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A Comprehensive Review of Basil (*Ocimum basilicum* L.) in Greenhouse Production: Bioactive Compounds, Pharmacological Properties, and Responses to Water Deficit Stress

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ABSTRACT

Basil (*Ocimum basilicum* L.), a member of the Lamiaceae family, is among the most commercially significant medicinal and aromatic plants worldwide. The increasing demand for standardized, high-quality raw material has driven a shift from open-field cultivation to greenhouse production. However, the literature on basil phytochemistry and pharmacology has rarely been connected to greenhouse cultivation and stress physiology, and no unified framework links these topics. This review therefore synthesizes current knowledge on basil's bioactive constituents, their pharmacological activities, and the responses of basil to water deficit stress in greenhouse and other controlled-environment systems, with emphasis on recent advances and Iranian landraces. Basil produces a large number of metabolites (830 volatile compounds were detected in a recent leaf study), including rosmarinic acid, flavonoids, and volatile terpenoids, many of which exhibit antioxidant, antimicrobial, anti-inflammatory, hypoglycemic, neuroprotective, and anticancer activities. In greenhouse systems, water deficit is not an unavoidable stress but a manageable tool: mild to moderate, controlled deficit increases secondary metabolite production through upregulation of phenylpropanoid pathway genes, raising total phenolics by up to 40% and rosmarinic acid by up to 30%, whereas severe stress reduces biomass by more than 45%. Soilless systems offer the precise water and nutrient control needed to apply such strategies, so that yield and phytochemical quality can be balanced. Iranian native landraces are promising genetic resources for stress tolerance and phytochemical quality in greenhouse breeding programs. We conclude that controlled, mild to moderate deficit irrigation combined with precise greenhouse management can raise the concentration of bioactive compounds in basil, provided that biomass losses are kept low; future research should prioritize multi-omics approaches, CRISPR-based breeding, and sustainable greenhouse cultivation strategies.

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1. Introduction

The genus *Ocimum* encompasses approximately 150 annual and perennial species within the Lamiaceae family, with centers of diversity in tropical Asia, Africa, and Central America (Simon *et al*., 1999; Dhama *et al*., 2023). Basil, frequently designated as the "queen of aromatic plants," has over 60 cultivars cultivated globally (Azizah *et al*., 2023; Zhakipbekov *et al*., 2024). Sweet basil (*Ocimum basilicum* L.) holds paramount economic importance owing to its superior organoleptic properties and medicinal value. This plant serves not only as an aromatic vegetable and flavoring agent but also as a source of bioactive constituents—phenolics, flavonoids, and volatile oils—for the pharmaceutical, perfumery, and cosmeceutical sectors (Shahrajabian *et al*., 2020).

Global demand for basil and its derived products has increased substantially over the past decade, driving a fundamental shift from open-field cultivation to greenhouse production systems. This transition is not merely a matter of environmental convenience; it reflects a deeper transformation in how this high-value medicinal and aromatic plant is produced, traded, and utilized. Greenhouse cultivation enables year-round production, protects plants from adverse weather events, reduces pest and disease pressure, and allows precise control over environmental factors such as temperature, light, humidity, and water supply (Savvas and Gruda, 2018). In arid and semi-arid regions, including Iran, greenhouse production is particularly important because it reduces water consumption while maintaining high productivity and quality (Goldani *et al*., 2021; Savvas and Gruda, 2018).

Basil has been utilized in traditional medicine systems for centuries. Persian medicine prescribes it for stomach strengthening, indigestion, and nervous system fortification (Ezeorba *et al*., 2024). Traditional Chinese medicine employs basil for kidney disorders and circulatory enhancement (Makri and Kintzios, 2008). In Ayurveda, holy basil (*O. tenuiflorum*) is revered as the "elixir of life," while common basil is used for cough, bronchitis, diarrhea, and fungal infections (Vasincu *et al*., 2025). Scientific interest in basil has grown steadily since the mid-twentieth century, and a large body of literature has accumulated over the past two decades (Sestili *et al*., 2018). Basil is native to tropical Asia and is now cultivated across temperate and tropical regions worldwide. In Iran, wild and cultivated populations exist in the northern provinces (Mazandaran, Gilan, and Golestan) and in some central and southern regions. High genetic diversity among basil germplasms has generated numerous chemotypes based on predominant essential oil constituents (Bernhardt *et al*., 2015). Iranian native landraces, particularly those from the northern provinces, possess significant genetic and chemical diversity owing to long-term adaptation to humid conditions (Ghasemi Pirbalouti, 2014). Some of these landraces demonstrate superior drought tolerance and phytochemical quality compared with foreign cultivars, making them valuable genetic resources for greenhouse breeding programs (Karimi *et al*., 2020; Khakdan *et al*., 2021).

Despite the growing importance of greenhouse basil production, the existing literature lacks a comprehensive synthesis that integrates greenhouse cultivation practices with the plant's phytochemistry, pharmacology, and stress physiology. Previous reviews have focused primarily on open-field cultivation, general phytochemistry, or pharmacological properties, without addressing the unique challenges and opportunities of greenhouse production systems (Dhama *et al*., 2023; Zhakipbekov *et al*., 2024). Furthermore, the interaction between greenhouse environmental control—deficit irrigation, light management, CO_2 enrichment—and secondary metabolite production remains poorly understood, limiting the optimization of greenhouse basil production for both yield and quality. This review aims to: (a) present the nature and scope of basil's bioactive compounds and pharmacological properties, with emphasis on greenhouse-produced material; (b) provide comprehensive background on water deficit stress responses specifically within greenhouse and controlled-environment systems; (c) identify critical knowledge gaps and future research priorities for greenhouse basil production; and (d) provide practical recommendations for greenhouse growers, industries, and policymakers. By integrating greenhouse cultivation practices with stress physiology and phytochemistry, this review provides a novel framework for optimizing basil production in controlled environments. In this review, "controlled environment" refers primarily to greenhouse production, including soilless culture; other controlled systems such as plant factories (vertical farms) and shade-net houses are mentioned only where evidence from them informs greenhouse practice.

2. Botanical and Ecological Characteristics

2.1. Botanical Characteristics

Basil is an annual herbaceous plant with an erect, branched stem reaching 30–60 cm in height. Leaves are opposite, ovate to lanceolate, measuring 5 cm × 1–3 cm, with margins varying from entire to dentate (Romano *et al*., 2022). Coloration ranges from light green to dark purple owing to anthocyanins in purple cultivars (Azizah *et al*., 2023). A distinctive feature is the presence of essential oil-secreting peltate glands as transparent dots on both leaf surfaces (Ezeorba *et al*., 2024). Essential oils are synthesized and stored in these peltate glands (Gang *et al*., 2002; Iijima *et al*., 2004), and gland density contributes to differences in oil content among cultivars (Romano *et al*., 2022). Glandular and non-glandular trichomes are the main epidermal secretory and defensive structures (Makri and Kintzios, 2008). The inflorescence is a terminal spike or compound raceme (Vasincu *et al*., 2025). Flowers are arranged in whorls with a green to purplish calyx, a bilabiate corolla (white, pink, purple, or burgundy),

four stamens (two long and two short), and a superior ovary (Dhama *et al*., 2023). Flowering occurs from late spring to early autumn, providing important nectar sources for honeybees (Simon *et al*., 1999). The fruit is a dry schizocarp dividing into four quadrangular nutlets (Tel *et al*., 2025). Nutlets are dark brown to black, elliptic, and smooth, with a 1000-seed weight of 1.5–2.5 g. Seeds form a gelatinous mucilage layer upon contact with water (Romano *et al*., 2022). The root system is fibrous with a shallow taproot (20–30 cm depth) and lateral spread reaching 40–50 cm, rendering the plant susceptible to drought (Khalid, 2006). Several chromosome numbers—48, 50, 52, 56, 72, and 74—have been reported for *O. basilicum* (Carović-Stanko *et al*., 2010; Gonda *et al*., 2020). In a study of 22 accessions, Carović-Stanko *et al*. (2010) found 2n=48 in twenty *O. basilicum* accessions, whereas two accessions of the purple variety *O. basilicum* var. *purpurascens* Benth. had 2n=72.

2.2. Environmental Requirements for Protected Cultivation and Distribution

In protected cultivation, temperature, light, humidity, water, and nutrition are managed rather than imposed by the environment, so the requirements below are best read as target setpoints for greenhouse management; soil- and climate-related information is relevant mainly to soil-based greenhouses, to site selection, and to comparison with open-field production. Basil prefers warm, humid climates and is highly frost-sensitive; temperatures below 5 °C cause severe damage (Azizah *et al*., 2023). The optimal temperature for growth and essential oil production is 20–30 °C (Al-Huqail *et al*., 2020). The plant requires abundant light; low light levels reduce vegetative growth, yield, and photosynthetic capacity, and the daily light integral (DLI) is a key determinant of growth and yield under controlled conditions (Dou *et al*., 2018; Pennisi *et al*., 2019). Basil prefers fertile, well-drained soils rich in organic matter with a slightly acidic to neutral pH (Makri and Kintzios, 2008). It is relatively salinity-sensitive (ECe threshold 1.7–2.25 dS m^{-1}), with significant growth reduction above 4 dS m^{-1} (Corrado *et al*., 2021; Tel *et al*., 2025). Waterlogging causes root rot and plant death (Makri and Kintzios, 2008). Water requirements range from 400–600 mm over the growing period (Ekren *et al*., 2012). Basil requires nitrogen (for vegetative growth), phosphorus (for root development and flowering), and potassium (for essential oil quality and stress resistance) (Marschner, 2012; Nguyen *et al*., 2010). Mineral fertilization can also modify the bioactivity of basil (Gürgan and Adiloğlu, 2021). Organic amendments such as vermicompost (Kosem *et al*., 2022) and mycorrhizal inoculation (Copetta *et al*., 2006) can improve growth and quality while reducing chemical inputs. In Iran, basil is found in the northern (Mazandaran, Gilan, and Golestan), central (Tehran, Alborz, Isfahan, and Qom), southern (Khuzestan, Fars, and Bushehr), and western (East Azerbaijan and West Azerbaijan) provinces. Native populations in the northern provinces possess significant genetic and chemical diversity owing to long-term adaptation to humid conditions (Ghasemi Pirbalouti, 2014). These landraces are therefore a valuable resource for breeding programs, and their drought responses have been characterized in several Iranian cultivars (Karimi *et al*., 2020; Khakdan *et al*., 2021).

2.3. Important Cultivars and Classification

Based on morphology and chemical composition, sweet basil is classified into several varieties (Simon *et al*., 1999; Zhakipbekov *et al*., 2024):

1. Common Green Basil (*O. basilicum* var. *basilicum*): The most widespread type, with light to dark green, elliptic leaves and a sweet aroma. The predominant chemotype is linalool or methyl chavicol (Azizah *et al*., 2023). Cultivars include 'Genovese', 'Sweet Basil', 'Napoletano', 'Thai Basil', and 'Italian Large Leaf' (Romano *et al*., 2022).

2. Purple Basil (*O. basilicum* var. *purpurascens*): Purple to dark burgundy leaves containing significant anthocyanins (cyanidin-3-glucoside and pelargonidin-3-glucoside) (Phippen and Simon, 1998; Ozcan *et al*., 2025). These basils have a more pungent aroma. Anthocyanins provide antioxidant properties and serve as natural colorants (Gould, 2004; Ozcan *et al*., 2025). Cultivars include 'Dark Opal', 'Purple Ruffles', 'Round Midnight', 'Red Rubin', and 'Purple Basil' (Kwee and Niemeyer, 2011).

3. Lemon Basil (*O. basilicum* var. *citriodorum*): Strong lemon aroma with citral (neral + geranial) as the predominant constituent (Dudai and Belanger, 2016). Used in food, perfumery, and herbal teas (Baby and Nair, 2025). Cultivars include 'Lemon Basil', 'Mrs. Burns' Lemon', and 'Sweet Dani' (Romano *et al*., 2022).

4. Dwarf Basil (*O. basilicum* var. *minimum*): Compact growth with very small leaves (1–2 cm), used as an ornamental (Makri and Kintzios, 2008). Cultivars include 'Bush Basil', 'Balkon Star', 'Spicy Globe', and 'Greek Basil' (Simon *et al*., 1999).

5. Cinnamon Basil (*O. basilicum* var. *cinnamon*): Cinnamon aroma with methyl cinnamate as the predominant constituent (Ezeorba *et al*., 2024). This type of basil is native to Mexico and Central America (Baby and Nair, 2025).

6. Holy Basil (*Ocimum tenuiflorum*, syn. *O. sanctum*): A distinct species with a special position in Ayurveda. Leaves are greenish-purple with a pungent, camphoraceous aroma; the predominant constituents are eugenol and β-caryophyllene (Vasincu *et al*., 2025).

2.4. Greenhouse Production Systems for Basil

2.4.1. The Rationale for Greenhouse Cultivation: A Critical Perspective

Several interconnected factors drive the shift from open-field to greenhouse cultivation of basil. First, the pharmaceutical and nutraceutical industries require consistent, standardized raw material with reproducible phytochemical profiles—a requirement that open-field cultivation cannot reliably meet due to uncontrolled environmental variation (Sangwan *et al*., 2001). Second, the increasing frequency of extreme weather events—droughts, heatwaves, and unseasonal frosts—has made open-field basil production increasingly risky in many regions, including Iran (IPCC, 2021). Third, greenhouse systems enable year-round production, allowing processors to maintain continuous supply chains without seasonal interruptions (Raviv *et al*., 2019). However, greenhouse production is not without challenges. The enclosed environment creates unique microclimatic conditions—elevated humidity, restricted air movement, and altered light spectra—that can predispose plants to fungal diseases, particularly downy mildew (*Peronospora belbahrii*), which remains the most devastating disease of greenhouse basil worldwide (Wyenandt *et al*., 2015; Hasley *et al*., 2021). Furthermore, the energy costs of heating and supplemental lighting can be substantial, particularly in temperate regions, making economic viability dependent on premium product pricing or subsidy support (Carron *et al*., 2025). These challenges underscore the need for integrated greenhouse management strategies that balance productivity, quality, and sustainability.

2.4.2 Environmental Control: A Critical Analysis

Temperature: While the optimal temperature range for basil growth (20–30 °C) is well established (Al-Huqail *et al*., 2020), root-zone temperature is often overlooked in greenhouse management. Root-zone temperature can affect water and nutrient uptake and thus plant growth (Raviv *et al*., 2019), but its effect on essential oil accumulation in basil has received little attention and requires study. This has practical implications for greenhouse operations: bottom heating or root-zone temperature control may be necessary in cooler climates to maintain productivity during winter months.

Light: The relationship between light and secondary metabolite production in greenhouse basil is more complex than previously recognized. While supplemental lighting—particularly LED with adjustable red/blue ratios—can enhance phenolic compound production (Pennisi *et al*., 2019; Teliban *et al*., 2025), excessive light intensity can induce photooxidative stress, reducing both biomass and essential oil quality. Daily light integral (DLI) strongly influences basil photosynthesis, morphology, and yield, with higher DLI generally promoting greater fresh mass accumulation (Dou *et al*., 2018), whereas its effect on essential oil concentration is less consistent. This suggests a trade-off between biomass and quality that greenhouse growers must carefully manage depending on their target market—fresh culinary herb versus essential oil extraction.

CO_2 Enrichment: CO_2 enrichment is widely used in greenhouse production to increase biomass accumulation (Ainsworth and Rogers, 2007). However, the interaction between CO_2 enrichment and water deficit stress remains poorly understood. Elevated CO_2 typically reduces stomatal conductance (Ainsworth and Rogers, 2007), which could mitigate drought stress effects, but its consequences for the accumulation of stress-induced secondary metabolites in basil have not been established. This represents a critical knowledge gap for greenhouse basil production, particularly in water-limited regions where deficit irrigation is used to enhance phytochemical quality.

Humidity: Relative humidity (RH) management in greenhouses presents a fundamental trade-off: high RH increases the risk of fungal diseases, particularly downy mildew (Wyenandt *et al*., 2015), while low RH increases transpirational demand and may induce water stress even under adequate irrigation (Raviv *et al*., 2019). The optimal RH for greenhouse basil is likely to vary depending on cultivar, growth stage, and disease pressure.

2.4.3. Soilless Cultivation: A Paradigm Shift

Soilless culture has emerged as the preferred production system for greenhouse basil, offering several advantages over soil-based cultivation: precise control over water and nutrient delivery, elimination of soilborne pathogens, and improved product cleanliness (Savvas and Gruda, 2018). However, the choice of soilless system has profound implications for plant physiology and secondary metabolism.

Hydroponics: Nutrient film technique (NFT) and deep-water culture (DWC) are widely used, but not all hydroponic systems are equivalent for basil production. Comparative studies have shown that NFT systems achieve higher yields and shorter growth cycles (34 days) compared to conventional soil cultivation, but essential oil composition may differ significantly due to differences in nutrient availability and root-zone environment (Carron *et al*., 2025). Furthermore, electrical conductivity (EC) management is critical: while basil is relatively salinity-sensitive, mild and controlled salinity stress can enhance phenolic compound accumulation without large reductions in biomass—a phenomenon known as eustress (Corrado *et al*., 2021).

Aeroponics: Aeroponic systems, where roots are suspended in air and misted with nutrient solution, have shown promising results for herb production (Lakhiar *et al*., 2018). However, aeroponic systems are technically complex

and require precise control of misting frequency, droplet size, and nutrient concentration—failure to maintain these parameters can lead to rapid plant death. The economic viability of aeroponics for basil production remains questionable outside of high-value niche markets.

Substrate Culture: Organic substrates, particularly vermicompost and flaxseed oil cake (FOC), have shown additional benefits beyond simple physical support. Vermicompost application (25–50%) enhances drought tolerance and rosmarinic acid content (Kosem *et al*., 2022), while FOC (10 g dm^{-3}) improves basil yield under drought stress (Dutra *et al*., 2025). These benefits are attributed to microbial communities in organic substrates that enhance nutrient availability and induce systemic stress tolerance—a phenomenon that warrants further investigation.

2.4.4. Irrigation Management: The Deficit Irrigation Paradox

Water management is arguably the most critical factor in greenhouse basil production, not only because water is a limited resource but because controlled water deficit can enhance phytochemical quality. This "deficit irrigation paradox"—where mild stress improves quality while severe stress reduces yield—is particularly relevant in greenhouse systems where precise water control is possible. Research has demonstrated that maintaining 70% field capacity (FC) optimizes biomass and essential oil yield while saving 30% water in greenhouse conditions (Mulugeta and Radacsi, 2022). More aggressive deficit irrigation (60% of readily available water) can be applied without significant yield loss in some cultivars (Khater *et al*., 2021; Mousavi, 2026). However, the optimal deficit irrigation strategy depends on the target product: for fresh culinary herb production, maximum biomass is prioritized; for essential oil or phenolic extract production, mild stress (50–75% FC) may be preferable to enhance secondary metabolite accumulation (Kleinwächter and Selmar, 2015). A critical unresolved question is whether deficit irrigation protocols developed for soil-based greenhouse systems can be directly transferred to soilless systems. In soilless culture, substrate moisture sensors and evapotranspiration models can be used to precisely monitor and control water delivery (Raviv *et al*., 2019), but the optimal moisture setpoints may differ due to differences in substrate water-holding capacity and root-zone aeration. This represents a priority area for future research.

3. Bioactive Compounds

A wide range of pharmacologically active compounds has already been identified in basil, classified into volatile essential oils (terpenoids) and non-volatile compounds (phenolics, flavonoids, anthocyanins, and other secondary metabolites) (Table 1) (Ezeorba *et al*., 2024). Advances in analytical platforms have enabled comprehensive metabolite profiling; for example, headspace SPME-GC-MS identified 830 volatile compounds in sweet basil leaves (Zhou *et al*., 2025).

Table 1. Major bioactive compounds identified in basil.

Compound Category	Subgroup	Major Compounds	Organ	Analytical Method	References
Volatile Compounds (Essential Oil)	Phenylpropanoids	Methyl chavicol (estragole), eugenol, methyl eugenol	Leaf, flower, stem	GC-MS	Kirci *et al*., 2025; Paudel *et al*., 2025
	Oxygenated Monoterpenes	Linalool, geraniol, geranyl acetate, citral, 1,8-cineole, camphor	Leaf, flower	GC-MS	Lee *et al*., 2005; Kirci *et al*., 2025
	Sesquiterpene Hydrocarbons	β-Caryophyllene, γ-cadinene, α-humulene, (E)-γ-bisabolene	Leaf	GC-MS	Klimánková *et al*., 2008; Kirci *et al*., 2025
	Other Sesquiterpenes	Germacrene D, trans-β-bergamotene, β-elemene	Leaf, flower	GC-MS	Paudel *et al*., 2025; Kirci *et al*., 2025
Non-Volatile Compounds	Phenolic Acids	Rosmarinic acid, caffeic acid, chlorogenic acid, ferulic acid, gallic acid	Leaf, flower, stem	HPLC/UPLC-MS	Qayid Alotaibi *et al*., 2026

Modern extraction techniques, including ultrasound-assisted extraction (UAE), microwave-assisted extraction (MAE), and supercritical fluid extraction (SFE), have demonstrated superior efficiency (20–40% higher yield) and better preservation of heat-sensitive compounds compared with conventional hydrodistillation. The application of response surface methodology (RSM), in conjunction with machine learning algorithms, has significantly

enhanced the extraction efficiency of target bioactive compounds (Handayani *et al*., 2025). Furthermore, nanoemulsion-based formulations of basil essential oils have shown promising biological and chemical stability (El-Sakhawy *et al*., 2025).

3.1. Essential Oil Composition and Chemotypes

The essential oil yield of basil varies from 0.2% to 4.2%, depending on genotype, environment, harvest stage, and extraction method (Handayani *et al*., 2025). GC-MS analysis reveals a predominance of oxygenated monoterpenes and phenylpropanoids (Qayid Alotaibi *et al*., 2026). Various cultivars of basil are distinguished by their unique volatile compounds, which correlate directly with their sensory attributes (Bernhardt *et al*., 2015). For instance, Genovese-type basil, used in traditional pesto from Italy, is known for its high levels of linalool and eugenol (Dudai and Belanger, 2016). By contrast, Thai basil has its own unique chemical marker, methyl chavicol, which gives it the distinct aroma of anise. Cinnamon basil is known for the presence of methyl cinnamate in its composition (Dudai and Belanger, 2016). The essential oil extracted from *O. basilicum var. citriodorum* (lemon basil) consists mainly of citral (neral + geranial), which is formed from geraniol (Iijima *et al*., 2004). The sweet basil chemotype is defined by the major phenylpropene volatiles: eugenol in the case of Genovese sweet basil (for instance, Perrie) and methyl chavicol in the case of Thai sweet basil (such as Cardinal). A genetic study of an F_2 segregating population obtained from the crossing of both basil types has shown the existence of a reciprocal dependence of both phenylpropenes; increased accumulation of one correlates with decreased levels of the other (Dudai *et al*., 2018). The function of chavicol synthase in the production of methyl chavicol was demonstrated by Vassão *et al*. (2006). The activities of p-coumaroyl shikimate transferase (CST) and p-coumarate 3′-hydroxylase (C3′H) were reported to be limited to eugenol-accumulating basil, and no CST or C3'H activity was observed in methyl chavicol-accumulating plants (Gang *et al*., 2002). However, the gene coding for CST, similar to the family of HCT genes, was not isolated from basil. Large-scale evaluation of basil genotypes has further confirmed significant chemotypic diversity and variation in antioxidant capacity (Ghasemi Pirbalouti, 2014; Barut and Tansi, 2026).

Table 2. Essential oil chemotypes of basil

Chemotype	Predominant Compound (%)	Other Major Compounds (%)	Indicator Cultivars	Geographical Distribution	Chemical Stability	References
Methyl chavicol	Methyl chavicol (50–80%)	Linalool (5–15%), methyl eugenol	Thai basil, Egyptian basil	Africa	Moderate	Paudel *et al*., 2025
Citral	Neral + Geranial (50–70%)	Linalool (10–15%), geranyl acetate (up to 10%)	Lemon basil (*O. basilicum var. citriodorum*)	Tropical regions, Thailand	Moderate	Dudai and Belanger, 2016
Camphor/Linalool	Camphor (51–66%)	Linalool (10–20%), β-caryophyllene	*O. americanum*, African basil	Africa, Tropical Asia	High	Paudel *et al*., 2025

3.2. Phenolic and Flavonoid Compounds

Recently, a study was carried out that evaluated the phenolic acid profile and antioxidant activity in 22 different basil (*Ocimum basilicum* L.) cultivars, representing five different morphotypes (true, small-leaf, lettuce-leaf, purple A, and purple B), all cultivated under the same greenhouse conditions (Bajomo *et al*., 2022). The total phenolic content (TPC) of the basil cultivars varied from 3.07 to 4.99 mg gallic acid equivalents (GAE)/g dry weight (DW), and the TPC was affected by cultivar and morphotype, along with the antioxidant activities (cupric reducing antioxidant capacity [CUPRAC] and oxygen radical absorbance capacity [ORAC]). Based on hierarchical clustering analysis of the phenolic acid profile, five chemotypes of basil were identified: rich in caftaric acid (cardinal chemotype), rich in rosmarinic acid (basil cultivar Dark Opal), rich in caffeic acid (true basil types mostly), rich in caffeic and ferulic acid (Indian and Romanesco cultivars), and rich in chicoric acid (Rosie cultivar). The highest amount of phenolics and the best antioxidant properties were detected in green Genovese-type true basil cultivars ('Dolly', 'Jolina', 'Eleanora', and 'Emily'), and the lowest in lettuce-leaf morphotypes. Caffeic acid was the dominant phenolic acid in antioxidant basil cultivars, and there were significant positive correlations between TPC and CUPRAC (R = 0.5) as well as ORAC (R = 0.8) activities. Tables 3, 4, and 5 summarize the major phenolic acids, flavonoids, and anthocyanins, detailing their concentration ranges, primary sites of accumulation, and biological activities.

3.3. Nutritional Composition

Basil contains sterols (β-sitosterol: 8–15 mg/100 g; stigmasterol: 3–7 mg/100 g), vitamins (A: 2640–4500 IU; C: 18–30 mg; K: 170–420 µg; B9: 68–135 µg/100 g fresh weight), and minerals (Ca: 2.41%; P: 1.41%; Mg: 0.32%; N: 2.82%; Fe: 281.29 ppm; Zn: 47.27 ppm; Cu: 6.62 ppm) (Othman *et al*., 2022). The proximate composition includes moisture (10.58%), ash (14.12%), crude protein (17.66%), crude fat (2.53%), crude fiber (18.09%), and carbohydrates (55.11%), with a calorific value of 313 kcal/100 g (Othman *et al*., 2022).

Table 3. Major phenolic compounds of basil.

Compound	Concentration Range (mg/g DW)	Organ with Highest Concentration	Primary Biological Activity	References
Rosmarinic acid	1.5–8.2	Leaf	Potent antioxidant, anti-inflammatory, neuroprotective	Qayid Alotaibi *et al*., 2026
Caffeic acid	0.3–1.8	Leaf	Antioxidant, antimicrobial	Moraz-Alderete *et al*., 2025
Chlorogenic acid	0.2–1.5	Flower	Antioxidant, hypoglycemic	Qayid Alotaibi *et al*., 2026
Caftaric acid	0.1–0.9	Leaf	Antioxidant, hepatoprotective	Moraz-Alderete *et al*., 2025
Gallic acid	0.5–8.4	Leaf, stem	Potent antioxidant, anticancer	

Table 4. Major flavonoids of basil

Compound	Concentration Range (mg/g DW)	Organ with Highest Concentration	Primary Biological Activity	References
Quercetin	0.5–3.2	Leaf	Potent antioxidant, anti-inflammatory, anticancer	Moraz-Alderete *et al*., 2025
Luteolin	0.3–2.8	Leaf, flower	Neuroprotective, anti-inflammatory, antioxidant	Qayid Alotaibi *et al*., 2026
Apigenin	0.2–1.5	Flower	Anxiolytic, anti-inflammatory, anticancer	Moraz-Alderete *et al*., 2025
Rutin	0.2–1.8	Leaf, flower	Vasoprotective, antioxidant	Qayid Alotaibi *et al*., 2026
Kaempferol	0.1–0.9	Leaf	Anti-inflammatory, cardioprotective	Moraz-Alderete *et al*., 2025

Table 5. Major anthocyanins of purple basil

Compound	Aglycone Form	Indicator Cultivar	Color	Biological Activity	References
Cyanidin-3-glucoside	Cyanidin	Dark Opal, Red Rubin	Red-purple	Potent antioxidant, anti-inflammatory	Ozcan *et al*., 2025
Pelargonidin-3-glucoside	Pelargonidin	Purple Ruffles	Orange-red	Antioxidant, antimicrobial	Ozcan *et al*., 2025

4. Towards Downy Mildew (*Peronospora belbahrii*) Resistance in Greenhouse Basil: A Review of Breeding and Gene-Editing Efforts

Downy mildew caused by *P. belbahrii* is the most destructive disease of basil worldwide, including in greenhouse production (Wyenandt *et al*., 2015). The humid, poorly ventilated microclimate of enclosed greenhouses favours the pathogen, and control currently relies mainly on fungicide programs, environmental management, and, increasingly, resistant cultivars (Wyenandt *et al*., 2015). Genetic resistance is therefore directly relevant to sustainable greenhouse production, because it protects yield and the quality of the harvested raw material while reducing dependence on chemical control. The key breeding and gene-editing studies are summarized below, with emphasis on what they imply for protected cultivation. Transcriptome-level studies of the basil–*Peronospora belbahrii* interaction are still at an early stage, and the molecular basis of host susceptibility remains incompletely understood (Wyenandt *et al*., 2015). Laura *et al*. (2023) developed a highly effective CRISPR/Cas9-based gene-editing technique for the advanced basil genotype 'FT Italiko', in which the susceptibility gene *ObDMR6* was targeted to impart resistance to downy mildew (*P. belbahrii*). With the help of an optimized *A. tumefaciens*-mediated transformation method for cotyledonary node tissues, the authors obtained 82.2% regeneration efficiency, while 84.6% of the regenerated shoots contained Cas9. Mutation analysis of 21 T0 transgenic genotypes showed various indels, of which 60% showed frameshift knockouts of the *ObDMR6* gene;

these mutations were inheritable and segregated in T1 progeny without any transgenes. Infection trials suggested that clone 22B showed lower disease incidence (41.7% at 14 dpi) than the wild type (100%), implying that this genotype has a higher resistance level. Volatile profiling suggested that edited plants had acceptable aromatic compounds, while oxygenated monoterpenoids dominated; however, gene editing had a marked effect on the phenylpropanoid compounds, including eugenol and methyl eugenol (Laura *et al*., 2023).

Another study established a highly efficient CRISPR/Cas9-mediated gene-editing system in allotetraploid sweet basil (*Ocimum basilicum*) by targeting the putative susceptibility gene *ObDMR1*, a homologue of *Arabidopsis DMR1* involved in downy mildew susceptibility (Navet and Tian, 2020). Using *Agrobacterium*-mediated transformation with constructs expressing one or two sgRNAs, the authors achieved a 92.6% mutation rate at the target site in T0 transgenic plants, with amplicon deep sequencing confirming diverse indels and one complete knockout line. Homozygous mutants with 1-bp frameshift insertions were obtained in the T1 generation, and transgene-free homozygous mutants were also identified. T2 homozygous mutants exhibited a dwarf phenotype at the seedling stage, consistent with *DMR1* functions in other species (Navet and Tian, 2020). In an investigation, editing the susceptibility gene *ObDMR6* in the allotetraploid sweet basil variety 'Genovese' increased resistance to downy mildew (*Peronospora belbahrii*). The authors found multiple copies of *ObDMR6* with polymorphisms and designed sgRNAs for the conserved parts of this gene. By using two different constructs with either one or two sgRNAs, they obtained 56 T0 transgenic plants and selected 13 mutants with complete knockout (>96% indel efficiency) of *ObDMR6*. Transgene-free homozygous mutant lines were generated in the T1 generation and verified via both Sanger sequencing (ICE analysis) and amplicon deep sequencing. Disease screening performed on T2 plants showed a 61–68% decrease in sporangia formation and a 69–93% decrease in relative pathogen biomass without significant growth penalties (Hasley *et al*., 2021).

Zhang *et al*. (2021) also utilized CRISPR/Cas9 gene-editing technology to mutate the *ObHSK* (homoserine kinase) gene, which is associated with susceptibility to downy mildew, in the sweet basil breeding line SB22. The researchers successfully regenerated 22 T0 plants, among which eight contained *ObHSK* gene mutations with an average indel frequency of 19–22%, and five T0 plants were confirmed to be transgene-free. Inoculated with *Peronospora belbahrii,* downy mildew resistance in T1 generations of 321-5 and 321-13 mutant lines was assessed based on symptom evaluation and qPCR-based pathogen quantification. It was found that some T1 lines had a considerable decline in the pathogen population of up to 90% and 96% in 321-13-1 and 321-13-2 lines, respectively, compared with wild-type plants, and symptom occurrence in T1 generations was considerably later (25 days post-inoculation) than in the WT (10 days post-inoculation). The scientists noticed that mutation in only a part of *ObHSK* alleles was sufficient to increase disease resistance without influencing plant growth, except for one T0 line with more mutations, which was sterile and growth-retarded (Zhang *et al*., 2021). While three independent studies (Laura *et al*., 2023; Hasley *et al*., 2021; Zhang *et al*., 2021) consistently demonstrated that knockout of susceptibility genes—*ObDMR6* and *ObHSK*—enhances downy mildew resistance in basil, the reported resistance levels varied substantially (from a disease incidence of 41.7% versus 100% in the wild type at 14 dpi to a 96% reduction in pathogen biomass). This variability likely reflects differences in basil genotype (FT Italiko vs. Genovese vs. SB22), sgRNA design and target sites, and pathogen inoculation conditions. Notably, Hasley *et al*. (2021) achieved transgene-free homozygous mutants in the T1 generation, whereas Laura *et al*. (2023) did not report transgene segregation data. A critical unresolved question is whether susceptibility gene knockout confers durable resistance across diverse *Peronospora belbahrii* isolates, as none of the studies conducted multi-isolate challenge tests. Furthermore, the long-term stability of resistance under commercial greenhouse conditions—where pathogen populations are diverse and evolving—remains unknown. These knowledge gaps must be addressed before gene-edited basil cultivars can be deployed in commercial greenhouse production.

5. The First Chromosome-Level Reference Genome of Basil (*Ocimum basilicum*): A Milestone for Unlocking Genetic Resources and Trait Improvements

Over the past decade, considerable efforts have been invested in scaffold-level genome assembly for sweet basil (Bornowski *et al*., 2020; Gonda *et al*., 2020) to identify fusarium resistance and the lack of anthocyanin trait; however, a contiguous chromosome-level reference genome remained elusive until a recent study successfully published a fully resolved, chromosome-scale assembly of *Ocimum basilicum*. Recently, the study by Zhang *et al*. (2025) released a chromosome-level, homeolog-phased reference genome assembly for tetraploid sweet basil (*Ocimum basilicum* L. cv. 'Perrie'), achieved through PacBio HiFi and Hi-C sequencing. The 2.2 Gbp genome was resolved into 26 pseudochromosomes and clearly partitioned into two distinct subgenomes (A and B), revealing high synteny between them but limited collinearity with other Lamiaceae species. In fact, the authors depicted high levels of synteny between the two basil sub-genomes, but comparisons with the rosemary genome revealed collinearity breakdown in near relatives. This high-quality reference genome, along with GFF, functional annotation, CDS, and protein files, publicly accessible via the Basil Genome Base platform (https://basil.breedbase.org), provides a robust foundation for future studies, including computationally less-demanding reference-guided RNA-seq alignments, fine-mapping of agronomically important traits, genome-wide association studies (GWAS) in diverse basil germplasm, elucidation of specialized metabolite biosynthesis

pathways at the single-cell level, evolutionary and polyploidization analyses, and accelerated molecular breeding programs for enhanced aroma, stress tolerance, and disease resistance in basil. Zhang *et al*. (2025) employed a bi-parental mapping population derived from a Perrie (Genovese type; eugenol-rich) × Cardinal (Thai type; methyl chavicol-rich) cross and identified a single major quantitative trait locus (QTL) on chromosome 5B governing the eugenol/methyl chavicol ratio, which possessed a genomic region with 95 genes, including 15 genes related to a shikimate O-hydroxycinnamoyl transferase (HCT/CST) enzyme. Within this QTL interval, they pinpointed *ObHCT1*, a trichome-specifically expressed shikimate O-hydroxycinnamoyl transferase gene, and functionally validated its role in eugenol biosynthesis through in vitro enzymatic assays. The chromosome-level genome assembly by Zhang *et al*. (2025) represents a genuine milestone for basil genomics, but its practical implications for greenhouse breeding programs remain limited. The identified QTL on chromosome 5B governs only the eugenol/methyl chavicol ratio—a quality trait—not the traits most critical for greenhouse production: drought tolerance, water-use efficiency, or yield stability under controlled environments. Furthermore, the genome assembly was derived from a single cultivar ('Perrie'), and the extent of structural variation across diverse basil germplasm—particularly Iranian landraces adapted to semi-arid conditions—remains unknown. Future research should prioritise genome-wide association studies (GWAS) for greenhouse-relevant traits, including water deficit stress tolerance, biomass accumulation under controlled environments, and essential oil yield stability. The integration of genomic data with multi-omics approaches (transcriptomics, proteomics, and metabolomics) will be essential to identify the regulatory networks governing these complex traits.

6. Pharmacological Effects

6.1. Summary of Pharmacological Effects with Evidence Levels

The pharmacological properties of basil have been extensively investigated through various experimental models, ranging from in vitro assays to human clinical trials. To provide a structured overview of the current evidence base, the pharmacological effects are categorized according to evidence levels: Level 1 (human randomized controlled trials), Level 2 (in vitro and animal studies with strong evidence), Level 3 (in vitro or animal studies with limited evidence), Level 4 (traditional use only), and Level 5 (insufficient evidence). This classification system enables researchers and clinicians to critically evaluate the strength of evidence supporting each therapeutic application. Table 6 summarizes the major pharmacological activities of basil, their underlying mechanisms, active compounds, and corresponding evidence levels, while Table 7 summarizes the limited human data available.

6.1.1. Detailed Pharmacological Activities

1. Antioxidant Activity (Level 2 Evidence)

Basil bioactive compounds demonstrate significant antioxidant activity in 2,2-diphenyl-1-picrylhydrazyl (DPPH), 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) (ABTS), ferric reducing antioxidant power (FRAP), and ORAC assays through: (i) direct free radical scavenging; (ii) increased endogenous antioxidant enzyme activity (superoxide dismutase [SOD], catalase [CAT], and glutathione peroxidase [GPX]); (iii) increased reduced glutathione (GSH); (iv) reduced lipid peroxidation products (malondialdehyde [MDA] and thiobarbituric acid reactive substances [TBARS]); and (v) protection against H_2O_2-induced cytotoxicity (Zhakipbekov *et al*., 2024). A strong correlation was observed between antioxidant activity and total phenolic content (Ahmed *et al*., 2019).

2. Antimicrobial Activity (Level 2 Evidence)

Basil essential oil exhibits broad-spectrum antibacterial activity against Gram-positive (*Staphylococcus aureus* and *Bacillus subtilis*) and Gram-negative (*Escherichia coli* and *Salmonella typhimurium*) bacteria through membrane disruption, efflux pump inhibition, and biofilm inhibition (Sestili *et al*., 2018). Antifungal activity has also been reported against *Aspergillus* species and *Candida albicans* (Poulios *et al*., 2025) and against *Trichophyton rubrum* (Poulios *et al*., 2025).

3. Anti-inflammatory Activity (Level 3 Evidence)

Basil inhibits lipoxygenase (LOX; IC50 = 18.28 μg/mL) and cyclooxygenase (COX), reduces proinflammatory cytokines (TNF-α, IL-1β, and IL-6), and inhibits the NF-κB pathway (Maoz *et al*., 2026).

4. Hypoglycemic Activity (Level 3 Evidence)

Basil inhibits α-amylase (IC50 = 50.51 μg/mL) and α-glucosidase (IC50 = 39.84 μg/mL), increases insulin secretion, and improves insulin sensitivity (Baby and Nair, 2025). The evidence for hypoglycemic activity is predominantly preclinical: studies in diabetic rodents reported blood glucose reductions of roughly 30–40%, whereas the few small human studies available (8–12 weeks) reported fasting glucose reductions of 18–28%

(Banerjee and Sharma, 2025). The methodological quality of these studies is variable, and well-designed randomized controlled trials of *Ocimum basilicum* are still lacking (Sestili *et al*., 2018).

5. Neuroprotective Activity (Level 3 Evidence)

Basil compounds reduce amyloid-β aggregation, decrease neuronal oxidative stress, increase SOD/CAT/GPx activity, and inhibit acetylcholinesterase (AChE), improving cognitive function (Vasincu *et al*., 2025).

6. Anticancer Activity (Level 3 Evidence)

Basil preparations induced apoptosis in breast (MCF-7) and pancreatic (MIA PaCa-2) cancer cells, were cytotoxic to liver (Hep3B) cells, and, in combination with cisplatin, induced G0/G1 cell cycle arrest in cervical cancer cells (Poulios *et al*., 2025). However, most of this evidence derives from in vitro studies, and selectivity towards non-tumorous cells needs confirmation in vivo (Sestili *et al*., 2018).

Table 6. Summary of pharmacological effects of basil and evidence levels

Pharmacological Effect	Active Compounds	Primary Mechanism	Evidence Level*	Key Studies	References
Antioxidant	Rosmarinic acid, luteolin, quercetin, caffeic acid, eugenol	Free radical scavenging; increased SOD, CAT, GPX activity	Level 2	In vitro + animal studies	Baby and Nair, 2025
Antimicrobial	Eugenol, linalool, methyl chavicol, 1,8-cineole	Membrane disruption; efflux pump inhibition; biofilm inhibition	Level 2	In vitro studies	Qasem *et al*., 2023
Anti-inflammatory	Rosmarinic acid, luteolin, eugenol	LOX inhibition (IC50 = 18.28 µg/mL); NF-κB pathway inhibition	Level 3	In vitro + limited animal	Maoz *et al*., 2026
Hypoglycemic	Rosmarinic acid, quercetin, methyl chavicol	α-Amylase inhibition (IC50 = 50.51 µg/mL); α-glucosidase inhibition (IC50 = 39.84 µg/mL)	Level 3	Mainly animal studies; 2 small human studies (8–12 weeks)	Banerjee and Sharma, 2025
Neuroprotective	Linalool, rosmarinic acid, luteolin, apigenin	Reduced amyloid-β aggregation; AChE inhibition; increased SOD, CAT, GPX	Level 3	Animal models	Vasincu *et al*., 2025
Anticancer	Eugenol, luteolin, apigenin, rosmarinic acid	Apoptosis induction; G0/G1 cell cycle arrest (with cisplatin); cytotoxic to breast (MCF-7), pancreatic (MIA PaCa-2), liver (Hep3B), and cervical cancer cell lines	Level 3	In vitro + limited animal	Poulios *et al*., 2025
Hepatoprotective	Rosmarinic acid, caffeic acid, quercetin	Reduced liver enzymes (ALT, AST, ALP); reduced oxidative stress	Level 3	Animal models	Baby and Nair, 2025
Skin protective	Methyl chavicol, trans-anethole	Tyrosinase inhibition (IC50 = 68.58 µg/mL); reduced melanogenesis	Level 3	In vitro studies	Qasem *et al*., 2023

*Evidence Level Classification: Level 1 = Human clinical trials (RCTs); Level 2 = In vitro + animal studies with strong evidence; Level 3 = In vitro/animal studies with limited evidence; Level 4 = Traditional use only; Level 5 = Insufficient evidence.

6.1.2. Toxicological Considerations and Safety

While basil is generally recognized as safe (GRAS) at culinary doses, several considerations warrant attention. First, estragole and methyl eugenol are hepatocarcinogenic in rodent models at high doses (SCF, 2001; Smith *et al*., 2002); the European Food Safety Authority (EFSA) recommends a margin of exposure (MOE) approach for substances that are both genotoxic and carcinogenic (EFSA, 2005). Second, no long-term human studies (>6 months) exist for therapeutic doses, and current human evidence is limited to a few short-term (8–12 weeks) studies

(Banerjee and Sharma, 2025). Third, safety data for pregnancy are insufficient, and therapeutic doses should be avoided in pregnant women as a precaution. Fourth, herb-drug interactions with anticoagulants (warfarin), antidiabetics (metformin and sulfonylureas), and antihypertensives require investigation (Qasem *et al*., 2023). Fifth, essential oil should never be consumed orally without dilution owing to its high phenolic concentration and potential mucosal irritation. Finally, individuals with Lamiaceae family sensitivity (mint, oregano, thyme, and sage) should exercise caution.

Table 7. Summary of human studies on basil reported in the diabetes literature

Indication	Number of human studies	Duration	Sample Size	Key Finding	Reference
Glycemic control (human studies)	2	8–12 weeks	80–100 per study	Fasting glucose reduced by 18% and 28%; HbA1c not reported	Banerjee and Sharma, 2025
Dyslipidemia (human studies)	1	12 weeks	80	HDL cholesterol increased by 12%	

Table 8. Summary of basil responses to different levels of water deficit stress in greenhouse systems

Stress Level	FC %	Morphological	Physiological	Biochemical	Molecular	References
Mild	75%	Slight reduction in biomass	Stomatal closure initiation; PSII efficiency maintained	Increased phenolics (up to 40%); rosmarinic acid (up to 30%); essential oil (up to 10%)	Upregulation of *PAL*, *RAS*, *GES* (2–3.8 fold)	You *et al*., 2025
Moderate	50–<75 %	Biomass reduction (20–30%)	Reduced photosynthesis; increased ROS	Enhanced secondary metabolites; anthocyanin increase (17–72% in purple)	*GES* upregulation (3.8 fold at 50% FC)	Palesh and Abdollahi Mandoulakani, 2020
Severe	30–<50 %	Biomass reduction >45%; RWC loss >14%	Stomatal closure; PSII damage	Oxidative stress; MDA increase; membrane damage	Downregulation of *CDS*, *SES*	Mulugeta *et al*., 2023

7. Water Deficit as a Managed Stress: Responses and Effects on Bioactive Metabolites in Greenhouse Production Systems

Water deficit is a potential constraint for basil production owing to its shallow root system (Irsyad and Pratiwi, 2026). In greenhouse systems, water deficit can be precisely controlled through irrigation scheduling, substrate moisture monitoring, and deficit irrigation strategies, enabling targeted application of stress to enhance secondary metabolite production without compromising yield (Goldani *et al*., 2021). Mild to moderate stress can enhance secondary metabolite production through complex physiological, biochemical, and molecular mechanisms (Selmar and Kleinwächter, 2013). Table 8 summarizes basil responses to different levels of water deficit stress in greenhouse and controlled-environment conditions. Two clarifications define the scope of this section. First, in well-managed greenhouses water deficit is rarely an unavoidable problem because irrigation can be scheduled precisely; it nevertheless occurs through irrigation failures, the low water-holding capacity of soilless substrates, and water scarcity in arid regions such as Iran, and it can be applied deliberately as regulated deficit irrigation. Second, the rationale for deliberate deficit is the stress-induced accumulation of secondary metabolites (Selmar and Kleinwächter, 2013; Kleinwächter and Selmar, 2015): mild to moderate stress can raise the concentrations of phenolics, rosmarinic acid, and essential oil, which determine the dietary and pharmaceutical value of basil,

whereas severe stress reduces biomass and quality (Table 8). Evidence is cultivar- and system-dependent, and not all studies report increases, so deficit strategies should be regarded as a quality-oriented option for specific markets rather than a general recommendation. Accordingly, the physiological and molecular subsections that follow are presented as mechanisms that explain when stress improves, and when it impairs, bioactive metabolite production.

7.1. Physiological Responses in Greenhouse Conditions

1. Water Relations and Membrane Stability

Under severe drought (30% FC), basil loses >14% relative water content (RWC), with leaf water potential reduction exceeding 60%, leading to stomatal closure and photosynthesis inhibition (Mulugeta *et al*., 2023). In greenhouse systems, substrate moisture sensors and evapotranspiration models can be used to precisely monitor and control water delivery, enabling the maintenance of target FC levels (Goldani *et al*., 2021). The membrane stability index (MSI) decreases by 34% in green basil versus 25% in purple basil under PEG-induced stress, indicating that anthocyanin-mediated membrane protection might be involved (Irsyad and Pratiwi, 2026).

2. Biomass and Growth

Severe drought reduces fresh and dry biomass by >45% (Mulugeta and Radacsi, 2022). The 'Genovese' cultivar shows the highest yield under optimal conditions (344.7 g/plant) (Mulugeta and Radacsi, 2022), while purple cultivars maintain better yield under stress owing to anthocyanins (Stefanov *et al*., 2026). In soilless greenhouse systems, biomass accumulation can be further optimized through precise nutrient management and CO_2 enrichment (Marschner, 2012; Ainsworth and Rogers, 2007).

3. Photosynthetic Responses

- ✓ **Pigment Content**

Drought reduces total chlorophyll by 19% in green basil and 10% in purple basil at 20% PEG treatment (Irsyad and Pratiwi, 2026). The carotenoid-to-chlorophyll ratio (Car/Chl) increases in purple basil under stress, indicating protective roles against reactive oxygen species (ROS) (Stefanov *et al*., 2026).

- ✓ **Photosystem II Performance**

Drought affects both the electron donor (Wk) and acceptor (Vj) sides of photosystem II (PSII), resulting in: (i) reduced photochemical efficiency (PIABS and PItotal); (ii) reduced electron transport rate (ETR) and photosynthesis rate (RFd); and (iii) increased dissipated energy at reaction centers (DIo/RC) (Stefanov *et al*., 2026). Photosynthetic limitation under water deficit is primarily stomatal under mild stress and increasingly metabolic under severe stress (Lawlor and Cornic, 2002); whether supplemental lighting or CO_2 enrichment can mitigate these effects in greenhouse-grown basil has not been systematically tested.

4. Anthocyanin-Mediated Protection

Purple basil shows superior tolerance through: (i) reduced photodamage via blue-green light absorption; (ii) ROS neutralization; (iii) protection of the oxygen-evolving complex (OEC); and (iv) nearly complete recovery after re-watering, compared with green basil's incomplete recovery (Irsyad and Pratiwi, 2026). Anthocyanin content increases by 17–72% under stress in purple basil (Stefanov *et al*., 2026). The photoprotective and antioxidant roles of anthocyanins in leaves are well established (Gould, 2004).

7.2. Biochemical Responses

- **Oxidative Stress**

Drought increases ROS production (H_2O_2 and O_2^-) and MDA levels (Sharma *et al*., 2012). Purple cultivars show less oxidative damage owing to higher anthocyanins (Irsyad and Pratiwi, 2026).

- **Secondary Metabolites**

Essential Oil: Mild to moderate drought increases essential oil concentration by up to 10%, with gland density increasing by >60% (Mulugeta *et al*., 2023). However, the qualitative pattern of major constituents may be preserved (Mulugeta and Radacsi, 2022). In sweet basil, the main volatiles (linalool, eucalyptol, and eugenol) remained relatively stable under drought, whereas flavonoid and flavonol contents increased significantly only under moderate and severe stress (Zhou *et al*., 2025). Linalool content reached 52.6% under mild stress (Khakdan *et al*., 2021). This pattern is consistent with the over-reduction hypothesis, according to which stress-induced limitation of CO_2 fixation increases the supply of reducing equivalents available for the synthesis of highly reduced metabolites such as terpenoids and phenolics (Selmar and Kleinwächter, 2013). In greenhouse systems, this may allow essential oil quality to be optimized through controlled stress application (Kleinwächter and Selmar, 2015).

Phenolics and Flavonoids: Mild to moderate drought increases total phenolics (up to 40%), total flavonoids (stress-dependent), and rosmarinic acid (up to 30%) (Irsyad and Pratiwi, 2026). Increased expression of phenylalanine ammonia-lyase (PAL), cinnamate 4-hydroxylase (C4H), 4-coumarate-CoA ligase (4CL), and rosmarinic acid synthase (RAS) mediates these changes (You *et al*., 2025).

7.3. Molecular Responses

- **Terpene Biosynthesis Genes**

Khakdan *et al*. (2021) showed diverse transcriptional patterns for HDR, LinS, GerS, and GadS genes under drought, with cultivar-dependent expression and significant correlation with RWC. Furthermore, comparative transcriptome analysis has revealed candidate gene modules involved in salt stress response in sweet basil, with overexpression of *ObWRKY16* and *ObPAL2* enhancing salt tolerance in transgenic *Arabidopsis* (Wang *et al*., 2024).

Table 9. Demonstrated differential expression of monoterpene/sesquiterpene biosynthesis genes (Palesh and Abdollahi Mandoulakani, 2020)

Gene	Expression Change at 50% FC	Expression Change at 75% FC
GES (geraniol synthase)	3.8-fold increase	2-fold increase

- **Multi-Omics Approaches**

You *et al*. (2025) identified convergent and divergent responses to drought and salinity, including core metabolic pathway remodeling (GS-GOGAT cycle, photorespiration, and TCA cycle) and stress-specific patterns in flavonoid and alkaloid accumulation.

Table 10. Combined stress interactions in greenhouse basil

Combined Stress	Effect on Basil	Proposed Mechanism	Key Studies
Drought + Salinity	Overlapping responses; combined growth effects not quantified in basil	Shared osmotic + ionic stress; additive effects on ROS production	Tel *et al*., 2025
Drought + Downy Mildew	Limited data in basil	Possible altered stomatal behavior and defense-related metabolism (cf. Suzuki *et al*., 2014)	Suzuki *et al*., 2014 (general); knowledge gap in basil
Drought + Heat	Limited data	Unknown	Knowledge gap
Drought + Nitrogen Deficiency	Limited data	Unknown	Knowledge gap

- **Combined Stress Interactions**

In natural agricultural systems, plants are rarely exposed to a single abiotic stress in isolation. In greenhouse systems, drought stress frequently coincides with other environmental constraints, including salinity (from nutrient solution accumulation), high temperature (in unshaded greenhouses), and pathogen attacks (particularly downy mildew), creating complex stress combinations that can have additive or synergistic effects on plant performance (Mittler, 2006; Suzuki *et al*., 2014; Tel *et al*., 2025). The response of plants to a combination of stresses is often unique and cannot be predicted from the responses to the individual stresses (Mittler, 2006; Suzuki *et al*., 2014). Understanding these combined stress interactions is crucial for developing realistic management strategies and breeding programs, as single-stress studies may not accurately predict field responses. Recent multi-omics approaches have begun to elucidate the complex regulatory networks governing plant responses to combined stresses (Varadharajan *et al*., 2025). Table 10 summarizes the documented interactions between drought and other environmental stresses in basil, highlighting their effects, proposed mechanisms, and key studies.

7.4. Genotypic Variation and Stress Tolerance Strategies

Purple basil cultivars show superior drought tolerance through higher anthocyanin accumulation (Stefanov *et al*., 2026). Vermicompost application (25–50%) enhances drought tolerance and rosmarinic acid content (Kosem *et al*., 2022). Flaxseed oil cake (FOC) as a substrate additive at 10 g dm^{-3} has been shown to significantly reduce biomass loss under drought stress in greenhouse-grown basil (Dutra *et al*., 2025). Melatonin treatment (50 µM) increases biomass by 100% and leaf area by 119%, and reduces MDA by 36% under salt stress (González Forte *et al*., 2025). Foliar ascorbic acid application has likewise been reported to improve morpho-physiological traits of

basil under water deficit (Esmaeilpour *et al*., 2023). In greenhouse systems, maintaining 70% FC optimizes biomass and essential oil yield while saving 30% water (Mulugeta and Radacsi, 2022). Studies on deficit irrigation in greenhouse basil have shown that the highest yield (7 t ha^{-1} fresh weight, 1.8 t ha^{-1} biological yield) was achieved at 100% readily available water, with no significant difference between 80% and 60% irrigation levels for most morphological traits (Khater *et al*., 2021; Mousavi, 2026). Drought and salinity show differential effects: drought primarily inhibits leaf growth, while salinity primarily inhibits root growth (You *et al*., 2025). Additionally, water deficit stress has been shown to alter drug yield, antioxidant enzyme activity, and essential oil quality and quantity in related aromatic plants such as tarragon (*Artemisia dracunculus* L.) (Mumivand *et al*., 2021).

7.5. Implications for Bioactive Metabolite Yield and Dietary Value

The central question for greenhouse producers is not only whether stress increases metabolite concentration, but whether the total yield and nutritional value of the harvested product improve. Mild to moderate deficit (50–75% FC) increased total phenolics by up to 40%, rosmarinic acid by up to 30%, and essential oil by up to 10% (Mulugeta *et al*., 2023), whereas severe stress (30–50% FC) reduced biomass by more than 45% (Mulugeta *et al*., 2023). Because the content of bioactive compounds per unit area is the product of concentration and biomass, gains in concentration are meaningful only when biomass losses remain small; the 70% FC regime reported to save about 30% of water while maintaining biomass and oil yield (Mulugeta and Radacsi, 2022) illustrates this balance. With respect to dietary value, the phenolic acids, flavonoids, and anthocyanins that increase under moderate stress are the compounds linked to the antioxidant capacity of basil (Kwee and Niemeyer, 2011), and purple cultivars combine higher anthocyanin content with better drought tolerance (Stefanov *et al*., 2026). Whether stress-induced increases translate into higher nutritional or therapeutic value of the final product has rarely been tested and remains an open question.

7.6. Conceptual Model of Basil Responses to Drought Stress

Based on the synthesized evidence from physiological, biochemical, and molecular studies, a comprehensive conceptual model has been developed to illustrate the integrated responses of basil to water deficit stress in greenhouse and controlled-environment systems (Figure 1). This model integrates findings from multiple research levels, including water relations, photosynthetic performance, oxidative stress responses, secondary metabolite accumulation, and gene expression changes. The model also incorporates genotype-specific responses, distinguishing between green and purple cultivars, as well as the effects of different stress severities (mild, moderate, and severe drought). Additionally, it highlights the protective roles of anthocyanins and the potential for agronomic interventions such as vermicompost application (Kosem *et al*., 2022) and melatonin treatment (González Forte *et al*., 2025). The model also accounts for greenhouse-specific factors, including controlled irrigation, soilless culture, CO_2 enrichment, and supplemental lighting, as well as combined stress interactions as summarized in Table 10. This integrated framework provides a holistic understanding of basil's adaptive mechanisms to drought stress in greenhouse production systems and identifies key targets for breeding and management strategies.

Conclusion, Knowledge Gaps, and Future Perspectives

❖ Summary of Key Findings

Basil (*O. basilicum* L.) is a valuable medicinal and aromatic plant containing a diverse array of bioactive compounds, including rosmarinic acid (the predominant phenolic acid in most cultivars), flavonoids (luteolin and quercetin), and volatile essential oils (linalool, methyl chavicol, and eugenol) (Kwee and Niemeyer, 2011). Pharmacological studies have confirmed multiple properties: antioxidant (Level 2 evidence), antimicrobial (Level 2), anti-inflammatory (Level 3), hypoglycemic (Level 3, mainly animal studies), neuroprotective (Level 3), anticancer (Level 3), hepatoprotective (Level 3), and skin protective (Level 3) (Vasincu *et al*., 2025). Greenhouse production systems offer significant advantages for basil cultivation, including year-round production, precise environmental control, reduced water consumption, and consistent product quality (Savvas and Gruda, 2018). Water deficit stress at mild to moderate levels (50–75% FC) can enhance phytochemical quality by up to 40% through the upregulation of PAL, RAS, and GES genes (You *et al*., 2025). Purple cultivars show superior drought tolerance and recovery capability owing to protective anthocyanins (Stefanov *et al*., 2026). Iranian native landraces represent valuable genetic resources with exceptional stress tolerance and phytochemical quality for greenhouse breeding programs (Karimi *et al*., 2020).

❖ Critical Knowledge Gaps

Despite significant advances, important knowledge gaps remain. First, human clinical trials are limited: most evidence is from in vitro and animal studies, and no pharmacological effect of *Ocimum basilicum* currently has Level 1 evidence from well-designed randomized trials (Banerjee and Sharma, 2025). Second, molecular and epigenetic mechanisms governing secondary metabolite biosynthesis induction under abiotic stresses—

particularly transcription factor roles and DNA methylation—remain incompletely understood (Zhou *et al*., 2025). Third, combined stress interactions—particularly drought with salinity, heat, and disease—are poorly studied, especially in greenhouse systems (see Table 10). Fourth, extract standardization based on marker compounds requires further research for industrial and pharmaceutical applications (Handayani *et al*., 2025). Fifth, long-term safety data are lacking: no human studies >6 months exist for therapeutic doses, and estragole and methyl eugenol hepatocarcinogenicity concerns remain (Qasem *et al*., 2023). Finally, greenhouse-specific gaps persist: the integration of greenhouse environmental factors (light quality, CO_2 enrichment, humidity, root-zone temperature) with stress response pathways remains poorly understood, and optimal deficit irrigation protocols for different greenhouse systems (hydroponics, aeroponics, substrate culture) and cultivars have not been systematically established.

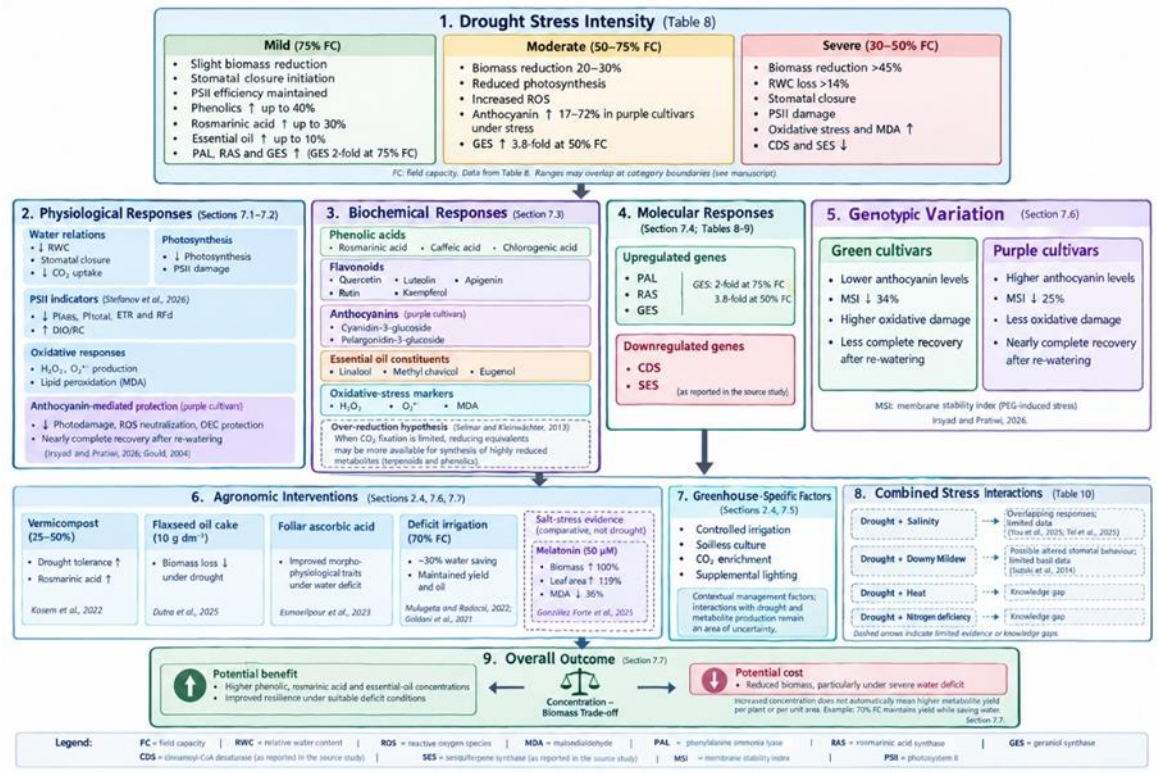


Figure 1. Conceptual model of basil (*Ocimum basilicum* L.) responses to drought stress, integrating drought intensity gradients (mild, moderate, severe; Table 8; Section 7), physiological responses (reduced RWC, stomatal closure, decreased photosynthesis, ROS and MDA accumulation, PSII photoinhibition; Section 7.1), biochemical responses (phenolic acids, flavonoids, anthocyanins, essential oil constituents; Section 7.2), and molecular responses (PAL, RAS, GES upregulated; CDS, SES downregulated; Section 7.3). The model also shows genotype-dependent differences between green and purple cultivars (MSI 34% vs. 25%; anthocyanin-mediated protection; Section 7.4), agronomic interventions (vermicompost, flaxseed oil cake, foliar ascorbic acid, deficit irrigation at 70% FC; Section 7.4), greenhouse-specific factors (Sections 2.4, 7.1, 7.2), combined stress interactions (Section 7.3; Table 10), and the overall concentration–biomass trade-off (Section 7.5). The over-reduction hypothesis is shown as an explanatory box (Section 7.2); FC, field capacity; RWC, relative water content; ROS, reactive oxygen species; MDA, malondialdehyde; PAL, phenylalanine ammonia lyase; RAS, rosmarinic acid synthase; GES, geraniol synthase; CDS, cinnamoyl-CoA desaturase (as reported in Table 8); SES, sesquiterpene synthase (as reported in Table 8); MSI, membrane stability index; PSII, photosystem II.

❖ Genetics and Breeding

The identification of drought- and salinity-tolerant native genotypes using molecular markers (SNP and SSR) represents a foundational step for greenhouse breeding programs. However, marker-assisted selection alone is insufficient; comprehensive phytochemical evaluation must accompany molecular characterization to ensure that tolerance traits are not associated with reduced quality. Multi-omics approaches (transcriptomics, proteomics, and metabolomics) offer unprecedented opportunities to identify associated genes and metabolic pathways under various biotic and abiotic stresses (Varadharajan *et al*., 2025). The integration of these approaches with CRISPR/Cas9 molecular breeding (Navet and Tian, 2020; Zhang *et al*., 2025) for enhanced production of valuable compounds (linalool and rosmarinic acid) could accelerate the development of greenhouse-adapted cultivars with superior quality and stress tolerance.

❖ Agronomy and Ecology

The interactive effects of combined stresses (drought + salinity, drought + heat, and drought + disease) represent a critical knowledge gap that must be addressed through systematic greenhouse experiments. Organic and biological fertilizer optimization (vermicompost, mycorrhizae, and *Azotobacter*) offers a sustainable pathway to enhance drought tolerance and phytochemical quality (Copetta *et al*., 2006). Soilless cultivation systems (hydroponics and aeroponics) provide precise control over water and nutrient delivery, enabling targeted application of deficit irrigation strategies (Goldani *et al*., 2021). The integration of CO_2 enrichment and supplemental lighting with stress management strategies requires further investigation to optimize the balance between biomass and quality.

❖ Clinical and Pharmacological

Large-scale randomized, placebo-controlled clinical trials are needed for type 2 diabetes, anxiety disorders, and cardiovascular diseases. Long-term toxicological studies should establish the maximum tolerated dose and chronic consumption side effects. Synergistic effects with conventional drugs (antidiabetics, antihypertensives, and anxiolytics) warrant systematic investigation.

❖ Technology and Industry

Green extraction methods (UAE, MAE, and SFE) using RSM and machine learning optimization can enhance yield and preserve heat-sensitive compounds (Handayani *et al*., 2025). Basil essential oil nano-formulations with high stability and controlled release offer promising applications in food and pharmaceutical industries. Micropropagation for mass multiplication and genetic uniformity is essential for greenhouse production (Siddique and Anis, 2008).

❖ Practical Recommendations

For Farmers: The selection of purple cultivars (drought-tolerant) and tolerant native genotypes is recommended for water-limited areas (Irsyad and Pratiwi, 2026). Mild deficit irrigation (70–75% FC) can save 30% water while improving quality (Mulugeta and Radacsi, 2022); for more aggressive water-saving strategies, 60% of readily available water may be applied without significant yield loss in some cultivars (Khater *et al*., 2021; Mousavi, 2026). Soil amendments such as vermicompost (25–50%) or flaxseed oil cake (10 g dm^{-3}) enhance drought tolerance and rosmarinic acid content (Dutra *et al*., 2025). Harvest timing should be chosen according to the target product: in one field study, herb yield was highest at 50% flowering, whereas essential oil content continued to increase towards the end of flowering (Kacar *et al*., 2024). Environmental control should target a temperature of approximately 20–30 °C, with relative humidity and daily light integral adjusted to the cultivar and production target (Al-Huqail *et al*., 2020; Dou *et al*., 2018). For Industries: Pharmaceutical companies should establish direct cultivation contracts for uniform, stable quality raw materials from greenhouse production. Food manufacturers can use basil essential oil as a natural preservative and antioxidant. Cosmeceutical companies can utilize basil extract for anti-aging, anti-spot, and anti-acne products. Extraction facilities should adopt UAE, MAE, or SFE for higher yield, heat-sensitive compound preservation, and environmental compatibility (Handayani *et al*., 2025). For Policymakers: Genetic conservation of native basil landraces should be a strategic priority. A basil gene bank storing superior genotypes for future breeding should be established. Extension programs should train farmers on drought-tolerant cultivars and optimal irrigation management in greenhouse systems. Research funding should be allocated for clinical studies, molecular breeding, and greenhouse-specific research on basil production.

❖ Final Perspective

Basil stands at the threshold of a new era of sustainable agriculture, evidence-based medicine, and green technologies. Greenhouse production systems, integrated with precision irrigation and stress management, offer a sustainable pathway for industrial-scale production of high-quality basil biomass. Climate change and increasing water limitations necessitate drought-tolerant cultivars and optimal irrigation guidelines for sustainable basil cultivation in Iran and worldwide. The convergence of traditional knowledge with modern scientific approaches (nanotechnology, metabolomics, and transcriptomics) creates unprecedented opportunities for discovering new drugs, producing functional foods, and developing natural cosmeceuticals. Realization of this vision requires close collaboration among researchers, farmers, industries, and policymakers within an integrated innovation ecosystem, where genetic resource conservation, sustainable production, quality processing, and intelligent commercialization are pursued in an interconnected value chain. Iran, with its rich basil genetic diversity, long tradition in traditional medicine, and growing greenhouse infrastructure, has high potential to become a regional and global hub for the production and processing of this valuable plant.

Conflict of Interest

The authors declare no conflict of interest.

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During the preparation of this manuscript, the authors used DeepSeek for language revision and text refinement, and ChatGPT for design support in developing the graphical abstract and Figure 1. These tools were used solely for editorial and visual assistance; all scientific content, labels, abbreviations, references, and final graphical elements of Figure 1 were created, verified, and approved by the authors, who assume full responsibility for the final content and presentation. No AI tool was used to generate, alter, or manipulate any scientific data, chemical structures, or graphical results presented in the manuscript. This use complies with the journal's AI policy, which permits AI tools for language editing and design support provided that such use is transparently disclosed and that the authors retain full responsibility for the scientific content.

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