High temperatures decrease flower numbers, pollen viability, and fruit directly reducing yields	[63]
Mango	Rising temperatures cause desiccation of pollen and poor pollinator activity resulting in low fruit set	[64]
	Mango cv. Chausa the rate of development of fruit fly increased with the increase in temperature from 20 to 35°C	[65]
Apple	In India and Nepal, traditional apple cultivation area is moving further up in elevation because of the warmer climate	[66]
	High-temperature climate reduces anthocyanin concentration in the peel of maturing apples	[67]
Mango and Guava	Changes in temperature have contributed to postponing of fruiting season. It is also true that in several cases, fruiting and the ultimate set have been badly affected.	[68, 69]
Guava	Temperatures lower and higher than this range (18–28°C) reduce fruit setting, and very low night temperatures (5–7°C) paralyze growth and turn leaves purple	[70]
Citrus	Temperatures above 37°C may cause serious damage to tender fruitlets, and between 44 and 45°C can slow down fruit growth and cause excessive fruit abscission	[71]
Mangosteen	High temperatures above 35°C cause some stresses on the trees	[72]
Papaya	In papaya, higher temperatures have resulted in flower drops in female and hermaphrodite plants as well as sex changes in hermaphrodite and male plants. The promotion of stigma and stamen sterility in papaya is mainly because of higher temperatures	[73]
Pineapple	The coincidence of long days with high temperatures results in irregular flowering, which emphasizes the role of temperature	[74]
	High-temperature stress of 38°C causes a significant reduction in the development of the F-leaf of pineapple during the vegetative stage	
Passion fruit	Sugar content in the juice was highest at 28/23°C and lowest at 33/28°C	[75]
Grape	Higher temperature regime, the number of clusters per shoot was greater and the number of flowers per cluster was reduced	[76]
	The loss of ovule viability in the varieties Pinot Noir and Carignane at 35 and 40°C as compared to 25°C	[77]
	The evapotranspiration rate increased with temperature and was highest at 30–35°C	[78]
Grape, Cape gooseberry, Mango	In grape vine, temperatures >35°C hinder fruit set, in cape gooseberry ≥30°C can inhibit flowering, in mango >35°C reduces the viability of pollen and fruit set	[53]
Peach	High temperature has a negative effect on breaking rest in dormant peach buds	[79]
	High temperatures above 25°C remarkably reduced fruit set in Hakuho peach variety	[80]
Dragon fruit	High summer temperatures (day/night: 40°C/30°C) are known to cause poor fruiting, reduced fruit/seed weight, and delayed fruit development in the 'Da Hong' red-fleshed pitaya (*Hylocereus polyrhizus*)	[81]

Table 2.
Effect of High temperature (°C) on different fruit crops.

10. Management practices to alleviate heat stress

Several strategies can be employed to mitigate the adverse effects of heat stress on fruit crops, focusing on selection, management, and direct protection [83].

Selection: Choosing the appropriate plant material is crucial. This includes:

- *Fruit crop selection*: Prioritize perennial fruit species adapted to high temperatures, exhibiting traits like deep root systems, leaf shedding, water binding mechanisms, thorns, specific leaf orientations (vertical or rolling), and well-formed canopies. Suitable crops for heat-prone areas include Ber, Pomegranate, Aonla, Fig, Ker, Tamarind, Karonda, Lasoda, Khejri, and Indian Fig.

- *Cultivar selection*: Select heat- and drought-tolerant cultivars. Examples include 'Ruby' pomegranate, 'Arka Sahan' annona, and drought-tolerant banana cultivars like 'Karpuravali' and 'Kanthali' [84]. In temperate fruits, examples include heat-tolerant strawberry cultivars like 'Elsanta', 'Khope', and 'Camarosa' [85] and peach cultivars like 'BR1 Chimarrita', 'Tropic Beauty', and 'Atens' [86].

- *Rootstock selection*: Utilizing tolerant rootstock genotypes is a key strategy. Heat- and drought-tolerant rootstocks minimize the immediate effects of dry conditions and enable faster recovery.

10.1 Management practices

- *Canopy management*: Canopy cover, which shades fruit, can be manipulated through cultivar selection, irrigation, fertilization, and pruning/training. Practices that reduce canopy cover (*e.g.*, foliar diseases, wilting, excessive pruning) increase sunburn risk. Maintaining adequate leaf cover is essential for fruit shading, especially during the afternoon.

- *Irrigation*: Irrigation timing is crucial. Irrigating just before or during heat waves can prevent heat stress and sunburn [87]. Meeting evapotranspiration demand through irrigation is essential. Overhead watering, sprinkling, and misting can further reduce tissue temperature and water vapor pressure deficit.

- *Nutrient management*: Proper nutrition alleviates heat stress [88]. Split applications of nitrogen (N) and potassium (K) fertilizers improve plant growth under moderate heat stress. Foliar sprays of 2% DAP + 1% KCl can also be used, ensuring sufficient soil moisture to prevent leaf scorching. Other beneficial foliar sprays include 0.5% zinc sulfate + 0.3% boric acid + 0.5% ferrous sulfate + 1% urea.

- *Mulching*: Mulches reduce transpiration and keep the canopy cool. Reflective, low-density organic mulches like straw reduce surface radiation and conserve moisture. Shading cloth provides partial shading by reducing advected heat and total incoming radiation.

10.2 Direct protection

- *Anti-transpirants*: Anti-transpirant chemicals minimize evapotranspiration. Foliar sprays of 3% kaolin can reduce heat stress by this mechanism.

- *Growth regulators*: Exogenous application of plant growth regulators (PGRs) can induce stress tolerance. Salicylic acid can maintain higher photosynthesis in grape leaves under heat stress and increase stem reserve utilization and harvest index [89].

- *Fruit bagging*: Shade cloth (10–30% shade) can protect a significant proportion of exposed fruits from sunburn.

- *Film sprays/sun protectants:* Film sprays, often kaolin clay-based (e.g., Surround, Screen Duo, Purshade), create a white particle film on the fruit to reduce sunburn. Other products, like Raynox, offer protection without leaving a white residue [87].

- *Bark painting*: Painting exposed trunks and branches with reflective white coatings can prevent high-temperature damage to the trunk cambium.

11. Conclusion

In conclusion, heat stress poses a significant challenge to fruit crop production worldwide. High temperatures adversely impact various aspects of plant growth and development, leading to reduced yield and compromised fruit quality. While the detrimental effects of heat stress are multifaceted, understanding the underlying mechanisms is crucial for developing effective mitigation strategies. This chapter has highlighted the diverse impacts of heat stress on fruit crops, ranging from morphological alterations to physiological and biochemical disruptions. Furthermore, various management practices, including cultivar selection, canopy management, and irrigation strategies, have been discussed as potential avenues to alleviate the negative consequences of heat stress. Continued research on heat stress tolerance mechanisms and the development of heat-tolerant cultivars through breeding and biotechnological approaches are essential to ensure sustainable fruit production in a warming climate.

Conflict of interest

The authors declare no conflict of interest.

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Author details

Yatinkumar N. Tandel*, Vijay R. Zala and Shivanand Koti
Department of Fruit Science, ASPEE College of Horticulture Navsari Agricultural University, Navsari, Gujarat, India

*Address all correspondence to: yatintandel1512000@nau.in

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Chapter 4

Medicinal Utilization and Suitability of Pumpkin (*Cucurbita maxima*) Seeds for the Development of Value-Added Products

Adeyanmola Oluwaseyi Faturoti and Clement Olusola Ogidi

Abstract

Pumpkin (*Cucurbita maxima*) seeds have attracted significant interest due to their potential in developing f value-added products and their diverse medicinal purposes. These seeds are abundant in essential nutrients such as proteins, vitamins, minerals and unsaturated fatty acids, making them an excellent raw material for functional foods and dietary supplements. Additionally, their bioactive compounds, such as antioxidants and phytosterols, offer various health benefits, including anti-inflammatory, antimicrobial and anticancer properties. Their versatility in applications, such as oil extraction, protein supplements, beverages and snacks, position them as sustainable and cost-effective resources for product development in both food and health industries. This chapter explores the utilization of *Cucurbita maxima* seeds and underscores their potential to enhance human health.

Keywords: *Cucurbita maxima* seeds, value-added products, medicinal purposes, supplements, development

1. Introduction

Recently, fruits and vegetables have notably gained interest due to high nutraceutical and therapeutic values of bioactive compounds present in them, including pumpkin [1]. Pumpkins, as an oily seed, belong to the Cucurbitaceae of about 118 genera and 825 species and is collectively among the top 10 leading vegetable crops worldwide [2]. Although there are different species grown in the world, the most economically of them are *Cucurbita maxima, Cucurbita moschata Duch., Cucurbita ficifolia, Cucurbita pepo* L., *Cucurbita mixta* and *Telfairia occidentalis* [3]. *Cucurbita maxima* is an underutilized crop and a medium-sized plant grown for its fruits and seeds for human consumption [4]. The fruits vary in shape, color, sizes and weight of different

species [5, 6]. Despite *Cucurbita maxima* seeds being regarded as agro-industrial waste, the seeds have a unique flavor and nutty taste. They are consumed as salted or roasted snacks in various parts of the world, including Canada, the United States and Nigeria [4, 5]. *Cucurbita maxima* seeds serve as a powerhouse of nutrients with interesting nutraceutical properties [7]. *Cucurbita maxima* seeds are composed of proteins (25.2–37.0%), dietary fiber (3–6%), carbohydrates (18–25%), lipids (37.8–45.4%) and ash (3–5%) [3]. They serve as a potential source for edible oil extraction and rich in essential macro and micro elements such as potassium, calcium, sodium magnesium, iron, zinc and copper [8, 9]. Furthermore, *Cucurbita maxima* seeds are abundant in bioactive compounds like phenolic compounds, squalene, phytosterols, tocopherols (α, β, γ and δ), tocotrienols, carotenoids and flavonoids [9]. These natural bioactive constituents contribute significantly to disease prevention and overall health promotion. As a result, *Cucurbita maxima* seeds are classified as functional foods due to their high concentration of health-promoting bioactive components [10].

2. Characteristics of pumpkin (*Cucurbita maxima*) seeds

The characteristics of *Cucurbita maxima* seeds provide critical insights into their nutritional composition, facilitating their potential use in various culinary applications, food formulations and oil extraction. The seeds are often referred to as nutritional powerhouses and are an exceptional source of protein, fiber, lipids, minerals, phytochemicals, antioxidants and other bioactive compounds [10]. Owing to their remarkable nutraceutical properties, *Cucurbita maxima* seeds once considered agro-industrial waste, have gained recognition as miracle seeds [3, 11].

2.1 Nutritional components of pumpkin (*Cucurbita maxima*) seeds

Cucurbita maxima seeds are rich source of valuable nutritional components. These nutrients act as primary metabolites essential for sustaining life, while the bioactive compounds in the seeds play significant roles in disease prevention [10, 12, 13]. *Cucurbita maxima* seeds contain approximately 6.37–6.56% moisture content, 35–50% lipids, 25–37% proteins, 18–25% carbohydrate, 3–6% fiber and 3–5% ash [9]. They are particularly rich in fats and proteins, making them effective in addressing nutritional disorders such as malnutrition and in preventing from various ailments [8, 9]. *Cucurbita maxima* seeds also contain lipids which are composed of many essential and non-essential fatty acids including ω-3, ω-6 and ω-9 fatty acids, rendering them a favorable ingredient for edible oil extraction. The extracted oil can be utilized as a cooking oil or as a fat replacer in food industry [8]. Furthermore, the high protein content in the *Cucurbita maxima* seeds is suitable for the production of protein isolates and for use in flour formulations for baked goods such as biscuits and cookies [8, 9, 14, 15]. Protein isolates derived from *Cucurbita maxima* seeds have been shown to mitigate the adverse effects of low-protein and CCl4 intoxication [15]. Pumpkin seeds contain approximately 0.95–16.84% fiber, as documented by various researchers [include ref]. They also contain variable amount of carbohydrates, ranging from 1.00% to 26.43%, which makes them valuable ingredients in food formulation. The carbohydrate content of *Cucurbita maxima* seeds allows their use in the development of various bakery products, such as cake, cookies and bread [14]. Ash content of the seed was reported in the range of 1.60–7.20%. *Cucurbita maxima* seeds have

been extensively studied for their nutritional composition, with various researchers highlighting their significant protein, lipid and fiber content and their potential applications in food and nutrition industries [8, 9, 14].

2.2 Mineral composition of pumpkin (*Cucurbita maxima*) seeds

Cucurbita maxima seeds contain a substantial of essential minerals. They are particularly rich in potassium while being relatively lower and in sodium and provide significant levels of high levels of calcium, phosphorus, magnesium, iron and copper. Additionally, they are valuable sources of zinc, iron and copper [7]. Minerals such as zinc, copper and iron exhibit antioxidant properties, serving as cofactors for vital antioxidation-dependent enzymes [16, 17]. The low sodium and high potassium content in *Cucurbita maxima* seeds has notable clinical implications, particularly for enhancing cardiovascular health [18]. Zinc plays a crucial role in male reproductive health, the structural integrity of proteins and cellular protection [19]. These mineral concentrations highlight the potential of *Cucurbita maxima* seeds as a valuable ingredient for food fortification, particularly in bakery products.

2.3 Amino acids (g/100 g) profiles of pumpkin (*Cucurbita maxima*) seeds

Cucurbita maxima seeds are rich in protein, containing approximately 35%, which contributes to a diverse and significant amino acid profile [20]. Amino acids are essential as they serve as both the building blocks of proteins and as intermediates in various metabolism processes. An adequate dietary supply of essential amino acids, in both quantity and quality, is vital for maintaining physiological functions in human body [21, 22]. Research indicates that protein isolates derived from *Cucurbita maxima* seeds are comparable to those of soybeans exhibiting high bioavailability of amino acids [7, 22]. Notably, the globulin structure of *Cucurbita maxima* seeds closely resembles that of legume seeds [22, 23]. This similarity is significant, as it supports the potential of *Cucurbita maxima* seeds to serve as a reliable ingredient in the development of nutritious food products, thereby addressing the challenges of protein malnutrition in vulnerable populations. Additionally, *Cucurbita maxima* seeds protein isolates exhibit antioxidative and chelating properties, further enhancing the nutritional and functional applications [23–26].

2.4 Fatty acid (mg/100 g) profiles of pumpkin (*Cucurbita maxima*) seeds

The primary fatty acids in *Cucurbita maxima* seed oil are linoleic, oleic, stearic and palmitic, which collectively account for more than 95% of the total fatty acids content, with 75% unsaturated [27, 28]. Trace amounts of arachidic and linolenic acid have also been identified [29, 30]. The fatty acid profile of the *Cucurbita maxima* seed oil is presented in **Table 1**. Unsaturated fatty acids have been extensively studied due to their protective effect against cardiovascular diseases [42, 43]. They play a vital role in the healthy growth and development of brain and nervous system. Furthermore, they are associated with health benefits such as mitigating hypertension, arthritis, coronary heart diseases, cancer, inflammation and autoimmune disorders [42–45]. Importantly, only linoleic]and alpha-linolenic acids are considered essential for humans, as they cannot be synthesized by the body and must be obtained through dietary source [7].

Industry	Food product	Function	Reference
Meat	Beef meat ball	Fat replacement	[31]
	Chicken burgers	Enhanced stability during storage	[32]
	Beef patties	No change in textural property and decrease moisture content	[33]
Bakery	Biscuits	Decrease serum blood glucose level	[34]
	Cookies	Prevent constipation, diabetes, prolong intestinal transit time and lower cholesterol	[35]
	Muffins	Had a better sensory profile and improved nutritional value	[36]
	Cake	Increase in firmness and moisture retention	[37]
	Sausage	Improvement in the water holding capacity and cooking quality	[3]
Diary	Ice cream	An increase in the protein content improves the degree of satiety and enhances sensory characteristics	[38]
	Cereal milk	Improved the sensory and nutritional value Extended shelf life	[39]
Spice	Bouillon cube	Improved sensory and nutritional value	[5]
Vegetable oil	Vegetable oil	Functional food used as culinary and traditional medicine	[40]
	Vegetable fat	Improvement in the fatty acid profile of meat batters with no much difference in the textural profile.	[41]

Table 1.
Development of value-added products Cucurbita maxima *seeds.*

2.5 Phytochemical composition of pumpkin (*Cucurbita maxima*) seeds

Cucurbita maxima seeds are rich in phytochemical composition, serving as essential metabolites for functional foods. These nutrients play a crucial role in promoting health and prevent diseases [3]. Notably, *Cucurbita maxima* seeds are an excellent source of phenolic compounds, which have garnered significant attention from researchers due to their promising health benefits for humans [46]. Phenolic represent a diverse group of secondary metabolic products in plants and are known for their potent antioxidant properties [47, 48]. Their hydroxyl functional groups provide radical-scavenging abilities, making them effective in reducing the risk of oxidative stress-induced degenerative diseases [46]. The predominant phenolic compounds in *Cucurbita maxima* seeds include ferulic, vanillic acids, vanillin, tyrosol, p-hydroxybenzoic, caffeic and smaller amounts of trans-p-coumaric, syringic acids, luteolin and protocatechuic. These compounds contribute to the *Cucurbita maxima* seeds health-promoting potential. *Cucurbita maxima* are also an excellent source of vitamin E, which includes four tocopherol and tocotrienol isomers (α, β, γ and δ) [48, 49]. These isomers differ only in the number and position of the methyl groups on their chromanol ring [49, 50]. However, only one isomer (d-RRR-α-tocopherol) meets the criteria to be classified as true vitamin E [48]. While sunlight facilitates the synthesis of vitamin E in the human body, many plants, including *Cucurbita maxima* seeds, serve as rich dietary sources of this essential nutrient. Tocopherols and tocotrienols in *Cucurbita maxima* seeds are potent antioxidants capable of neutralizing highly reactive radicals by donating H + ion from their rings [7, 47]. Additionally, *Cucurbita maxima*

seeds are a valuable source of phytosterols. Phytosterols have been extensively studied for their cholesterol-lowering effects, particularly in reducing low-density lipoprotein (LDL) [51, 52], which translates to a decreased risk of cardiovascular diseases. Furthermore, numerous studies suggest that phytosterols may lower the risk of certain cancers [47, 53] and improve the management of prostate complications [54]. This high phytosterol content in *Cucurbita maxima* seeds makes them a promising and suitable nutraceutical option for managing various non-communicable diseases in humans [55].

3. Nutraceutical benefits of pumpkin (*Cucurbita maxima*) seeds

Cucurbita maxima is a well-known medicinal plant and is considered a functional food that promotes human health when consumed safely as shown in **Figure 1**. Its numerous biologically active components such as proteins, peptides, polysaccharides, sterols, fixed oils and para-aminobenzoic acid make it highly beneficial for human consumption [1]. The therapeutic potential of *Cucurbita maxima* seeds against various human diseases is attributed to their bioactive compounds, which produce distinct physiological effects in the human body.

3.1 Antihypertensive and cardio-protective activity

Blood pressure in the arteries remains persistently high due to a long-term health condition known as hypertension, which is a major risk factor for cardiovascular diseases. *Cucurbita maxima* seed oils are rich in bioactive medicinal component compounds, including monounsaturated and polyunsaturated fatty acids like omega 3, omega 6, oleic acid and linoleic acid, which play a significant role in reducing the risk of hypertension and cardiovascular illness [56]. Studies have shown that *Cucurbita maxima* seeds exhibit hypotensive effects and demonstrate favorable drug interaction outcomes when administered in animal models alongside commonly used antihypertensive medications, with commonly, such as felodipine [57].

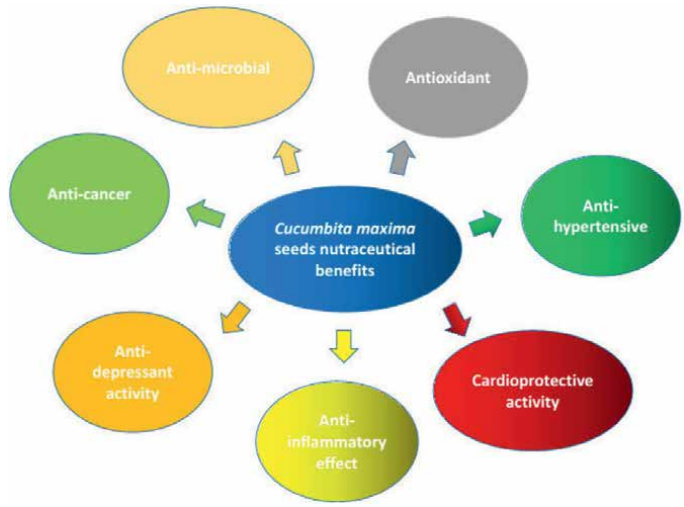

Figure 1.
Nutraceutical benefits of Cucurbita maxima *seeds.*

3.2 Anticancer activity

The phytoestrogenic compounds present in *Cucurbita maxima* seeds make them a promising candidate for preventing hormone-dependent cancer. The anticancer activity of the *Cucurbita maxima* seeds extract was evaluated on MCF7, Jeg3 and BeWo (chorionic carcinoma) cell lines, demonstrating significant cytotoxic activity and notable estradiol production. These results suggest that, like many phytoestrogenic substances, *Cucurbita maxima* seeds, rich in lignans and flavones, exhibit a biphasic effect through various pathways, possessing both estrogenic and antiestrogenic activities [58]. It is reported that consuming 20–40 mg/kg of pumpkin seed oil orally for 20 days can help reduce testosterone-induced prostate gland enlargement [59]. Additionally, the application of *Cucurbita maxima* seed oil has been shown to slow the progression of testosterone-induced hyperplasia. These findings highlight the potential of *Cucurbita maxima* seed oil in managing benign prostatic hyperplasia [60].

3.3 Anti-inflammatory effect

The management of numerous diseases can be supported by preventing inflammation, which is a significant risk factor for various pathological conditions such as cancer, cancer and other concerns. The anti-inflammatory effects of *Cucurbita maxima* seeds are primarily attributed to their rich content of polyphenols and other antioxidant compounds. These bioactive components help reduce inflammation by neutralizing free radicals and modulating inflammatory pathways [59].

3.4 Antidepressant activity

Depression is the most common brain disorder, characterized by disruptions in sleep, eating habits, interests and desires. *Cucurbita maxima* seeds have gained pharmacological importance as a natural source of antidepressant properties. They exhibit an antidepressant food score of 47%, primarily due to the presence of 5-hydroxytryptophan, a tryptophan intermediate that aids in serotonin (a neurotransmitter) formation [61]. Furthermore, *Cucurbita maxima* seeds are a remarkable source of zinc, which plays a crucial role in brain's conversion of tryptophan into serotonin, thereby promoting a sense of well-being.

3.5 Antioxidant activity

Cucurbita maxima seeds contain β-carotene, making them both nutritionally and pharmacologically balanced. β-Carotene, tocopherols and other carotenoid components in *Cucurbita maxim* seeds exhibit antioxidant activities, protecting cells from damage caused by reactive oxygen species and other free radicals [62]. Additionally, *Cucurbita maxima* seed extracts demonstrate antioxidant and geno-protective effects [63].

3.6 Antimicrobial activity

Cucurbita maxima seed oil, rich in linoleic and oleic acids, exhibits strong antibacterial properties against *Staphylococcus aureus*. It demonstrated a zone of inhibition of 15 mm. *Cucurbita maxima* seed extract in tests against *Bacillus subtilis*, *Staphylococcus aureus* and *Escherichia coli*, pumpkin seed extracts in petroleum ether and methanol, tested at concentrations of 10, 50, 100, 200, 500 and 1000 g/mL were

effective against *Pseudomonas aeruginosa*, *Candida albicans*, *Acinetobacter baumanii*, *Enterococcus faecalis*, *Klebsiella pneumonia*, *Escherichia coli* and *Staphylococcus aureus* are successful. Additionally, *Cucurbita maxima* seed oil has shown significant antibacterial activity against *Pseudomonas aeruginosa, Candida albicans, Acinetobacter baumanii, Enterococcus faecalis, Klebsiella pneumonia, E. coli and Staphylococcus aureus.* A polysaccharide derived from *Cucurbita maxima* seeds also display antibacterial properties, with a dosage of 0.5 mg/mL, significantly suppressing against *Escherichia* coli (12.8 ± 1.0 mm) and *Bacillus subtilis* (7.2 ± 0.3 mm), while showing a modest zone of inhibition against *Pichia fermentans* (2.3 ± 0.2 mm) and *Staphylococcus aureus* (2.3 ± 0.2 mm) [59].

3.7 Other nutraceutical benefits

In addition to the thematic nutraceutical benefits discussed above, the *Cucurbita maxima* seed exhibits ameliorative effects on hepato-inflammation, lipotoxicity and healing wounds [7, 64]. Furthermore, the seeds contribute to the prevention of Alzheimer's and Parkinson's diseases, anemia, benign prostate hyperplasia, hypercholesterolemia and hyperlipidemia [3].

4. Development of value-added products from *Cucurbita maxima* seeds

Food is a fundamental necessity of all living organisms. In everyday life, we consume food in both raw and processed forms. Nowadays, we mostly consume artificial foods that have some side effects [65]. *Cucurbita maxima* seeds are cultivated for their nutritional and medicinal benefits and are widely used in the production of various food items, including jellies, purees, jams, syrups, etc. In recent decades, utilizing *Cucurbita maxima* wastes, particularly the seeds as a functional food ingredient, have introduced new opportunities and challenges. These are incorporated into crackers, cookies, cakes, snacks, bread, muffins, cereal bars and other baked goods are all made with pumpkin seeds. The nutritional profile of these products is enhanced by the addition of *Cucurbita maxima* seeds, which also serve as a taste enhancer in dressings, soups and baked good [66–68]. Food producers are increasingly using *Cucurbita maxima* seed to create innovative and nutrient-rich products, as shown in **Table 1** and **Figure 2**. Its nutty flavor and appealing green hue make it a versatile ingredient in modern food applications [69]. Various studies have been conducted to develop value-added products including dietary supplements and food additives using *Cucurbita maxima* seeds.

4.1 Additional value-added products from *Cucurbita maxima* seeds

Cucurbita maxima seeds have significant potential for transformation into high-value products such as edible or biodegradable film. Defatted *Cucurbita maxima* seed meal has been effectively utilized in bio-based films, which not only provide an eco-friendly alternative but also help mitigate environmental issues relating to composting. These films are particularly suitable for applications in cakes, desserts and baked goods. The waste generated from *Cucurbita maxima* rich in carbon content, making it a desirable renewable substrate for producing added-value products [59]. The seed cake of *Cucurbita maxima,* a byproduct of oil extraction, can be used to develop edible coating materials with enhanced properties such as gas permeability, protein

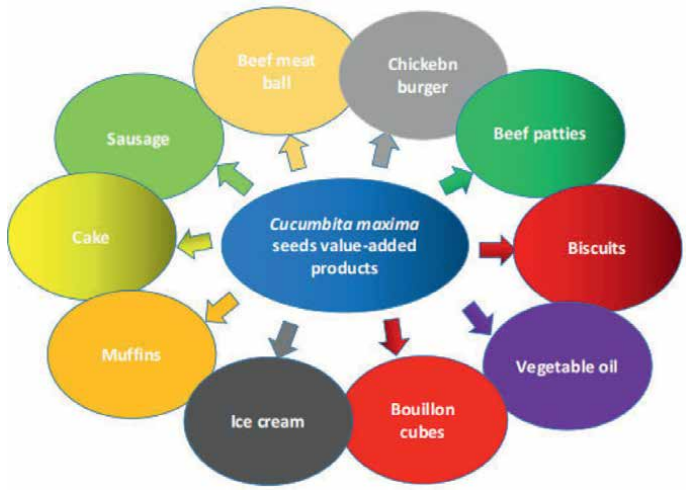

Figure 2.
Development of value-added products Cucurbita maxima *seeds.*

concentration, film thickness and mechanical barrier [70]. Using H_3PO_4 as a chemical agent, the pore structure of the activated carbon can be significantly influenced by adjusting the impregnation ratio and activation temperature [71]. This demonstrates that *Cucurbita maxima* seed shells are promising raw materials for producing commercially viable activated carbon.

5. Conclusion

Cucurbita maxima seeds are highly nutritious and categorized as super-food due to their exceptional properties. Their nutritional and bioactive components make them valuable nutraceutical foods. Once considered waste and underutilized, the nutraceutical potential of *Cucurbita maxima* seed is now widely recognized, leading to their incorporation into various applications. *Cucurbita maxima* seeds possess numerous – health promotion and are beneficial in managing ailments such as cancer, cardiovascular disease, benign prostate hyperplasia, Alzheimer's disease, Parkinson's disease, diabetes and hyperglycemia. They are a rich source of antioxidant compounds that enhance overall health and help prevent a range of diseases. The development of value-added products from *Cucurbita maxima* seeds has highlighted their suitability and utilization, creating market opportunities while promoting their beneficial nutritional and nutraceutical properties.

Conflicts of interest

The authors declare no conflict of interest.

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Author details

Adeyanmola Oluwaseyi Faturoti* and Clement Olusola Ogidi
Department of Food Science and Technology, Olusegun Agagu University of Science and Technology, Okitipupa, Nigeria

*Address all correspondence to: oluwaseyiakintade@gmail.com

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Chapter 5

Microgreens Technology and Automation

N. Malligarjunan and A. Anandkumar

Abstract

In the twenty-first century, rising lifestyle-related health issues such as obesity, diabetes, hypertension, and cancer are closely linked to changing socio-economic and cultural patterns. A major contributing factor is limited access to fresh, chemical-free vegetables, especially in urban areas. Cities often rely on long supply chains from rural regions, affecting the freshness and nutritional value of perishable produce. As a result, many urban zones are considered "food deserts," with limited availability of fresh fruits and vegetables. This leads to increased consumption of processed foods, contributing to hidden hunger and deficiencies in essential nutrients. In India, this issue is particularly pressing, with the country ranked 107 out of 121 in the 2022 Global Hunger Index. To address this, microgreens have emerged as a viable solution. These young vegetable greens are rich in bioactive compounds and nutrients, offering high nutritional value despite their small size. Their short growth cycle, minimal space requirements, and suitability for urban farming make them ideal for improving nutrition in cities. Microgreens are increasingly recognized as "smart foods" that can bridge nutritional gaps and combat lifestyle diseases, offering a sustainable and accessible approach to enhancing public health nutrition.

Keywords: urban agriculture, nutritional security, lifestyle diseases, food deserts, microgreens, sustainable nutrition

1. Introduction

Microgreens, those tiny, nutrient-packed powerhouses, have become increasingly popular in recent years, adding a burst of flavor and vibrant color to dishes around the world. These miniature greens are not just a pretty garnish; they are a culinary delight that can elevate the flavor of any dish. Microgreens are young vegetables harvested just after the cotyledon leaves have developed, typically between seven and 21 days after germination. This sets them apart from sprouts, which are germinated seeds harvested much earlier, usually within 2 to 7 days. The difference in harvesting time is significant.

Microgreens are allowed to grow until they develop their first true leaves, giving them a more developed root system and stronger stem structure. This extra time in the growing cycle allows them to absorb more nutrients from their growing medium, often soil or a soil substitute like coco coir. As a result, microgreens generally contain a higher concentration of vitamins, minerals, and antioxidants compared to sprouts.

Microgreens are a versatile ingredient that can be used in a variety of dishes, from salads and sandwiches to soups and stir-fries. They are also incredibly easy to grow, requiring very little physical effort and space. In fact, we can produce a significant amount of product from a small vertical setup. The popularity of microgreens is not just due to their taste and convenience; they are also a nutritional powerhouse. They are a great source of fibers, essential minerals, vitamins, and antioxidant compounds. Microgreens have been shown to have elevated levels of vitamins E, C, and K, as well as concentrated levels of beta-carotene and lutein [1].

In fact, they can contain up to 40 times more nutrients than a mature plant. Growing microgreens at home is a fun and rewarding experience. We can start with a seed tray, growing medium (soil or soilless), and seeds. Keep the tray in a sunny location, water often, and within 7–21 days we will have delicious, nutritious microgreens ready for harvest. With a little effort, we can enjoy the benefits of these tiny, mighty greens in our own home. In the twenty-first century, lifestyle changes associated with the improved standard of living in terms of social, economic, and cultural standards have been linked to major lifestyle-associated problems such as obesity, diabetes, hypertension, cardiovascular diseases, and various types of cancer. Alongside, the unavailability of fresh and chemical-residue-free vegetables for consumption has been identified as a significant issue for the urban population. Reliance is primarily placed on long food chains that originate in distant rural areas, thereby limiting the availability of fresh commodities with short shelf lives and poor shipping ability.

2. History

Microgreens were not known before the 1980s. **Figure 1** shows a simple microgreens farm. They were not even referred to as microgreens at that time. As the second major stage of plant growth, microgreens remained undiscovered while sprouts and full-grown vegetables were given all the attention. Microgreens began being featured on chefs' menus as early as the 1980s in San Francisco. In Southern California, microgreens were grown starting in the mid-90s.

The term "Microgreens" was coined by Craig Hartman in 1992. Initially, a few varieties such as arugula, basil, beets, kale, and cilantro were offered in a colorful mixture known as "Rainbow Mix." As these tiny, flavorful plants were included by Californian chefs in high-end restaurant dishes, their popularity grew rapidly and was spread westward across the U.S. over the next 30 years.

In India, microgreen farming and its consumption are still considered to be at a very nascent stage. Awareness is largely restricted to a few metro and larger cities where some knowledge about microgreens exists. As a result, microgreens are strictly regarded as a component of "urban horticulture" without any doubt. **Figure 1** shows the microgreen farm under suitable temperature conditions.

3. Differences among sprouts, microgreens, and baby greens

Microgreens are distinguished from sprouts in the sense that sprouts are germinated seeds consumed along with the embryonic root and seeds. Microgreens are also differentiated from baby greens by their size, as they are much smaller than baby greens. Their status is regarded as being between sprouts and baby greens [2]. Microgreens are considered much healthier and more nutritionally valuable than

Figure 1.
Microgreens farm.

sprouts and baby greens because they are concentrated with enzymes, flavonoids, and natural flavors [3]. The potential for bacterial growth is reported to be much lower in microgreens compared to the other two [4].

3.1 Why microgreens?

At the tiny stage of a plant, the development of the epidermis is minimal, and as a result, the bioavailability of nutritional compounds is considered much higher in microgreens than in mature plants. Microgreens are recognized as essential because:

i. *Rich in nutrients*

Microgreens are acknowledged for having a higher concentration of nutrients than mature vegetables and herbs. For example, the content of lipophilic vitamins like vitamin E is reported to be 40 times higher in microgreens than in mature plants. Microgreens are noted as rich sources of minerals such as K, Fe, Zn, Mg, and Cu [5]. Spinach microgreens are observed to have higher levels of phytonutrients and carotenoids than mature leaves. Microgreens from the Brassica genus are recognized as good sources of phenols. After 7 days of germination, lettuce microgreens have been found to contain the highest antioxidant and total phenolic concentrations compared to mature plants [6]. Concentrations of ascorbic acid, carotenoids, phylloquinone, and tocopherols in red cabbage, cilantro, amaranthus, and daikon radish microgreens, respectively, are significantly higher when compared to their fully grown vegetable counterparts [7]. In general, microgreens are considered rich sources of α-carotene, β-carotene, neoxanthin, violaxanthin, and lutein [8].

ii. *Low in anti-nutritional factors*

The concentration of anti-nutritional factors like nitrate and nitrite is reported to be significantly lower in microgreens compared to mature plants.

iii. *Packed with flavors*

Despite being tiny, microgreens are noted for their concentrated flavors, making them a favorite of chefs and food enthusiasts worldwide [4].

iv. *Year-round cultivation*

Microgreens can be cultivated throughout the year since, at young stages, seedlings generally do not require specific weather conditions. Additionally, microgreens can be produced using limited inputs, making them very useful for individuals residing in urban and peri-urban areas where land availability is minimal.

v. *Easy to grow*

Microgreens are recognized as easy to grow inside residential areas. Due to their short growth cycle, they can be successfully cultivated without soil or external inputs like chemical fertilizers, fungicides, and pesticides. Thus, they are regarded as a potentially "chemical-free product."

vi. *Quick to harvest*

Microgreens are ready for harvest within 2 weeks of seed sowing at the maximum.

vii. *Low start-up costs*

Microgreen farming is considered a low-investment business as the input requirements are minimal.

viii. *High-value crops*

Crops grown as microgreens are generally regarded as high value. Farmers can fetch premium prices by selling their products to high-end restaurants and malls.

4. Health benefits of microgreens

Since microgreens are recognized as being rich in nutrients, vitamins, minerals, and antioxidants (**Table 1**), their consumption at regular intervals is associated with a reduction in the risk of many diseases, including:

i. *Heart disease:*

A high concentration of antioxidants, such as polyphenols, found in microgreens is believed to reduce the risk of heart disease. It has been reported by Huang et al. [9] and Tangney and Rasmussen [8] that the levels of triglycerides and "bad" LDL cholesterol may be lowered by microgreens. Moringa and beet microgreens are noted for their role in controlling blood pressure, while moringa microgreens are also associated with aiding weight management and lowering cholesterol levels.

Microgreen	Days to harvesting	Antioxidant activity (μmol TE/g)
Bottle gourd	11	8.35
Cucumber	9	4.65
Pumpkin	10	8.92
Katwa	12	4.58
Sweet corn	19	15.90
Basella	12	3.90
Jute	9	21.55
Waterspinach	9	20.23
Radish	9	17.77
Palak	11	6.71
Carrot	15	26.81
Fennel	14	16.88

Table 1.
Antioxidant potential of microgreens.

ii. *Diabetes:*

The presence of antioxidants in microgreens has been linked to a reduced risk of type II diabetes. Fenugreek microgreens have been found to suppress the activity of the enzyme responsible for glucose production, thereby aiding in the management of blood glucose levels [10].

iii. *Alzheimer's disease:*

Microgreens, being rich in antioxidants including polyphenols, are believed to decrease the probability of memory-related diseases such as Alzheimer's [11].

iv. *Several types of cancer:*

Microgreens such as broccoli, chickpea, buckwheat, flax, mustard, and rutabaga, which are high in polyphenols, are regarded as having the potential to lower the risk of various types of cancer.

v. *Weight management:*

Microgreens are considered helpful in avoiding weight-related problems. Red cabbage microgreens are reported to hinder weight gain. Although the mechanism remains uncertain, the effects of this microgreen might be linked to its ability to reduce adipogenesis. Phytochemicals present in microgreens, such as I3C and a carotene metabolite, retinoic acid (RA), have been shown to reduce adipogenesis [12].

vi. *Microgreens constipation problems*:

They are noted for their effectiveness in improving vision and are reported to exhibit strong antiseptic and anti-inflammatory properties. They are also recognized for their significant role in treating anemia and alleviating. **Table 1** depicts the antioxidant potential of microgreens, expressed in μmol TE/g.

5. Selection of crops for microgreens

Selection criteria:

i. Crops must be raised through seeds.

ii. The crops should be characterized by a quick germination process and ease of growth.

iii. Crops with high nutritional value should be selected.

The most suitable microgreens are identified in vegetable crops belonging to the families Brassicaceae, Amaranthaceae, Apiaceae, and Chenopodiaceae [6]. Species commonly used for microgreen farming from various plant families are listed in **Table 2**. Different color shades are noted in these families due to the presence of pigments such as chlorophyll, anthocyanins, carotenoids, and betalains.

Chlorophyll is responsible for providing light green to dark green colors, whereas carotenoids are associated with yellow hues in microgreens. Two yellow-colored microgreens, yellow popcorn shoots and yellow pea tendrils, are gaining popularity in western markets; these colors are achieved through etiolating. Anthocyanins impart purple hues to microgreens belonging to the families Apiaceae and Brassicaceae. Betalains are noted for providing vivid red-pink to yellow shades, primarily in plants of the families Amaranthaceae and Chenopodiaceae.

Microgreens from the families Brassicaceae and Apiaceae are recognized for their distinct flavors, making them suitable for garnishing various dishes. Microgreens are also cultivated from cereal crops such as rice, oats, wheat, corn, and barley, as well as from legumes like chickpeas, beans, and lentils. These crops

Family	Name	Scientific name	Color	Bioactive compounds
Brassicaceae	Arugula	*Eruca sativa* Mill.	Green	Glucosinolates, Phenolics
Fabaceae	Lentil	*Lens culinaris Medikus*	Green	Phenolics, folic acid
Amaranthaceae	Amaranthus	*Amaranthus tricolor* L.	Greentored	Phenolics, betalains
Chenopodiaceae	Swiss chard	*Belavulgaris varicla* L.	Green	Phenolics, betalains
Apiaceae	Carrot	*Daucus carota* L.	Greento purplish green	Phenolics, polyacetylene
Poaceae	Popcorn shoots	*Zea mays* L.	Yellow	Carotenoids
Lamiaceae	Basil	*Ocimum basilicum* L.	Greento Greenish-purple	Phenolics
Convolvulaceae	Waterspinach	*Ipomoea aquatica* Forssk.	Green	Phenolics
Polygonaceae	Sorrel	*Rumex acetosa* L.	Greento reddish-green	Phenolics, betalains

Table 2.
Commonly used microgreens and predominant bioactive compounds present in those species.

exhibit varied tastes, which are described as ranging from neutral to spicy, slightly sour (e.g., chickpeas or Bengal gram), or even bitter (e.g., fenugreek), depending on the crop.

6. Microgreens automation technology

6.1 Literature summary

Microgreens are gaining popularity due to their nutritional density and vibrant flavors, making them a promising avenue for urban farmers seeking sustainable and innovative solutions.

Automation is revolutionizing microgreens farming by providing precise control over growing conditions, leading to consistent yields and quality, and enabling vertical farming techniques.

Various automated systems, such as the *Kratky method*, *InstaGreen*, and *Microwth*, offer efficient and scalable solutions for home and urban microgreens cultivation, utilizing hydroponics, smart watering, and advanced technology.

6.2 Automated system descriptions

The world of microgreens is experiencing a surge in popularity, driven by their nutritional density and vibrant flavors. These tiny powerhouses, harvested just weeks after germination, offer a sustainable and innovative solution for urban farmers and enthusiasts alike. As space becomes a premium and the demand for local, fresh produce grows, microgreens farming stands out as a promising avenue. However, like any emerging industry, challenges exist alongside opportunities.

To overcome the challenges of cultivating microgreens, farmers are turning to automation. Microgreens, with their short growth cycles and delicate nature, require precise conditions to thrive. Traditional farming methods often struggle to maintain consistency, leading to inconsistent yields and quality. The need for a controlled environment paved the way for the integration of automation into microgreens farming.

Automation bridges the gap between the unpredictable nature of agriculture and the precision of technology. Sensors monitor factors like soil moisture, humidity, light intensity, and temperature in real time, allowing for immediate adjustments to ensure optimal growth conditions. This tight monitoring leads to more predictable harvests in both quantity and quality, crucial for farmers supplying consistent produce to demanding markets.

The introduction of automation has also unlocked the potential for vertical farming in microgreens cultivation. As urban spaces shrink and the demand for local produce rises, vertical farming offers a solution that maximizes yield per square foot. Automated systems ensure that each layer in a vertical setup receives the exact amount of water, nutrients, and light it needs. This multilayered approach not only multiplies the yield but also embodies the essence of sustainable agriculture.

The *Kratky method*, a passive hydroponic system, provides a simple and efficient way to cultivate nutritious plants at home. This method involves growing plants suspended over a nutrient-filled water reservoir, eliminating the need for electricity, pumps, and airstones. The Kratky method is particularly well-suited for microgreens due to their short growth cycle, minimizing the risk of root rot that can occur in mature crops.

The Kratky method is a simple hydroponic technique that involves growing plants in net pots filled with an inert medium above a reservoir of nutrient-rich water, allowing the roots to access oxygen through an air gap created by the decreasing water level.

This method is particularly well-suited for growing microgreens and leafy vegetables due to its low maintenance and cost-effectiveness, and its ability to minimize the risk of root rot.

The Kratky method is a sustainable and efficient way to grow plants, using less water than traditional soil-based gardening and allowing for increased plant density in limited spaces.

The *InstaGreen* cultivation system offers a low-tech, scalable design for urban farmers. This system utilizes smart watering trays, watering slides, and natural phenomena like capillarity and gravity to deliver water, oxygen, and nutrients to the growing greens. The system focuses on high-quality LED lighting and automated irrigation, ensuring efficient growth while minimizing energy consumption.

The InstaGreen cultivation system is a low-tech, scalable design for urban farmers, which utilizes natural phenomena like capillarity and gravity to deliver water, oxygen, and nutrients to plants.

The system's focus on high-quality LED lighting and automated irrigation ensures efficient growth while minimizing energy consumption, promoting a circular economy approach to urban farming.

The InstaGreen system's design promotes a more sustainable and resilient food system in urban areas by addressing the challenges of urban agriculture through its practical and environmentally friendly approach.

The *Microwth* system provides a comprehensive approach to indoor microgreens cultivation. It features a pump to keep the grow medium moist, lighting to optimize growth speed, and an user interface with internet connectivity to create custom grow cycles and receive notifications. The system also includes a camera to monitor growth progress and identify potential problems.

The Microwth system is an indoor microgreen cultivation system that utilizes technology to optimize growth and yield.

The system features a pump for consistent moisture, specialized lighting for accelerated growth, and an intuitive user interface with internet connectivity for customized grow cycles.

The Microwth system also includes a built-in camera for remote monitoring of growth progress, allowing for early detection of potential problems and ensuring the production of healthy microgreens.

Table 2 shows the bioactive compounds in microgreens are known to aid in reducing oxidative stress, improving cardiovascular health, and boosting immunity. Their compact size and intense nutrient profile make them a valuable addition to diets aimed at enhancing overall well-being. Integrating microgreens into meals offers a simple yet effective way to harness their health-promoting properties.

Table 3 provides an overview of commonly grown microgreens, detailing their estimated germination and harvest times. Germination time refers to the number of days required for the seeds to sprout and emerge as seedlings, while harvest time indicates the total duration from sowing to the point when the microgreens are ready for consumption.

Table 4 provides insights into the germination percentage of various microgreen species grown on different substrates. Germination percentage reflects the proportion

Microgreen name	Germination time	Estimated time to harvest
Amarantha red desi	3–5 Days	9–12 Days
Amarantha red garnet	2–3 Days	7–10 Days
Alfa alfa	1–2 Days	7–9 Days
Carrot	3–5 Days	10–12 Days
Chia	2–3 Days	8–10 Days
Flax	2–3 Days	8–10 Days
Garden cress	2–3 Days	8–12 Days
Lettuce green	1–2 Days	7–9 Days
Mustard yellow	1–2 Days	7–9 Days
Redonion desi	2–3 Days	8–12 Days
Pak choi/Bak choy	1–2 Days	8–12 Days
Radish daikon	1–2 Days	7–10 Days
Radish desi	1–2 Days	7–10 Days
Radish purple	1–2 Days	7–10 Days
Radish pink	1–2 Days	7–10 Days
Red cabbage	2–3 Days	9–12 Days
Sesame white	2–3 Days	7–10 Days
Spinach/palak	3–5 Days	10–14 Days
Swiss chard	3–5 Days	10–14 Days
Turnip desi	1–2 Days	7–10 Days

Table 3.
List of microgreens with estimated germination and harvest time.

Species	Growing substrate	Germination percent
Red radish	Peat70% + Perlite30%	85%
	Cellulose	80%
Red basil	Peat70% + Perlite30%	90%
	Cellulose	80%
Peas	Peat70% + Perlite30%	70%
	Cellulose	65%
Sunflower	Peat70% + Perlite30%	70%
	cellulose	80%

Table 4.
Germination percentage of microgreens depending on species and growing substrate.

of seeds that successfully sprout under given conditions, offering a measure of seed viability and suitability for a specific growing medium.

Table 5 highlights the average height and weight of microgreens based on their species and the growing substrate used. These parameters are crucial for evaluating

Species	Growing substrate	Growing model	Average height of the plants (cm)	Average weight of the plants when sold (g/pot)
Red radish	Peat 70% + Perlite 30%	Growing benches	11.2	22.3
	cellulose		10	21.5
	Peat 70% + Perlite 30%	Vertical system	12.9	23.6
	cellulose		12.1	22.4
Red basil	Peat 70% + Perlite 30%	Growing benches	10.5	20.1
	Cellulose		9.6	19.6
	Peat 70% + Perlite 30%	Vertical system	12	21.5
	Cellulose		10.9	20.6
Peas	Peat 70% + Perlite 30%	Growing benches	11.7	12.4
	Cellulose		10.4	11.9
	Peat 70% + Perlite 30%	Vertical system	12.7	12.8
	Cellulose		11.8	12.2
Sunflower	Peat 70% + Perlite 30%	Growing benches	11	28.2
	Cellulose		10.4	27.4
	Peat 70% + Perlite 30%	Vertical system	13.3	28.9
	cellulose		12.6	27.5

Table 5.
Average height and weight of microgreens depending on species and growing substrate.

the quality and yield of microgreens, as height often indicates proper growth, while weight reflects the biomass and nutritional output.

7. Production technology of microgreens

Growing media: Microgreens are cultivated in pots, containers, baskets, and pro-trays/plug trays containing soil or various types of soilless growing media. A wide range of soilless media, such as coconut coir, wood fiber, paper fiber, bark, peat moss, rock wool, sphagnum moss, vermiculite, perlite, and vermicompost, is available in India for microgreen production. Media selection must be done carefully to ensure maximum seed germination. A mixture of cocopeat, vermiculite, and perlite in a ratio of 2:1:1 is recommended [6]. Before sowing, media must be sterilized completely to eliminate the risk of damping-off disease caused by fungal pathogens. Heat pasteurization is traditionally performed using steam, whereas inherently sterile media like vermiculite and perlite do not require sterilization. The release of macro- and micronutrients from the media is slow, enabling reuse for multiple crop cycles. Microgreen seeds typically do not require additional nutrition but need ideal conditions such as appropriate temperature and water moisture for germination [2]. Seed treatment with biocontrol agents like *Trichoderma virens* and *Trichoderma harzianum* is preferred when non-sterilized media are used.

Sowing: Seeds for microgreen production are procured from authentic sources. Seeds of vegetables such as cabbage, beet, alfalfa, knolkhol, radish, mustard,

and amaranth germinate easily and grow quickly. Adequate natural sunlight, low humidity, and good air circulation are required, as these conditions prevent the growth of pathogenic microorganisms. Seeds with hard coats are soaked in water for 4–24 hours, depending on the thickness of the seed coat. Seed sowing can be done year-round based on demand. When reusing media from previous sowings, roots and remnants must be removed completely. The media must be dried in sunlight before being refilled in trays or containers. Proper spacing during sowing is essential, as excessive density results in soft, elongated microgreens with smaller leaves and shorter shelf life. Approximately 10–12 seeds per square inch for smaller seeds and 6–8 seeds per square inch for larger seeds are recommended. Seeds are spread on the media surface and covered with a thin layer of decomposed farmyard manure or vermicompost for stability.

Aftercare: Containers with sown seeds are kept at room temperature until germination, after which they are shifted to sunny locations receiving 3–4 hours of sunlight daily. Watering is done twice daily to maintain media moisture until harvest. Care must be taken to prevent overwatering, which may lead to seedling wilting or death. Pests, diseases, and weeds are minimal due to the use of sterilized soilless media. Fertilizer application is generally unnecessary, although diluted organic nutrients like seaweed extract can enhance growth.

Harvesting: Microgreens are harvested 7–14 days after germination in tropical climates and 14–28 days in temperate conditions, depending on crop and environmental factors. Harvesting involves cutting microgreens with cotyledons, true leaves, and central stems using sharp blades or scissors to avoid damage. Proper hygiene practices during harvesting, such as wearing gloves and cleaning equipment, are essential to minimize contamination. Harvesters are required to use washable or disposable clothing and hair/beard nets. If not harvested timely, microgreens elongate and lose their color and flavor [13].

Postharvest operations: Due to high perishability, proper postharvest handling is critical. Microgreens are washed with cold running water and used fresh to maximize nutritional benefits. Pre-cooling techniques like hydro-cooling are applied to extend shelf life. NaOCl solution (100 mg chlorine/L, pH 6.5) treatment is used during hydro-cooling for microbial protection. After pre-cooling, moisture is removed, and microgreens are packed in plastic containers or biodegradable packaging. Modified atmospheric packaging (MAP) may extend shelf life, but optimization for individual commodities is required to prevent physiological disorders. Packaging labels must include cultivation details, harvesting date, and expiry.

Consumption: Microgreens are primarily consumed raw to preserve heat-sensitive micronutrients. They are used in salads, plate presentations, and cooked dishes as flavor enhancers. Proper hygiene practices must be maintained throughout production to prevent contamination.

Hydroponic cultivation: Hydroponics is considered a superior method to soil-based cultivation, eliminating issues like mold and reduced shelf life [14]. Comparative studies have shown better results in germination, plant height, and weight with peat-perlite mix of substrates and vertical hydroponic systems compared to growing benches and cellulose substrates [15].

Problems associated with microgreens:

- Short shelf life after harvest due to rapid dehydration and decay.
- High seed cost limits affordability for small farmers.

- Need for timely harvesting to maintain nutrient levels.
- Potential mild toxicity with excessive consumption.

Future scope:

- Expanded research on photoperiodism, nighttime temperatures, and food safety.
- Systematic studies on postharvest light treatments and their effects on nutrients.
- Optimization of washing and drying techniques for ready-to-eat products.

Conclusion: Microgreens, rich in bioactive compounds, serve as a "smart food" addressing nutritional deficiencies and lifestyle-related health issues. Increasing consumer awareness has boosted demand, making commercial cultivation a viable entrepreneurial option. Large-scale cultivation can support nutritional security and contribute to "Aatmanirbhar Bharat" by creating opportunities for young entrepreneurs.

8. Conclusion

Microgreens, often referred to as "vegetable confetti," are young seedlings of edible plants harvested within a short timeframe, typically 7–14 days after sowing [16]. They are distinguished by their fully expanded cotyledons (seed leaves) and the emergence of their first true leaves [16, 17]. This unique stage of development results in a concentrated burst of nutrients, making microgreens a nutritional powerhouse [18].

The popularity of microgreens has surged in recent years, driven by a growing awareness of their health benefits and the desire for fresh, functional foods [18, 19]. Chefs have embraced microgreens for their vibrant colors, delicate textures, and intense flavors, adding a touch of culinary sophistication to dishes [16, 18].

Microgreens are a versatile food source, capable of being grown in a variety of settings, including urban and peri-urban areas [20]. Their short growth cycle and minimal production requirements make them an attractive option for both home gardeners and commercial producers [18, 20].

The nutritional profile of microgreens is impressive, often exceeding that of their mature counterparts by a significant margin [20]. They are rich in vitamins, minerals, and bioactive compounds, including ascorbic acid, tocopherol, carotenoids, folate, and glucosinolates [18]. These compounds have been linked to a range of health benefits, including antioxidant, anticancer, antibacterial, anti-inflammatory, and anti-diabetic properties [19].

The potential of microgreens extends beyond their nutritional value. They offer a sustainable food source, particularly in urban environments where space is limited [19]. Their ability to be grown indoors, using controlled environment agriculture, reduces reliance on traditional farming practices and minimizes environmental impact [19, 21].

The future of microgreens is bright, with ongoing research exploring their nutritional properties, shelf life, sustainable production methods, and innovative growing and processing approaches [22, 23]. As interest in microgreens continues

to grow, we can expect to see further advancements in their cultivation, processing, and utilization, solidifying their place as a vital component of a healthy and sustainable food system.

Author details

N. Malligarjunan* and A. Anandkumar
Department of Electronics and Communication Engineering, Jai Shriram Engineering College, Tiruppur, Tamil Nadu, India

*Address all correspondence to: vkt.arjun@gmail.com

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Edited by Marcos Soto-Hernández, Mariana Palma-Tenango and Eva Aguirre-Hernández

Explore the complex world of medicinal and aromatic plants, where physiological development is intertwined with the biosynthesis of secondary metabolites. These extraordinary compounds, essential for plant defense and adaptation, are also invaluable sources of active pharmaceutical ingredients that enhance the medicinal and nutritional value of fruits, seeds, and cereals. This book provides a comprehensive overview of the factors that influence the production and variability of these bioactive compounds. Explore the dynamics of plant growth and the impact of biotic and abiotic factors, and discover how plants respond to stress and environmental interactions.

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