

Physiological and Phytochemical Responses of *Vernonia Amygdalina*, *Moringa Oleifera* and *Ocimum Gratissimum* to Waterlogging-Induced Hypoxia: A Comparative Review

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ABSTRACT

Climate change-associated with flooding and prolonged soil waterlogging reduce oxygen availability in the root zone and can disrupt root respiration, nutrient uptake, photosynthesis, and plant growth. This review examines the physiological and phytochemical responses of *Vernonia amygdalina*, *Moringa oleifera*, and *Ocimum gratissimum* to waterlogging-induced hypoxia, with emphasis on species-specific responses, the strength of available evidence, and current research gaps. Literature from PubMed, Scopus, ScienceDirect, Google Scholar, and FAO AGRIS, primarily covering publications from 2009 to 2026, was critically synthesized. Evidence from the three selected species was considered alongside studies from related species where direct evidence was unavailable. The available literature indicates that *M. oleifera* has comparatively more direct evidence on physiological responses to waterlogging, including reductions in growth and photosynthetic performance, whereas direct evidence for *V. amygdalina* and *O. gratissimum* remains limited. Although hypoxia and associated oxidative stress can alter secondary metabolism, the available evidence is insufficient to conclude that waterlogging consistently increases specific medicinally relevant compounds such as chlorogenic acid, eugenol, vernodaline, or quercetin derivatives in these species. The review therefore distinguishes experimentally demonstrated responses from responses inferred from related species and those that remain hypothetical and require experimental validation. The resilience–remedy continuum proposed in this review is presented as a conceptual framework for relating plant stress adaptation to possible changes in phytochemical composition, rather than as a validated physiological or pharmacological relationship. Future research should employ controlled waterlogging experiments, soil oxygen measurements, physiological monitoring, and quantitative chromatographic, transcriptomic, and metabolomic analyses to clarify species-specific responses and determine whether waterlogging alters phytochemical composition and medicinal quality.

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INTRODUCTION

Contextual Background

Climate change has become one of the major challenges facing agricultural production worldwide. Among its many effects, flooding and prolonged soil waterlogging have become important environmental constraints in many agricultural regions. These conditions reduce the availability of oxygen in the soil and can create hypoxic or, under severe conditions, anoxic conditions around plant roots. Hypoxia refers to a condition of reduced oxygen availability, whereas anoxia represents a more severe condition in which oxygen is nearly or completely depleted. When soil pores become saturated with water, oxygen diffusion to the root zone is greatly restricted, thereby impairing aerobic respiration and reducing the availability of ATP required for normal cellular activities. Consequently, prolonged oxygen deficiency can disrupt root respiration, nutrient uptake, root development, photosynthesis, and plant growth (Bailey-Serres *et al.*, 2012; Striker, 2012; Dichio *et al.*, 2025). According to the Food and Agriculture Organization (FAO, 2025), natural disasters have caused substantial agricultural losses over the past three decades, with flooding accounting for a significant proportion of these losses.

The search for crops that can better withstand this environmental challenge has increased interest in indigenous leafy vegetables (ILVs). In many tropical countries, species such as *Vernonia amygdalina* (bitter leaf), *Moringa oleifera* (moringa), and *Ocimum gratissimum* (scent leaf) are widely cultivated and consumed because of their nutritional value and medicinal importance (Obboh *et al.*, 2019; Akinola *et al.*, 2020; Ukom *et al.*, 2023). Besides serving as important food crops, these plants contain a wide range of bioactive compounds that have been associated with antimicrobial, antioxidant, anti-inflammatory, and other biological activities (Obboh *et al.*, 2019; Ijeh & Ejike, 2011; Gopalakrishnan *et al.*, 2016; Ijindu *et al.*, 2023).

Environmental stresses do not always produce only negative effects on plants. Moderate abiotic stress can induce defence-related metabolic responses and alter the production and accumulation of secondary metabolites (Ramakrishna & Ravishankar, 2011). Since many secondary metabolites contribute to the biological activities associated with medicinal plants, understanding how waterlogging-induced hypoxia affects their production and accumulation is important. However, a stress-induced increase in the concentration of a particular phytochemical should not

automatically be interpreted as an improvement in medicinal quality, because changes in metabolite concentration may occur alongside reductions in plant growth and biomass. The physiological cost of stress and the resulting phytochemical response therefore need to be considered together (Ramakrishna & Ravishankar, 2011; Dichio *et al.*, 2025).

Under hypoxic conditions, plant roots cannot sustain mitochondrial oxidative phosphorylation, leading to a severe energy crisis characterized by depleted adenosine triphosphate (ATP) production. ATP deprivation halts energy-dependent root processes, including active nutrient transport and water uptake, which triggers secondary physiological stress in shoot tissues. Furthermore, oxygen starvation impairs the electron transport chain in both mitochondria and chloroplasts, causing excess electron leakage to molecular oxygen and generating reactive oxygen species (ROS) such as hydrogen peroxide (H₂O₂), superoxide anions (O₂⁻), and hydroxyl radicals (OH[•]). Uncontrolled ROS generation induces lipid peroxidation, protein denaturation, and nucleic acid degradation. However, ROS also function as critical secondary messengers that trigger defense-related metabolic pathways.

Knowledge Gap

Although the medicinal properties of *Vernonia amygdalina*, *Moringa oleifera*, and *Ocimum gratissimum* have been widely investigated, much less is known about how flooding and soil oxygen deficiency influence their physiological performance and phytochemical composition, particularly when both responses are considered together.

Among the three species, *M. oleifera* has received comparatively greater attention in relation to waterlogging. Studies have reported changes in its growth, photosynthetic performance, chlorophyll content, antioxidant enzyme activity, and other physiological responses under waterlogged conditions (Ren *et al.*, 2021; Mudasir *et al.*, 2025; Dichio *et al.*, 2025). In contrast, direct experimental information on the responses of *V. amygdalina* and *O. gratissimum* to soil-induced hypoxia remains limited. Consequently, some of the available interpretations for these species are derived from general plant responses or studies involving related species rather than from direct waterlogging experiments on the focal species.

This distinction between direct and indirect evidence is important because responses to waterlogging can vary among plant species according to differences in root structure, oxygen transport, metabolic adjustment, antioxidant capacity, and tolerance mechanisms (Bailey-Serres *et al.*, 2012; Striker, 2012; Dichio *et al.*, 2025). Evidence obtained from a related species may therefore provide useful mechanistic context but should not be presented as experimental evidence for the response of *V. amygdalina*, *M. oleifera*, or *O. gratissimum* itself.

The limited species-specific evidence also makes it difficult to determine whether waterlogging primarily reduces plant performance and medicinal value or whether stress-induced metabolic adjustments modify the accumulation of particular bioactive compounds. The major gap addressed by this review is therefore the lack of an integrated, species-specific comparison of physiological responses and phytochemical changes under waterlogging-induced hypoxia. The review also seeks to distinguish experimentally demonstrated responses from those inferred from related studies and those that remain hypothetical and require experimental validation. By comparing *V. amygdalina*, *M. oleifera*, and *O. gratissimum* within the same framework, this review aims to identify common responses to waterlogging, species-specific

differences, and areas in which evidence remains insufficient. Such a comparison provides a basis for developing more targeted experimental studies on the relationship between waterlogging tolerance, biomass production, and phytochemical composition in medicinal and indigenous leafy vegetables.

Objectives of the Review

This review aims to examine the relationship between soil waterlogging-induced hypoxia, physiological responses, and phytochemical changes in selected tropical indigenous leafy vegetables.

Specifically, the review seeks to:

- i. Examine the nutritional, culinary, ethnobotanical, and reported pharmacological importance of *Vernonia amygdalina*, *Moringa oleifera*, and *Ocimum gratissimum*, including their major bioactive compounds and reported biological activities;
- ii. Compare the available evidence on the physiological, biochemical, and phytochemical responses of the three species to waterlogging-induced hypoxia, with particular emphasis on growth, photosynthetic performance, oxidative stress, antioxidant responses, and secondary-metabolite production; and
- iii. Identify gaps and limitations in the existing evidence and propose priorities for future research, particularly controlled waterlogging experiments and integrated physiological, phytochemical, transcriptomic, and metabolomic approaches.

MATERIALS AND METHODS

Literature Search Strategy

This review was based on published literature retrieved from PubMed, Scopus, ScienceDirect, Google Scholar, and the FAO AGRIS database. The literature search covered publications primarily published between 2009 and 2026. The searches were conducted from June 2026 to August 2026. The selected period was used to capture both established information on the nutritional, ethnobotanical, pharmacological, physiological, and phytochemical characteristics of the three focal species and more recent research on plant responses to waterlogging and hypoxia.

Searches were conducted using combinations of keywords relating to the three focal species, waterlogging and hypoxia, physiological responses, secondary metabolites, phytochemicals, antioxidant responses, and medicinal properties. The principal search terms included “*Vernonia amygdalina*,” “*Moringa oleifera*,” “*Ocimum gratissimum*,” “waterlogging,” “soil waterlogging,” “hypoxia,” “anoxia,” “flooding,” “physiological response,” “secondary metabolites,” “phytochemicals,” “antioxidant enzymes,” and “traditional medicine.” These terms were combined using Boolean operators such as AND and OR.

Representative search combinations included:

- i. (“*Vernonia amygdalina*” OR “*Moringa oleifera*” OR “*Ocimum gratissimum*”) AND (waterlogging OR flooding OR hypoxia OR anoxia);
- ii. (“*Vernonia amygdalina*” OR “*Moringa oleifera*” OR “*Ocimum gratissimum*”) AND (“secondary metabolites” OR phytochemicals OR “antioxidant enzymes”);
- iii. (“*Moringa oleifera*”) AND (waterlogging OR flooding OR hypoxia) AND (growth OR photosynthesis OR physiology);

- iv. (“*Vernonia amygdalina*” OR “*Ocimum gratissimum*”) AND (hypoxia OR waterlogging OR flooding) AND (physiology OR phytochemistry).

The search strategy was adapted to the indexing and search functions of each database rather than assuming that an identical search string would operate in exactly the same manner across all databases.

Eligibility and Selection of Literature

Studies were considered eligible when they provided information relevant to at least one of the major objectives of the review, including the nutritional, ethnobotanical, pharmacological, physiological, biochemical, or phytochemical characteristics of the three focal species or their responses to waterlogging-induced stress. Priority was given to peer-reviewed research articles and relevant scholarly reviews.

Studies were excluded when their content was unrelated to the focal plants, waterlogging/hypoxia, or the physiological and phytochemical themes of the review. Studies were also excluded where the available information was insufficient to establish relevance to the review objectives.

Because direct evidence concerning waterlogging responses in *V. amygdalina* and *O. gratissimum* was limited, studies involving related species were considered where they provided relevant mechanistic or comparative information. However, evidence obtained from related species was not treated as direct experimental evidence for the focal species.

Evidence Classification and Data Synthesis

Information extracted from the selected literature included plant species, experimental or study context, waterlogging or hypoxia conditions were reported, physiological responses, biochemical responses, phytochemical constituents, and reported biological activities. Particular attention was given to growth, biomass, photosynthetic performance, chlorophyll responses, antioxidant enzymes, reactive oxygen species, and changes in secondary metabolites.

For the comparative analysis, evidence was classified into three categories: (i) experimentally demonstrated responses reported directly for the focal species; (ii) responses inferred from studies of related species or broader plant-waterlogging literature; and (iii) proposed or hypothesized responses for which sufficient experimental evidence is currently unavailable.

The information was then qualitatively synthesized across the three species to identify similarities, species-specific differences, strength of evidence, and major research gaps. Where quantitative findings were reported in the source literature, they were considered in the comparative interpretation rather than assuming that a qualitative description represented a measurable increase or decrease.

The review was therefore conducted as a critical narrative synthesis rather than being described as a systematic review or meta-analysis. No quantitative statistical pooling of study outcomes was performed.

Table 1: Morphological, Nutritional, and Socio-Culinary Characteristics of *Vernonia Amygdalina*, *Moringa Oleifera*, and *Ocimum Gratissimum*

Characteristic	<i>Vernonia amygdalina</i> Delile	<i>Moringa oleifera</i> Lam.	<i>Ocimum gratissimum</i> L.
Family	Asteraceae (Ijeh & Ejike, 2011)	Moringaceae (Gopalakrishnan et al., 2016)	Lamiaceae (Prabhu et al., 2009)
Common names	Bitter leaf; Ewuro; Olugbu; Shiwaka (Ijeh & Ejike, 2011)	Moringa; drumstick tree; horseradish tree; miracle tree (Gopalakrishnan et al., 2016)	Scent leaf; clove basil; African basil; Nchanwu/Efirin (Prabhu et al., 2009)
Growth habit	Perennial shrub or small tree, commonly occurring in tropical Africa (Ijeh & Ejike, 2011; Ogwu & Ikhajagbe, 2024)	Fast-growing tree occurring widely in tropical and subtropical regions (Gopalakrishnan et al., 2016; Leone et al., 2015)	Aromatic perennial herb or shrub, generally about 1–3 m tall and woody at the base (Prabhu et al., 2009)
Leaf characteristics	Leaves generally elliptic to lanceolate with finely toothed or serrated margins and a pubescent surface (Ogwu & Ikhajagbe, 2024)	Compound, 2–3-pinnate to tripinnate leaves with numerous small leaflets (Leone et al., 2015; Gopalakrishnan et al., 2016)	Opposite, ovate to elliptic leaves with serrated margins and glandular structures associated with essential-oil production (Prabhu et al., 2009)
Root system	Root architecture is less well characterized than above-ground morphology; available literature does not provide sufficient evidence to assign a specific waterlogging-adaptive root architecture.	Taproot system with a thick central root and lateral roots (Leone et al., 2015; Gopalakrishnan et al., 2016)	A primary taproot with secondary roots has been described; however, its structural response to prolonged waterlogging remains poorly characterized.
Geographical origin/distribution	Indigenous to tropical Africa and widely cultivated in sub-Saharan Africa (Ijeh & Ejike, 2011; Ogwu & Ikhajagbe, 2024)	Native to the Indian subcontinent and now widely cultivated throughout tropical and subtropical regions (Gopalakrishnan et al., 2016; Leone et al., 2015)	Distributed widely across tropical Africa and Asia (Prabhu et al., 2009)
Nutritional characteristics	Leaves provide dietary fibre, vitamins, minerals, and other phytochemicals (Ijeh & Ejike, 2011; Ukom et al., 2025)	Leaves are notable for protein, essential amino acids, vitamins, minerals, and other phytochemicals (Gopalakrishnan et al., 2016)	Leaves contain protein, fibre, minerals, vitamins, and diverse phytochemicals (Prabhu et al., 2009)
Reported antinutritional/phytochemical constituents	Tannins, saponins, phytates, oxalates, and other secondary metabolites have been reported in the leaves; composition varies with plant material and extraction	Oxalates, phytates, saponins, and tannins have been reported in the leaves; the available evidence does not support describing the species simply as having “low overall”	Tannins, saponins, alkaloids, phenolics, and other phytochemicals have been detected in the leaves (Prabhu et al., 2009)

Characteristic	<i>Vernonia amygdalina</i> Delile	<i>Moringa oleifera</i> Lam.	<i>Ocimum gratissimum</i> L.
Culinary use	method (Ijeh & Ejike, 2011; Ogwu & Ikhajagbe, 2024) Leaves are commonly washed, squeezed, or otherwise processed to reduce bitterness before incorporation into traditional dishes such as <i>ofe onugbu</i> (Nigeria) and <i>ndolé</i> (Cameroon) (Ijeh & Ejike, 2011; Ogwu & Ikhajagbe, 2024)	antinutritional factors (Leone <i>et al.</i> , 2015) Leaves are consumed fresh or cooked and may also be dried and powdered for incorporation into foods (Gopalakrishnan <i>et al.</i> , 2016)	Fresh leaves are used as a culinary seasoning in soups and other dishes because of their characteristic aroma and essential-oil constituents (Prabhu <i>et al.</i> , 2009)
Relevance to the present review	Widely used medicinal and food plant, but direct experimental evidence on physiological and phytochemical responses to waterlogging remains limited.	Nutritionally and medicinally important species for which direct physiological evidence under waterlogging is available (Ren <i>et al.</i> , 2021).	Important culinary and medicinal species, but direct evidence concerning physiological and phytochemical responses to waterlogging remains limited.

Comparative Ethnopharmacology and Molecular Bioactivity

Ethnopharmacological Importance

For many generations, *Vernonia amygdalina*, *Moringa oleifera*, and *Ocimum gratissimum* have been used in traditional medicine across Africa and parts of Asia. Their widespread use is largely based on indigenous knowledge and reported therapeutic applications. These traditional uses should, however, be distinguished from experimentally demonstrated pharmacological activities and from clinically established therapeutic benefits.

Vernonia amygdalina is traditionally used in the management of malaria, diabetes, gastrointestinal disorders, intestinal worms, and fever. Its leaves are also consumed as bitters and have been associated with appetite stimulation and digestive health (Ijeh & Ejike, 2011; Zulkefli *et al.*, 2025). Experimental studies have subsequently investigated some of these traditional applications, including antidiabetic and antimicrobial activities, but such findings should not be interpreted as evidence of established clinical efficacy in humans.

Moringa oleifera has a broad range of traditional applications involving its leaves, seeds, roots, and pods. These include uses associated with malnutrition, inflammation, infections, hypertension, and other health conditions (Ramappa *et al.*, 2025). The reported health effects of *M. oleifera* have also been investigated experimentally, particularly in relation to its nutritional and phytochemical composition; however, evidence from laboratory and animal studies remains distinct from clinically established therapeutic effects.

Ocimum gratissimum is widely recognized as both a culinary herb and a medicinal plant. Traditionally, its leaves are prepared as infusions or decoctions for conditions including diarrhoea, respiratory infections, stomach discomfort, skin infections, and fever (Ijenu *et al.*, 2023; Liu *et al.*, 2025). Experimental investigations have reported antimicrobial, antioxidant, anti-inflammatory, and other biological activities, but these findings primarily represent preclinical evidence rather than clinically validated treatments.

The ethnopharmacological importance of these species therefore provides a basis for investigating their phytochemical constituents and biological activities, but traditional use, experimental pharmacology, and clinical efficacy should not be treated as equivalent levels of evidence.

Pharmacological Activities and Bioactive Compounds

Phytochemical studies have shown that these indigenous leafy vegetables contain diverse secondary metabolites, including flavonoids, phenolic acids, alkaloids, terpenoids,

saponins, and essential oils. These compounds have been associated with several biological activities reported in laboratory and animal studies.

Antimicrobial Activity

Several studies have reported antimicrobial activity in extracts or essential oils from *V. amygdalina*, *M. oleifera*, and *O. gratissimum*. In *V. amygdalina*, sesquiterpene lactones such as vernodalin and vernolepin have been associated with antibacterial and antiparasitic activities. These findings represent activity observed in experimental systems and do not by themselves establish therapeutic effectiveness in humans.

The antimicrobial activity of *M. oleifera* has been associated with compounds including moringin, chlorogenic acid, lanosterol, and other phytochemicals. Experimental studies have reported inhibitory effects of leaf and seed extracts against drug-resistant bacterial isolates, including methicillin-resistant *Staphylococcus aureus* and extended-spectrum β -lactamase-producing *Escherichia coli* (Apenteng-Takyiako *et al.*, 2025; Ramappa *et al.*, 2025). The magnitude of antimicrobial activity varies with plant material, extraction solvent, concentration, and test organism, making direct comparison between studies difficult.

For *O. gratissimum*, antimicrobial activity has been associated particularly with essential-oil constituents such as eugenol, thymol, carvacrol, and chavibetol. Experimental studies have reported activity against bacterial and fungal organisms (Sharma *et al.*, 2024; Odeniyi *et al.*, 2025). For example, Sharma *et al.*, (2024) reported minimum inhibitory concentrations of 1.25% against *E. coli* and 5.0% against *Candida albicans* for *O. gratissimum* essential oil.

Antioxidant and Anti-inflammatory Activities

Oxidative stress and inflammation contribute to the development of several chronic diseases, and extracts from the selected indigenous leafy vegetables have demonstrated antioxidant and anti-inflammatory activities in experimental systems. In *V. amygdalina*, flavonoids and polyphenols have been investigated for their effects on oxidative stress and inflammatory responses (Dejene *et al.*, 2024; Bũrũ *et al.*, 2025). Dejene *et al.* (2024), for example, reported an IC₅₀ value of 0.81 μ g/mL for albumin-denaturation inhibition in a *V. amygdalina* extract; this represents an in-vitro assay result rather than clinical anti-inflammatory efficacy.

Similarly, quercetin, kaempferol, chlorogenic acid, and related compounds in *M. oleifera* have demonstrated antioxidant activity in laboratory and animal studies (Aljadaan *et al.*, 2025). For *O. gratissimum*, antioxidant activity has been associated with rosmarinic acid, eugenol,

and other phenolic constituents (Isono & Jadesimi, 2017; Liu et al., 2025).

These findings are relevant to the present review because waterlogging-induced hypoxia can disturb cellular redox balance and alter reactive oxygen species (ROS) metabolism. However, the presence or reported antioxidant activity of these compounds under non-waterlogged conditions does not demonstrate that waterlogging will increase their concentration in any of the three species.

Potential Roles in Chronic Disease Management

Beyond antimicrobial and antioxidant activities, experimental studies have investigated the potential roles of these plants in metabolic and inflammatory disorders. *V. amygdalina*, for example, has demonstrated antihyperglycaemic effects in streptozotocin-induced diabetic rats. Ong et al. (2011) reported increased GLUT4 translocation and inhibition of hepatic glucose-6-phosphatase following administration of *V. amygdalina* extract. These findings provide experimental

evidence for biological activity but should not be interpreted as proof of clinical efficacy.

Similarly, studies of *M. oleifera* have investigated effects related to inflammation, and intestinal protection (Feng et al., 2025). Extracts of *O. gratissimum* have also demonstrated antihypertensive, antioxidant, and gastroprotective activities in experimental models (Ijindu et al., 2023). Overall, the evidence supports biological activity in experimental systems, while evidence for safety, dosage, efficacy, and therapeutic effectiveness in humans remains comparatively limited.

From the perspective of waterlogging-induced hypoxia, these pharmacological observations establish the baseline phytochemical and biological importance of the three species. They do not, however, establish that waterlogging enhances medicinal quality. Whether hypoxic stress changes the concentration, composition, or total yield of these bioactive constituents remains a separate physiological and phytochemical question addressed in subsequent sections.

Table 2: Reported Bioactivities and Phytochemical Constituents of the Focus ILVs

Species	Primary extract type	Reported bioactive constituents/markers	Experimental model or target	Reported biological activity/parameter
<i>Vernonia amygdalina</i>	Aqueous, methanolic and ethyl-acetate extracts	Vernodalinal, vernolepin, luteolin and other phenolic constituents	Experimental microbial, inflammatory and diabetic models	Albumin-denaturation inhibition IC ₅₀ = 0.81 µg/mL in an in-vitro assay (Dejene et al., 2024); GLUT4 translocation increased by 35.7% and hepatic G6Pase activity was inhibited by 40% in a diabetic-rat study (Ong et al., 2011).
<i>Moringa oleifera</i>	Aqueous, ethanolic and hydroethanolic extracts	Moringin, quercetin, chlorogenic acid and other phenolic compounds	Antimicrobial, antioxidant and metabolic experimental models	Reported antimicrobial activity against drug-resistant bacterial isolates and antioxidant activity in experimental systems (Biru et al., 2025; Apenteng-Takyiako et al., 2025). Numerical values should be interpreted in relation to the specific extract and assay used.
<i>Ocimum gratissimum</i>	Hydrodistilled essential oil and aqueous extracts	Eugenol, thymol, rosmarinic acid, carvacrol, chavibetol	Bacterial and fungal models; experimental vascular and cellular models	Essential-oil MIC values of 1.25% against <i>E. coli</i> and 5.0% against <i>C. albicans</i> were reported by Sharma et al., (2024). Other reported activities include antioxidant and experimental anti-inflammatory effects (Isono & Jadesimi, 2017; Liu et al., 2025).

Note. The values presented in this table are study-specific experimental observations rather than validated clinical efficacy measures. Differences in extraction procedures, plant material, concentration, experimental model, and assay conditions limit direct quantitative comparison among species.

Adaptive Plant Physiology and Secondary Metabolism Under Soil Hypoxia

Effects of Soil Hypoxia on Plant Metabolism

Flooding and prolonged soil waterlogging reduce oxygen availability in the root zone, creating hypoxic and, under more severe conditions, anoxic environments. Because oxygen is required for aerobic respiration, its depletion restricts ATP production and disrupts metabolic processes required for nutrient uptake, root maintenance, growth, and other physiological functions (Bailey-Serres et al., 2012; Striker, 2012).

Under oxygen limitation, plants may increase their reliance on anaerobic metabolic pathways to maintain a limited supply of ATP. This metabolic adjustment represents a survival response rather than a complete replacement for aerobic respiration, because anaerobic metabolism produces substantially less energy. Prolonged oxygen deprivation can therefore result in impaired nutrient acquisition, altered root development, reduced growth, and, depending on species and stress severity, tissue injury.

Reactive oxygen species (ROS) also have an important but complex role during flooding stress. ROS should not be considered exclusively as damaging products of hypoxia. Low-oxygen conditions can alter cellular redox balance and ROS production, and ROS may participate in stress signalling

and acclimation. Following the restoration of oxygen during reoxygenation, however, rapid changes in ROS production can contribute to oxidative damage when antioxidant capacity is exceeded (Blokhina & Fagerstedt 2010; Voeselek & Bailey-Serres, 2015). Thus, plant survival under waterlogging depends on the capacity to maintain energy metabolism, regulate redox status, and activate appropriate adaptive responses.

Morphological and Physiological Responses to Waterlogging

Plants differ considerably in their responses to soil oxygen deficiency. Established adaptations in waterlogging-tolerant species include aerenchyma formation and, in some species, the development of adventitious roots. Aerenchyma provides internal pathways that facilitate oxygen movement from aerial tissues towards oxygen-deficient roots, while adventitious roots can contribute to continued water and nutrient uptake under flooded conditions (Yamauchi et al., 2018). The presence and magnitude of these adaptations, however, are species-specific and should not be assumed for the three indigenous leafy vegetables considered in this review.

Among the three species, *Moringa oleifera* currently has the clearest direct evidence relating specifically to waterlogging.

Ren *et al.* (2021) reported reductions in photosynthetic performance, chlorophyll content, and growth at the seedling stage under waterlogging conditions. These findings demonstrate physiological sensitivity to waterlogging but do not, by themselves, establish the absence of specific anatomical adaptations such as aerenchyma or adventitious rooting.

Information on the direct responses of *Vernonia amygdalina* to prolonged soil waterlogging remains limited. The available literature does not provide sufficient species-specific experimental evidence to establish whether this species forms aerenchyma, develops adventitious roots, or maintains photosynthetic function through specific structural adaptations under waterlogging. Evidence from studies of general flooding responses and related species can provide physiological context, but such evidence should be distinguished from direct observations in *V. amygdalina* (Bailey-Serres *et al.*, 2012; Yamauchi *et al.*, 2018).

A similar limitation applies to *Ocimum gratissimum*. Although related species and members of the Lamiaceae may possess responses to water deficit or flooding, the available evidence reviewed here is insufficient to establish the presence or absence of aerenchyma, adventitious rooting, or specific photosynthetic adjustments in *O. gratissimum* under prolonged waterlogging. These responses should therefore be regarded as uncharacterized rather than categorically absent. Photosynthetic performance is particularly relevant because oxygen deficiency in the root zone can indirectly affect shoot carbon assimilation through impaired water and nutrient relations and altered root-to-shoot signalling. Chlorophyll fluorescence parameters such as the maximum quantum efficiency of photosystem II (Fv/Fm) can be used to assess changes in photosynthetic function (Maxwell & Johnson, 2000). However, predicted changes in Fv/Fm for *V. amygdalina* or *O. gratissimum* should not be presented as experimentally demonstrated responses unless species-specific waterlogging experiments have established them.

Secondary Metabolism and Phytochemical Responses

Abiotic stress can alter plant secondary metabolism, and changes in phenolic compounds, flavonoids, terpenoids, and other specialized metabolites have been reported across different plant species under environmental stress (Ramakrishna & Ravishankar, 2011). Waterlogging-induced changes in cellular redox status and defence signalling could therefore influence the biosynthesis or accumulation of secondary metabolites.

For the three species examined in this review, however, direct evidence demonstrating that waterlogging consistently increases particular medicinally important compounds remains limited. The presence of vernodalin and related sesquiterpene lactones in *V. amygdalina*, phenolic compounds and isothiocyanates in *M. oleifera*, and eugenol and related phenylpropanoids in *O. gratissimum* establishes their phytochemical importance under normal or previously

studied conditions. It does not demonstrate that waterlogging will necessarily increase their concentrations.

Phytochemical responses to environmental stress can depend on stress intensity, duration, genotype, developmental stage, tissue type, environmental conditions, and the timing of sampling (Ramakrishna & Ravishankar, 2011). Consequently, a moderate stress treatment may produce a different phytochemical response from prolonged or severe waterlogging, and the direction of change cannot be assumed to be the same across species.

An additional distinction is required between phytochemical concentration and total metabolite yield. A stress treatment could increase the concentration of a compound in surviving tissues while simultaneously reducing total plant biomass. In such a situation, the concentration of the metabolite per unit dry mass may increase even though the total quantity of that metabolite produced by the plant declines. Therefore, increased phytochemical concentration should not automatically be interpreted as improved medicinal quality or increased medicinal productivity.

The relationship between stress tolerance and medicinal quality proposed in this review as the resilience–remedy continuum should therefore be regarded as a conceptual framework rather than an established physiological or pharmacological relationship. Its validation would require experiments that simultaneously measure stress intensity, plant survival and biomass, physiological responses, and quantitative changes in relevant phytochemicals.

Comparative Interpretation of Physiological and Phytochemical Responses

The available evidence supports three levels of interpretation for the responses of the selected species: experimentally demonstrated responses, responses inferred from broader or related-species literature, and hypotheses requiring direct validation. This distinction is particularly important because the quantity of direct evidence differs substantially among the three species.

For *M. oleifera*, direct waterlogging research provides evidence of reductions in growth, chlorophyll content, and photosynthetic performance (Ren *et al.*, 2021). For *V. amygdalina* and *O. gratissimum*, comparable species-specific waterlogging evidence is limited. Their potential responses can therefore be discussed using established mechanisms of plant responses to oxygen deficiency, but should not be presented as experimentally confirmed species-specific traits. Similarly, the occurrence of antioxidant enzymes, phenolic compounds, flavonoids, terpenoids, and other secondary metabolites in these plants does not establish that their abundance will increase under waterlogging. The principal research gap is therefore not simply whether these plants contain medicinally important compounds, but whether controlled waterlogging changes the concentration, composition, and total yield of those compounds while maintaining economically meaningful biomass production.

Table 3: Evidence-Based Comparative Physiological and Phytochemical Responses to Waterlogging-Induced Hypoxia

Response/Indicator	<i>Vernonia Amygdalina</i>	<i>Moringa Oleifera</i>	<i>Ocimum Gratissimum</i>
Aerenchyma formation	Uncharacterized; insufficient direct experimental evidence under waterlogging.	Not sufficiently established from the available evidence; direct waterlogging studies should be used to determine whether anatomical adaptation occurs.	Uncharacterized; insufficient species-specific evidence to classify the trait as present or absent.
Adventitious rooting	Uncharacterized under waterlogging.	Uncharacterized as a specific waterlogging adaptation in the evidence reviewed; claims of extremely low capacity should be experimentally verified.	Uncharacterized under waterlogging.

Response/Indicator	<i>Vernonia Amygdalina</i>	<i>Moringa Oleifera</i>	<i>Ocimum Gratissimum</i>
Photosynthetic response	Species-specific waterlogging response remains insufficiently characterized.	Experimentally reported reduction in photosynthetic performance and chlorophyll content under waterlogging (Ren et al., 2021).	Species-specific response remains insufficiently characterized.
PSII photochemical efficiency (Fv/Fm)	Requires direct measurement under controlled waterlogging.	Potentially affected by waterlogging; species-specific quantitative measurements should be used to establish the magnitude of change.	Requires direct measurement under controlled waterlogging.
Antioxidant response	Potential involvement of antioxidant defence is biologically plausible, but species-specific waterlogging evidence is limited.	Requires quantitative measurement of antioxidant enzymes and redox markers under defined waterlogging conditions.	Potential involvement is plausible, but direct waterlogging evidence is limited.
Phytochemical response	Potential changes in sesquiterpene lactones and phenolic compounds are hypothesized and require quantitative validation.	Potential changes in phenolics, flavonoids, chlorogenic acid and other constituents require controlled quantitative assessment.	Potential changes in eugenol, rosmarinic acid and other phenylpropanoids require direct experimental validation.
Biomass–phytochemical relationship	Requires simultaneous measurement of biomass and metabolite concentration.	Requires simultaneous measurement of biomass and metabolite concentration.	Requires simultaneous measurement of biomass and metabolite concentration.
Resilience–remedy relationship	Conceptual hypothesis requiring validation.	Conceptual hypothesis requiring validation.	Conceptual hypothesis requiring validation.
Evidence classification	Limited direct waterlogging evidence; several responses remain uncharacterized.	Comparatively stronger direct physiological evidence, particularly for growth, chlorophyll and photosynthetic responses (Ren et al., 2021).	Limited direct waterlogging evidence; several responses remain uncharacterized.

Note: “Experimentally demonstrated” refers to observations directly reported for the species under waterlogging. “Inferred” refers to mechanisms supported by broader plant-waterlogging literature but not directly demonstrated in the species. “Hypothesized” refers to responses that require controlled experimental validation.

Challenges and Future Research Directions

Standardization of Experimental Approaches

A major limitation in comparing the responses of *Vernonia amygdalina*, *Moringa oleifera*, and *Ocimum gratissimum* to waterlogging is the lack of standardized experimental conditions. Existing studies differ in plant material, developmental stage, soil or growth medium, waterlogging intensity, duration of exposure, recovery period, extraction procedure, solvent system, and analytical method. These differences can substantially influence both physiological and phytochemical measurements and make direct comparison among studies difficult.

Future waterlogging experiments should therefore clearly define the duration and severity of waterlogging, soil or growth-medium characteristics, plant developmental stage, environmental conditions, and recovery period. Where possible, soil oxygen availability should be measured rather than assuming that a particular waterlogging treatment produces the same level of hypoxia across experiments. This would allow physiological and phytochemical responses to be related to the actual oxygen status experienced by the roots. Physiological measurements should include biomass accumulation, root development, chlorophyll content, photosynthetic performance, and appropriate indicators of oxidative stress and antioxidant defence. Measurements of photosynthetic efficiency using chlorophyll fluorescence can provide additional information on the effects of waterlogging on photosynthetic function (Maxwell & Johnson, 2000).

Phytochemical investigations should also employ standardized sampling and analytical procedures. Quantitative HPLC, GC-MS, or other validated chromatographic approaches should be used to determine changes in individual compounds rather than relying only on total phenolic or total flavonoid measurements. Importantly, both metabolite concentration and plant biomass should be measured so that changes in concentration can be distinguished from changes in total metabolite production.

Another limitation is the predominance of laboratory and animal evidence for many of the reported pharmacological activities. Such evidence provides a basis for further investigation but should remain distinguished from clinical evidence concerning safety, dosage, and therapeutic effectiveness.

Opportunities for Integrated Physiological, Transcriptomic and Metabolomic Research

The limited species-specific information available for *V. amygdalina* and *O. gratissimum* provides an opportunity for controlled experiments that integrate physiological and molecular measurements. Rather than examining phytochemical changes in isolation, future studies should simultaneously measure plant growth, photosynthetic performance, root responses, oxidative status, and quantitative metabolite profiles under defined levels and durations of waterlogging.

Transcriptomic approaches could help identify genes and regulatory pathways associated with oxygen sensing, anaerobic metabolism, antioxidant defence, root adaptation, and secondary metabolism. Metabolomic analyses could then identify broader changes in primary and secondary metabolites associated with these physiological responses.

The integration of transcriptomic and metabolomic data with physiological measurements would be particularly useful for determining whether changes in medicinally relevant metabolites are associated with adaptive responses to hypoxia, general tissue injury, or recovery after reoxygenation. Such studies could also determine whether the same stress treatment produces similar or contrasting responses among the three species.

A particularly important experimental question is whether a waterlogging treatment can produce a measurable change in phytochemical composition without causing an unacceptable reduction in biomass. This requires simultaneous assessment of stress intensity, physiological performance, biomass, metabolite concentration, and total metabolite yield. Such

evidence would provide a stronger basis for evaluating the “resilience–remedy” continuum proposed in this review.

Comparative Research Priorities for the Three Species

Research priorities should differ according to the current strength of evidence for each species. *M. oleifera* has comparatively more direct evidence concerning physiological responses to waterlogging, including changes in growth, chlorophyll content, and photosynthetic performance (Ren et al., 2021). Further work should therefore focus on linking these physiological responses to quantitative phytochemical changes and molecular mechanisms.

For *V. amygdalina*, the major priority is to establish basic species-specific responses to controlled waterlogging, including root development, biomass production, photosynthetic performance, antioxidant responses, and changes in major medicinally relevant metabolites. For *O. gratissimum*, similar experiments are required, with particular attention to its essential-oil and phenylpropanoid composition.

Comparative experiments involving all three species under identical environmental conditions would be particularly valuable. Such experiments could determine whether differences in waterlogging tolerance are associated with differences in biomass maintenance, antioxidant regulation, root adaptation, or secondary-metabolite responses.

Conservation and Sustainable Utilization

The long-term value of indigenous leafy vegetables depends not only on their nutritional and medicinal importance but also on their conservation and sustainable utilization. Conservation of genetically diverse populations through seed banks, field collections, and community-based programmes could provide valuable genetic resources for future research and breeding.

Production systems should also consider how environmental stress affects both yield and phytochemical composition. Future breeding and cultivation programmes should therefore avoid selecting solely for waterlogging tolerance or solely for high phytochemical concentration. Instead, selection should consider the combined traits of biomass production, stress tolerance, and stable phytochemical composition.

Improved cultivation practices, post-harvest handling, and processing may further support the sustainable utilization of these species. However, claims concerning enhanced medicinal value should be based on quantitative evidence rather than on stress exposure alone. Establishing the relationship between environmental conditions, crop yield, phytochemical composition, and biological activity will be necessary before waterlogging can be considered a useful cultivation strategy for improving medicinal quality.

CONCLUSION

This review shows that soil waterlogging and the resulting oxygen limitation can substantially affect the physiology, growth, and potentially the secondary metabolism of indigenous leafy vegetables. However, the strength of evidence differs considerably among the three species examined. *Moringa oleifera* has the most direct evidence of waterlogging-related physiological responses, including reduced growth and photosynthetic performance under waterlogged conditions (Ren et al., 2021). In contrast, direct experimental evidence for the physiological responses of *Vernonia amygdalina* and *Ocimum gratissimum* to soil hypoxia remains limited, making species-specific conclusions about their tolerance mechanisms premature.

The review also indicates that hypoxia, oxidative signalling, and subsequent reoxygenation may influence secondary metabolism, but evidence that waterlogging consistently increases particular medicinally important compounds remains insufficient. Reported or proposed changes in phenolics, flavonoids, terpenoids, essential oils, and related metabolites should therefore be regarded as species-, tissue-, genotype-, and stress-dependent rather than as predictable improvements in medicinal quality. In addition, increased metabolite concentration should not be interpreted as increased medicinal value where waterlogging simultaneously reduces biomass or total metabolite yield.

The “resilience–remedy” continuum proposed in this review is consequently a conceptual framework rather than a validated physiological or pharmacological relationship. Future research should prioritize controlled waterlogging experiments with measured soil oxygen, growth and photosynthetic assessments, oxidative-stress and antioxidant measurements, and quantitative HPLC/GC-MS profiling. Integrating these measurements with transcriptomic and metabolomic analyses, particularly in *V. amygdalina* and *O. gratissimum*, will help establish whether waterlogging-induced physiological adaptation is accompanied by reproducible changes in phytochemical composition and medicinal quality.

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