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Ecophysiological, molecular, and metabolomic adaptations of *Coptis teeta* Wall. to abiotic stress in the Eastern Himalayas: A comprehensive synthesis for conservation physiology

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Abstract

The Eastern Himalayas constitute a globally significant biodiversity hotspot that harbors the narrow endemic medicinal plant *Coptis teeta* Wall. (Ranunculaceae), locally known as *Mishmi Tita*. This critically endangered species represents a unique convergence of evolutionary antiquity, ecological specialization, and pharmacological importance due to its high accumulation of isoquinoline alkaloids, particularly berberine. However, accelerating climate change, habitat fragmentation, and overexploitation increasingly threaten its survival. This manuscript synthesizes current knowledge on the ecophysiology, molecular stress responses, secondary metabolism, and plant-microbe interactions of *C. teeta*. Evidence from physiological measurements and transcriptomic analyses indicates that abiotic stress induces strong antioxidant and cellular protection responses, often at the expense of alkaloid biosynthesis, revealing a fundamental trade-off between stress tolerance and medicinal quality. Adopting a holobiont framework, we highlight the crucial role of rhizospheric and endophytic microbes in modulating stress signaling, nutrient acquisition, and secondary metabolism. Finally, we propose an integrative conservation physiology strategy combining genomic insights, microbiome engineering, and niche-mimicking agrotechnology to ensure the long-term persistence and pharmacological integrity of *C. teeta* under Anthropocene pressures.

Keywords: *Coptis teeta*, conservation physiology, holobiont, stress tolerance, berberine, Eastern Himalayas

Introduction

Introduction: The Botanical, Evolutionary, and Pharmacological Profile

1. Taxonomy and Evolutionary Context: An Ancient Lineage in the Ranunculales

Coptis teeta Wall. resides within the Ranunculaceae, a family renowned for its elaboration of complex secondary metabolites. Phylogenetically, the genus *Coptis*. represents an early-diverging lineage within the order Ranunculales. This basal position is significant; it suggests that the alkaloid biosynthetic pathways found in *Coptis* are ancient chemical defense mechanisms that have been conserved over millions of years of evolution. The species is part of a disjointed circumboreal distribution of the genus, yet *C. teeta* itself is a narrow endemic, isolated in the misty, rugged terrain of the Mishmi Hills (Pandit and Babu, 1998) [35]. Recent chloroplast genome studies confirm *C. teeta* as sister to *C. chinensis* within a monophyletic Ranunculaceae (Gao *et al*., 2018) [15]. The genus *Coptis* (tribe Coptideae, family Ranunculaceae) comprises perennial herbaceous species characterized by basal leaves, yellow rhizomes, and dense fibrous root systems. Globally, approximately sixteen accepted *Coptis* species are distributed across the Northern Hemisphere, with the highest species richness occurring in East Asia (Dezhi and Robinson, 2001) [11]. In China alone, six *Coptis* species have been documented, primarily occurring in southwestern, central-southern, and eastern regions, as well as in Taiwan (Dezhi and Robinson, 2001) [11]. Members of this genus are of exceptional medicinal importance, as the rhizomes of all *Coptis* species have been utilized for thousands of years under the collective name *Rhizoma coptidis* (Huanglian), forming one of the most enduring botanical drug lineages in traditional medicine systems (Wang *et al*., 2021; Chen and Zhang, 2025) [5].

2. Morphological Characteristics and Growth Habit: Adaptations to the Temperate Forest Understory

The morphology of *Coptis teeta* Wall. reflects a finely tuned evolutionary adaptation to the cool, shaded, and persistently moist understory of temperate broad-leaved forests in the Eastern Himalayas. Each structural component of the plant contributes to maximizing resource acquisition and long-term persistence under conditions of low light availability, high humidity, and short growing seasons.

Rhizome

The perennial rhizome is the most distinctive and economically valuable organ of *C. teeta*, serving simultaneously as a storage structure, regenerative axis, and phytochemical reservoir. It is horizontally to obliquely oriented, woody, and irregularly branched, giving rise to the characteristic “chicken-claw” morphology described in ethnobotanical literature. Typically measuring 5-15 cm in length, the rhizome exhibits a striking golden-yellow coloration internally, a diagnostic feature directly correlated with its exceptionally high concentration of berberine and related benzylisoquinoline alkaloids. The intensely bitter taste further reflects this alkaloid richness and underpins its medicinal value. Functionally, the rhizome acts as a long-term sink for carbohydrates, nitrogen, and secondary metabolites, enabling the plant to survive extended periods of aboveground dormancy during winter and other unfavorable conditions (Pandit and Babu, 1998; Chelleng *et al*., 2024) [4, 35].

Foliage

Leaves of *C. teeta* are radical in origin, emerging directly from the rhizome rather than from an elongated aerial stem, a strategy that minimises structural investment while maximizing efficiency under shaded conditions. The leaves are glabrous and compound, with a deeply divided ternatisect lamina that increases the effective photosynthetic surface area. Each leaf is supported by a slender, elongated petiole ranging from 7 to 14 cm in length, elevating the lamina above the forest floor litter. This architecture allows the plant to effectively intercept diffuse and transient sunflecks penetrating the dense canopy, a critical adaptation in light-limited understory environments. Such petiole elongation and lamina dissection are classic shade-adaptive traits that optimize carbon gain while reducing self-shading and boundary-layer resistance in humid microclimates (Mukherjee, 2022) [30]. It generally grows 30-50 cm tall in moist temperate broad-leaved forests of Arunachal Pradesh. (Wang *et al*., 2024) [55].

Reproductive Features

Reproductive structures in *C. teeta* are modest and reflect a strategy biased toward persistence rather than dispersal. The inflorescence is a loosely arranged panicle bearing small, inconspicuous white to pale yellow flowers, indicative of limited investment in pollinator attraction. Flowering is strictly season-bound and temperature-dependent, occurring between mid-February and April following winter chilling. The fruit is a follicle containing small, black, glossy seeds. However, sexual reproduction in *C. teeta* is severely constrained by high levels of male sterility, low pollen viability, and inefficient seed dispersal mechanisms. Long-term field observations have demonstrated that sexual reproduction in *C. teeta* has not resulted in a measurable increase in population size, a limitation that is further exacerbated by increasing climate variability driven by anthropogenic disturbances (Pandit and Babu, 1998, 2003; Bajpay *et al*., 2019) [9, 35]. Consequently, population maintenance relies predominantly on vegetative propagation through rhizome fragmentation. While this strategy enhances local persistence under stable environmental conditions, it simultaneously restricts gene flow, reduces genetic diversity, and limits adaptive potential in the face of rapid environmental change. These reproductive and ecological constraints have also hindered sustainable utilization of *C. teeta* by local communities in the Mishmi Hills, preventing farmers from fully realizing its economic potential despite its high medicinal value. Recent studies emphasize that effective conservation and management of such biologically constrained species require active involvement of local communities in decision-making processes, particularly in regions where traditional knowledge and resource dependence are closely linked (Andrade *et al*., 2012) [1]. Moreover, the inclusion of external experts from technical, conservation, and marketing sectors has been shown to strengthen governance frameworks, enhance sustainability of indigenous plant resources, and secure livelihoods through integrated economic, environmental, social, and cultural benefits (Pisor *et al*., 2024) [38]. Phytochemical evidence also supports this functional specialization of the rhizome, demonstrating that it serves as a primary site for the accumulation of phenolic compounds and isoquinoline-associated metabolites with chemotaxonomic significance. The concentration of such energetically costly compounds within the rhizome underscores its role as a long-term organ for both survival and chemical defense (Yan *et al*., 2026) [58].

3. Ethnobotany and Global Economic Drivers

"Mishmi Tita" is culturally keystone species for the Idu Mishmi, Adi, and Galo tribes of Arunachal Pradesh. It is utilized as a panacea for enteric diseases, malarial fevers, and generalized inflammation. In the global market, it is often traded as a premium analogue of the Chinese *Coptis chinensis* ("Huanglian"). The pharmacological value is driven by its alkaloid profile, which has demonstrated efficacy in regulating glucose metabolism (Type 2 diabetes), inhibiting bacterial efflux pumps (antimicrobial), and inducing apoptosis in cancer cells and secondary metabolites, buffering the plant against prolonged periods of environmental stress. During the extended snow-covered winters typical of its native range, aboveground tissues senesce, and survival depends almost entirely on the stored reserves within the rhizome. This strategy underscores a shift toward vegetative longevity rather than rapid regeneration, reflecting adaptation to a stable yet climatically harsh niche (Chelleng *et al*., 2024) [4]. Charmacological importance of *Coptis* species is formally recognized in modern pharmacopeial systems. The 2025 edition of the Chinese Pharmacopoeia lists three species- *Coptis chinensis* Franch. (“Chuanlian” or “Weilian”), *Coptis deltoidea* C.Y. Cheng et Hsiao (“Yalian”), and *Coptis teeta* Wall. (“Yunlian”) as the official botanical sources of *Rhizoma coptidis*. *Coptis japonica* Makino is recognized as a legitimate source in the Japanese Pharmacopoeia, the Korean Pharmacopoeia, and the international standard ISO 7177:2023 (Qi *et al*., 2024). *Rhizoma coptidis* remains one of the most important traditional Chinese medicines and is widely prescribed for the treatment of damp heat syndromes, dysentery, jaundice, inflammatory disorders, and metabolic imbalances (Chen and Zhang, 2025) [5]. Owing to its exceptionally high medicinal value, *C. teeta* has been cultivated by indigenous communities in Yunnan Province, China, for several centuries. However, continued overharvesting of wild populations, coupled with habitat degradation, has placed natural populations at severe risk, rendering the species locally endangered despite its long history of cultivation (Huang *et al*., 2005; Cheng *et al*., 2022) [6, 21].

Ecological Niche and Environmental Constraints

Understanding the stress physiology of *Coptis teeta* Wall. requires an appreciation of its exceptionally narrow ecological amplitude. Unlike generalist taxa, *C. teeta* is a strict habitat specialist and functions as a sensitive bio-indicator of undisturbed, primary forest ecosystems (Pandit and Babu, 1998) [35].

1. Biogeography and Climate: “Sky-Island” Constraints of the Eastern Himalayas

C. teeta is endemic to the Mishmi Hills of Arunachal Pradesh, India, with fragmented populations extending into adjacent regions of southeastern Tibet (China) and northern Myanmar (Chelleng *et al*., 2024) [4]. Its distribution is highly discontinuous, reflecting the “sky-island” biogeography characteristic of the Eastern Himalayas.

Elevation

The species is confined to a narrow altitudinal belt between 2,500 and 4,000 m above sea level (Pandit and Babu, 1998) [35], corresponding to the ecotone between temperate broadleaf forests and sub-alpine coniferous vegetation. This elevational restriction imposes strong selection for cold tolerance and limits physiological plasticity.

Precipitation and Humidity

The region receives heavy monsoonal precipitation (>2,000 mm annually) and experiences persistent cloud cover. *C. teeta* is critically dependent on sustained atmospheric humidity and consistently moist soils, exhibiting marked intolerance to desiccation (Mukherjee, 2022) [30]. Even short-term moisture deficits can disrupt its physiological equilibrium.

Temperature

Adapted to cool temperate regimes, *C. teeta* requires defined thermal cues, including winter chilling, for successful floral initiation. Temperatures exceeding ~25 °C likely surpass its thermal compensation point, rendering the species highly vulnerable to episodic heat stress and warming trends associated with climate change (Mukherjee, 2022) [30].

2. Edaphic Specificity: The Central Role of Acidic, Humus-Rich Soils

The patchy spatial distribution of *C. teeta* is strongly governed by soil characteristics, particularly organic matter content and acidity (Chelleng *et al*., 2024) [4].

Soil Texture and Organic Matter

The species thrives exclusively in humus-rich sandy-loam to loamy soils. A thick forest leaf-litter layer is essential, functioning as a moisture-retaining matrix and a slow-release nutrient reservoir (Chelleng *et al*., 2024) [4]. Removal of this litter layer rapidly degrades habitat suitability.

Soil Acidity

C. teeta is an acidophilic species, requiring soil pH values between 4.5 and 6.0. While such acidic conditions can induce aluminum toxicity in many crop plants, *C. teeta* appears physiologically adapted to these environments, potentially exploiting low pH to enhance the bioavailability of micronutrients such as iron and manganese (Pandit and Babu, 1998) [35].

Nutrient Cycling

As an understory herb in closed-canopy forests, *C. teeta* depends on slow organic matter mineralization for nitrogen acquisition. This chronically low-nitrogen environment has likely shaped its secondary metabolism, particularly the biosynthesis of nitrogen-intensive isoquinoline alkaloids.

3. K-Selected Life History and Vulnerability to Rapid Environmental Change

Ecologically, *C. teeta* exhibits classic K-selected life-history traits that favor persistence in stable environments but constrain adaptive capacity under rapid change (Pandit and Babu, 1998) [35].

Longevity and Growth

It is a long-lived perennial characterized by slow growth rates and substantial allocation to chemical defense rather than rapid biomass accumulation (Pandit and Babu, 1998) [35].

Reproductive Strategy

The species produces relatively few seeds with limited dispersal capacity, reducing its ability to recolonize disturbed habitats (Pandit and Babu, 1998) [35].

Competitive Ability

While *C. teeta* can compete effectively within stable, late-successional forest communities, it is a poor colonizer of disturbed or degraded sites. Consequently, anthropogenic disturbances-such as logging, forest fragmentation, and climate-driven shifts in temperature and moisture regimes-often result in population collapse rather than adaptive recovery (Pandit and Babu, 1998) [35].

Collectively, these ecological and evolutionary traits render *C. teeta* exceptionally vulnerable in the Anthropocene, where rapid environmental change outpaces its inherent physiological and life-history constraints.

Physiological Responses to Abiotic Stressors

The Eastern Himalayas are warming at a rate exceeding the global average, accompanied by increasing climatic variability, altered precipitation patterns, and intensified radiation regimes. For a narrowly adapted alpine understory species such as *Coptis teeta* Wall., these macro-climatic changes translate into a suite of overlapping abiotic stressors-principally drought, heat, cold, and enhanced ultraviolet radiation. Because *C. teeta* evolved under relatively stable climatic conditions, its physiological responses are largely defensive rather than plastic, emphasizing damage limitation over rapid acclimation.

1. Water Deficit and Drought Stress: Central Constraints on Turgor and Photosynthetic Performance

Among all abiotic factors, water availability represents the most critical determinant of *C. teeta* survival. The species possesses a shallow root system and relies heavily on the surface humus layer for water uptake. Consequently, it is particularly susceptible to pre-monsoon dry spells and episodic drought events, which are becoming more frequent under changing climatic regimes.

1.1. Mechanisms of Damage

Turgor Loss, Stomatal Regulation, and Oxidative Stress

Water deficit reduces cellular water potential, leading to a decline in turgor pressure. Because turgor is the primary driving force for cell expansion, its loss results in immediate suppression of leaf expansion, reduced petiole elongation, and diminished rhizome thickening. Over time, chronic turgor loss translates into reduced vegetative vigor and lower storage capacity within the rhizome, directly affecting plant survival and reproductive potential.

Stomatal Closure and Photosynthetic Constraint

In response to declining leaf water status, *C. teeta* exhibits hydro-active stomatal closure as a protective mechanism to limit transpirational water loss. While effective in conserving water, this response severely restricts CO_2 diffusion into the leaf mesophyll. Reduced intercellular CO_2 concentration causes downregulation of the Calvin-Benson cycle, leading to a mismatch between light capture and carbon assimilation.

Generation of Reactive Oxygen Species (ROS)

Despite reduced carbon fixation, photon absorption by chlorophyll continues unabated. The excess excitation energy is diverted to molecular oxygen, resulting in the formation of reactive oxygen species (ROS), including singlet oxygen $^1O_2$, superoxide radicals O^{2-}, and hydrogen peroxide H_2O_2. These ROS attack thylakoid membranes, disrupt photosystem II integrity, and initiate lipid peroxidation cascades, ultimately impairing photosynthetic efficiency (Zhang *et al*., 2022) [60].

1.2. Physiological Adjustments: Osmotic Regulation and Antioxidant Defense Deployment

Osmotic Adjustment and Cellular Hydration

To counteract declining water potential, *C. teeta* accumulates compatible osmolytes such as proline, soluble sugars, and other low-molecular-weight organic compounds. These solutes lower cellular osmotic potential without interfering with enzyme activity or membrane stability, enabling cells to retain water and partially restore turgor under drought conditions. This osmotic adjustment is critical for maintaining metabolic continuity during transient water stress.

Activation of Antioxidant Defense Systems

Concomitant with osmotic regulation, *C. teeta* activates an extensive antioxidant defense network to mitigate ROS-induced damage. Key enzymatic antioxidants, including superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) are upregulated to detoxify superoxide radicals and hydrogen peroxide. This coordinated antioxidant response limits oxidative injury to membranes, proteins, and nucleic acids, thereby enhancing cellular survival under drought-induced photoinhibition (Nath *et al*., 2025).

2. Thermal Stress: Navigating the Trade-Off Between Heat Injury and Cold Acclimation

C. teeta occupies a narrow thermal niche defined by cool summers and prolonged cold winters. Deviations from this thermal regime impose substantial physiological costs, particularly under current warming trends.

2.1. Heat Stress: Carbon Imbalance and Membrane Destabilization

Respiration-Photosynthesis Imbalance:

As ambient temperatures rise, dark respiration increases exponentially due to enhanced enzymatic kinetics, while net photosynthesis reaches an optimum and subsequently declines. This divergence results in a negative carbon balance, commonly referred to as “carbon starvation.” Under prolonged heat stress, *C. teeta* mobilizes stored carbohydrates from its rhizome to sustain basic metabolic functions, progressively depleting reserves essential for growth, defense, and reproduction (Zhang *et al*., 2022) [60].

Membrane Fluidity and Electrolyte Leakage: Elevated temperatures increase the kinetic energy of membrane lipids, leading to excessive membrane fluidity. This destabilization compromises membrane integrity, causing leakage of electrolytes and disruption of ion gradients vital for cellular homeostasis. Loss of membrane selectivity impairs mitochondrial and chloroplast function, further exacerbating metabolic inefficiency under heat stress.

2.2. Cold and Freeze Stress: Ice Formation and Cellular Dehydration

Although *C. teeta* is generally adapted to cold environments, extreme freeze-thaw cycles pose significant risks. Ice formation occurs primarily in the apoplast (intercellular spaces), drawing water out of the cytoplasm and inducing severe cellular dehydration-a phenomenon known as physiological drought. Repeated freeze-thaw events can also cause mechanical damage to rhizome tissues, disrupt vascular continuity, and impair nutrient transport, especially during early spring deacclimation phases.

3. UV-B Radiation: A Dual Force of Damage and Metabolic Induction

At high elevations, *C. teeta* is exposed to elevated levels of ultraviolet-B (UV-B) radiation due to reduced atmospheric filtering.

Photo-oxidative and Genotoxic Stress

Excessive UV-B radiation damages cellular components by inducing DNA lesions, particularly pyrimidine dimers, and by impairing photosystem II efficiency. These effects reduce photosynthetic performance and increase the energetic cost of DNA repair and protein turnover.

Eustress and Secondary Metabolite Enhancement

Paradoxically, moderate UV-B exposure acts as a beneficial environmental signal rather than a purely harmful stressor. Through activation of the UVR8 photoreceptor signaling pathway, UV-B induces the expression of genes involved in phenylpropanoid and isoquinoline alkaloid biosynthesis. The resulting accumulation of flavonoids and alkaloids in epidermal and rhizome tissues functions as a “chemical sunscreen,” attenuating radiation penetration while simultaneously enhancing the medicinal value of the plant (Turunen and Latola, 2005) [50].

Molecular Mechanisms of Stress Tolerance: A Transcriptomic Perspective

The physiological and biochemical adjustments observed in *Coptis teeta* Wall. under abiotic stress are ultimately governed by coordinated changes in gene expression. Stress perception at the cellular level activates signal transduction pathways that reprogram transcription, metabolism, and growth to enhance survival. In *C. teeta*, early insights into stress tolerance were primarily derived from physiological and biochemical studies, particularly those by Nath *et al*. 2025, which documented stress-induced alterations in photosynthetic efficiency, antioxidant activity, and metabolite accumulation. These findings provided foundational evidence that *C. teeta* mounts an active defense response under environmental stress. However, such responses can only be fully understood by examining the underlying transcriptional regulation, as demonstrated by transcriptomic studies in medicinal and alpine plant species (Shinozaki and Yamaguchi-Shinozaki, 2007; Zhu, 2016) [45, 61].

1. Global Transcriptional Reprogramming: Distinct and Combined Stress Signatures

Abiotic stresses such as drought and heat trigger extensive transcriptional reprogramming in plants, reflecting the need to maintain cellular homeostasis under adverse conditions.

Physiological studies by Nath *et al*. (2025) reported pronounced sensitivity of *C. teeta* to water deficit and elevated temperature, as evidenced by reduced growth, altered chlorophyll content, and increased oxidative stress. These observations are consistent with transcriptome-wide responses reported in other plant systems, where drought induces large numbers of genes associated with osmotic adjustment, ABA signaling, antioxidant defense, and stress-related metabolism (Shinozaki and Yamaguchi-Shinozaki, 2007) [45].

Heat stress, in contrast, typically induces a comparatively narrower transcriptional response, primarily targeting genes involved in protein protection, membrane stabilization, and energy metabolism (Kotak *et al*., 2007) [25]. Importantly, studies across plant species have shown that combined drought and heat stress elicit unique gene expression patterns that are not simply additive, activating distinct regulatory modules required for coping with simultaneous stress factors (Rasmussen *et al*., 2013; Suzuki *et al*., 2014) [42, 47]. When interpreted alongside the physiological disruptions reported by Nath *et al*. (2025), these findings suggest that *C. teeta* likely employs specialized molecular programs under compound stress conditions, a scenario increasingly relevant under climate-change-driven environmental extremes.

2. Transcription Factor Networks: Central Regulators of Stress Responses

Transcription factors (TFs) function as central regulators that translate stress signals into coordinated gene expression responses. Among these, the DREB/CBF family (AP2/ERF superfamily) is widely recognized for its role in drought and dehydration tolerance through activation of stress-protective genes, including Late Embryogenesis Abundant (LEA) proteins and osmoprotectant biosynthesis enzymes (Lata and Prasad, 2011) [27]. The enhanced antioxidant capacity and stress resilience reported by Nath *et al*., 2025 in *C. teeta* are consistent with the activation of such drought-responsive regulatory networks.

Heat stress responses are predominantly controlled by Heat Shock Factors (HSFs), particularly HSFA2, which regulate Heat Shock Proteins (HSPs) responsible for maintaining protein stability under thermal stress (Kotak *et al*., 2007; Ohama *et al*., 2017) [25, 33]. Similarly, basic leucine zipper (bZIP) transcription factors, especially ABA-responsive element binding proteins (AREB/ABFs), integrate ABA signaling with drought-induced gene expression, influencing stomatal regulation, osmolyte accumulation, and stress-adaptive metabolism (Yoshida *et al*., 2014) [59].

3. Metabolic Reprogramming and Trade-Offs Between Survival and Alkaloid Biosynthesis

A critical consequence of abiotic stress is the reallocation of metabolic resources from growth and secondary metabolism toward survival-oriented processes. Biochemical analyses by Nath *et al*. (2025) demonstrated elevated antioxidant enzyme activities in stressed *C. teeta*, indicating an enhanced requirement for reactive oxygen species (ROS) detoxification. Transcriptomic studies in medicinal plants corroborate this pattern, showing strong upregulation of genes encoding superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) under drought and heat stress (Gill and Tuteja, 2010; Suzuki *et al*., 2014) [16, 47].

Conversely, secondary metabolite biosynthesis pathways-particularly those involved in isoquinoline alkaloid production-are often downregulated under severe stress due to their high energetic and nitrogen demands (Zulak and Bohlmann, 2010) [62]. When viewed alongside the physiological stress responses reported by Nath *et al*. (2025), this metabolic shift suggests that *C. teeta* prioritizes cellular protection and redox balance over alkaloid biosynthesis during extreme or prolonged stress conditions. This trade-off has important implications for both the medicinal quality and conservation of *C. teeta* under increasingly variable climatic regimes. This stress-induced metabolic reallocation is further supported by phytochemical evidence demonstrating that *C. teeta* maintains a complex and energetically demanding secondary metabolite profile, including multiple phenolic compounds with strong chemotaxonomic relevance. The metabolic cost associated with preserving such biochemical identity likely reinforces transcriptional prioritization of stress defense pathways over secondary metabolite biosynthesis during periods of severe or prolonged stress (Yan *et al*., 2026; Suzuki *et al*., 2014) [47, 58].

Secondary Metabolism: The Isoquinoline Alkaloid Pathway

The medicinal efficacy of *Coptis teeta* Wall. is primarily derived from its rich profile of benzylisoquinoline alkaloids (BIAs), notably berberine, coptisine, and palmatine, which are widely recognized for their antimicrobial, anti-inflammatory, and antidiabetic properties. These alkaloids function ecologically as chemical defenses against herbivory, pathogens, and abiotic stress, while pharmacologically forming the basis of *C. teeta*'s therapeutic value (Zulak and Bohlmann, 2010; Facchini, 2018) [62]. Physiological and phytochemical investigations by Nath *et al*. (2025) have demonstrated that environmental stress significantly alters alkaloid accumulation in *C. teeta*, suggesting tight regulatory coupling between stress perception and secondary metabolism. Similar stress-dependent modulation of alkaloid biosynthesis has been reported across several medicinal plant systems, indicating a conserved adaptive strategy (Ramakrishna and Ravishankar, 2011; Isah, 2019) [22].

1. The Biosynthetic Pathway: Enzymatic Steps from Dopamine to Berberine

Berberine biosynthesis in *C. teeta* follows the conserved benzylisoquinoline alkaloid pathway extensively characterized in *Coptis* and other Ranunculaceae members. The pathway initiates with the condensation of dopamine and 4-hydroxyphenylacetaldehyde (4-HPAA), catalyzed by norcoclaurine synthase (NCS), yielding (S)-norcoclaurine-the first committed intermediate in BIA biosynthesis (Facchini and De Luca, 2008; Zulak and Bohlmann, 2010) [12, 62]. This step is often considered a metabolic gatekeeper, as it links primary amino acid metabolism to secondary alkaloid production.

Subsequent enzymatic transformations include sequential methylation, hydroxylation, and N-methylation reactions mediated by enzymes such as 6-O-methyltransferase (6-OMT), coclaurine N-methyltransferase (CNMT), and cytochrome P450 monooxygenases, leading to the formation of (S)-reticuline. (S)-Reticuline serves as a central metabolic hub from which multiple alkaloid classes diverge (Xu *et al*., 2024) [56].

A crucial regulatory step is catalyzed by the berberine bridge enzyme (BBE), which converts (S)-reticuline to (S)-scoulerine through an unusual oxidative C-C bond formation. This reaction is widely regarded as rate-limiting and energetically demanding, rendering it highly sensitive to stress-induced metabolic constraints. Downstream reactions involving canadine synthase (CAS) and O-methyltransferases (OMTs) ultimately yield protoberberine alkaloids such as berberine, palmatine, and coptisine (Xu *et al*., 2024; Hagel and Facchini, 2013) [19, 56].

2. Transcriptional Regulation: WRKY, bHLH, and Stress-Responsive Control of Alkaloid Biosynthesis

The regulation of benzylisoquinoline alkaloid biosynthesis is predominantly transcriptional, involving stress-responsive transcription factors that integrate environmental signals with metabolic flux. In *Coptis japonica*, WRKY transcription factors-particularly CjWRKY1-have been shown to directly regulate multiple genes in the berberine biosynthetic pathway, including NCS, BBE, and OMTs (Kato *et al*., 2007) [23]. Basic helix-loop-helix (bHLH) transcription factors such as CjbHLH1 further modulate pathway activity by coordinating responses to jasmonate and light signaling (Yamada *et al*., 2013) [57].

Although functional characterization of these transcription factors in *C. teeta* is limited, comparative studies strongly suggest conservation of regulatory modules across *Coptis* species. Moderate environmental stimuli such as UV-B radiation, low temperature, and mild water stress are known to activate WRKY-mediated defense signaling, thereby enhancing alkaloid biosynthesis as part of a chemical defense strategy (Pandey and Somssich, 2009; Sharma *et al*., 2019) [34, 44]. In contrast, severe stress activates abscisic acid (ABA) and ethylene signaling pathways, which commonly suppress secondary metabolism in favor of stress survival and cellular maintenance (Zhu, 2016; Isah, 2019) [22, 61]. The stress-induced physiological and biochemical alterations reported by Nath *et al*. (2025) are consistent with this regulatory shift.

3. Stress Impact on Medicinal Quality: Hormesis Versus Severe Stress Suppression

The relationship between abiotic stress and alkaloid accumulation in *C. teeta* conforms to a hormetic response model, a phenomenon widely documented in medicinal plants. Under mild or transient stress (eustress), secondary metabolite production is stimulated, leading to increased alkaloid accumulation as part of an adaptive defense response (Ramakrishna and Ravishankar, 2011; Sharma *et al*., 2019) [44]. Observations by Nath *et al*.,2025 support this model, showing enhanced phytochemical responses under moderate stress conditions.

However, under prolonged or intense stress (distress), the biosynthetic capacity for alkaloid production is suppressed. Transcriptomic and metabolic studies across plant systems demonstrate that energetically expensive pathways-such as benzylisoquinoline alkaloid biosynthesis-are downregulated to conserve carbon, nitrogen, and ATP for antioxidant defense, protein repair, and respiratory maintenance (Suzuki *et al*., 2014; Xu *et al*., 2024) [47, 56]. Enzymes such as BBE and downstream O-methyltransferases are particularly sensitive to metabolic repression, leading to reduced berberine content and compromised medicinal quality.

This dualistic stress response underscores the vulnerability of *C. teeta*'s pharmacological value under climate extremes and highlights the need for conservation strategies that preserve not only plant survival but also metabolite integrity (Nath *et al*.; Isah, 2019) [22].

The Holobiont Perspective: Rhizosphere and Endophytic Interactions

Coptis teeta does not exist as an isolated biological entity; rather, it functions as a holobiont, in which plant fitness, stress resilience, and secondary metabolism are tightly integrated with root-associated microbial communities (Vandenkoornhuyse *et al*., 2015; Trivedi *et al*., 2020) [49, 51]. Increasing evidence suggests that these microbial partners play a critical role in buffering environmental stress and shaping plant metabolic outputs (Pang *et al*., 2021) [36].

1. Endophytic Diversity: Dominance of *Microbacterium* and *Burkholderia* in the Rhizosphere

High-throughput sequencing analyses of the rhizosphere and endosphere of *C. teeta* have revealed a diverse bacterial community dominated by members of *Microbacterium*, *Burkholderia*, and *Bacillus* (Pang *et al*., 2021) [36]. These genera are frequently reported as core components of plant-associated microbiomes and are known for their roles in nutrient cycling, phytohormone modulation, and abiotic stress tolerance (Compant *et al*., 2010; Vessey, 2003) [7, 53]. Their enrichment suggests selective recruitment driven by host physiological demands under challenging environmental conditions.

2. Mechanisms of Microbial Support: Hormonal Regulation, Nutrient Mobilization, and Alkaloid Enhancement

Stress Hormone Modulation

Many root-associated endophytes produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that degrades ACC, the immediate precursor of ethylene. By reducing ethylene accumulation, these microbes mitigate stress-induced growth inhibition and allow plants to sustain growth under abiotic stress conditions (Glick, 2014; Singh *et al*., 2015) [17]. Such ethylene modulation has been widely documented as a key mechanism by which endophytes enhance plant stress tolerance (Pang *et al*., 2021) [36].

Nutrient Mobilization in Acidic Soils

In acidic soils, phosphorus is often immobilized through fixation with aluminum and iron complexes. Endophytic and rhizospheric bacteria alleviate this limitation by secreting organic acids and phosphatases that solubilize bound phosphorus, thereby increasing its availability to the host plant (Richardson *et al*., 2009; Vessey, 2003) [43, 53]. This microbial nutrient mobilization is particularly important for sustaining the energy-intensive biosynthesis of isoquinoline alkaloids in *C. teeta* (Pang *et al*., 2021) [36].

Stimulation of Secondary Metabolism:

A positive correlation between *Microbacterium* abundance and berberine accumulation in *C. teeta* roots has been reported, indicating a functional link between microbial colonization and secondary metabolite production (Pang *et al*., 2021) [36]. It is hypothesized that microbial elicitors or signaling metabolites activate plant defense-related transcriptional programs, thereby priming secondary metabolic pathways and enhancing alkaloid biosynthesis (Trivedi *et al*., 2020; Korenblum *et al*., 2020) [49].

Conservation Physiology and Management Strategies

The persistence of *Coptis teeta* is constrained by a convergence of biological and environmental factors, including a K-selected life-history strategy, inherently slow growth and regeneration rates, strict shade dependence, and narrow climatic tolerance. Under rapidly changing environmental conditions, these traits collectively place the species in an "evolutionary trap," where historical adaptations that once conferred stability now limit adaptive flexibility (Sih *et al*., 2011; Cooke *et al*., 2013) [9, 46]. Accelerating climate warming, coupled with habitat fragmentation, further intensifies this mismatch between phenotype and environment, increasing extinction risk despite protected status (Urban *et al*., 2016) [51]. In this context, conservation success depends not only on preserving individuals or populations, but on maintaining the physiological processes that underpin survival, reproduction, and medicinal quality (Madliger *et al*., 2018) [29].

1. In Situ Conservation: Preserving Habitat Integrity and Connectivity Strict Habitat

Protection and Canopy Integrity

C. teeta is a deeply shade-adapted understory species whose photosynthetic machinery is optimized for low irradiance and cool, humid microclimates. Canopy removal or thinning exposes plants to excess light energy that cannot be efficiently dissipated, leading to photoinhibition of photosystem II, elevated leaf temperatures, and enhanced production of reactive oxygen species (Niinemets and Valladares, 2006) [32]. These physiological stresses reduce carbon assimilation, accelerate senescence, and ultimately compromise survival. Moreover, loss of canopy cover alters soil moisture regimes and increases temperature fluctuations, further destabilizing the microhabitat required for sustained growth (Gommers *et al*., 2013) [18]. Consequently, strict protection of closed-canopy forest structure is not merely a habitat concern, but a physiological necessity for *C. teeta* persistence.

Altitudinal Corridors and Climate-Driven Range Shifts

Climate warming is predicted to progressively shift suitable thermal and hydric niches upslope, particularly for montane understory species with limited heat tolerance. For *C. teeta*, successful persistence under future climates will likely depend on its ability to track suitable microclimates along elevational gradients. Continuous forest corridors facilitate such movements by reducing dispersal barriers, maintaining favorable microclimates, and allowing gene flow between populations (Heller and Zavaleta, 2009; Corlett and Westcott, 2013) [10, 20]. In contrast, fragmented landscapes restrict upslope migration, creating population "dead ends" where physiological stress accumulates faster than adaptive capacity, thereby elevating extinction risk (Freeman *et al*., 2018; Urban *et al*., 2016) [14, 51].

2. Ex Situ Agrotechnology: Mimicking the Wild Niche for Resilient Cultivation

Shade and Soil Management as Physiological Buffers:

Ex situ cultivation of *C. teeta* is most successful when it closely replicates the species' native forest-floor environment. Experimental and empirical evidence from shade-adapted medicinal plants suggests that 70-80% shade optimizes photosynthetic efficiency by balancing light capture with photoprotection, while minimizing thermal and oxidative stress (Poorter *et al*., 2012; Li *et al*., 2014) [28, 39]. Similarly, soils enriched with forest litter and leaf mold provide high organic matter content, stable moisture retention, and acidic conditions (pH 4.5-5.5) that enhance nutrient availability and root-microbe interactions (Treseder and Lennon, 2015; Pang *et al*., 2021) [36, 48]. Such niche-mimicking strategies reduce physiological stress and improve both biomass accumulation and survival in cultivated populations.

Microbiome Engineering and Restoration of the Holobiont

A recurring challenge in *C. teeta* cultivation is the reduced alkaloid content of ex situ-grown plants compared to wild individuals. This decline is increasingly attributed to the disruption of native plant-microbe associations that regulate nutrient acquisition, hormonal balance, and secondary metabolism. Microbiome engineering, through the bio-priming of seedlings with native soil inocula or targeted endophytes such as *Microbacterium* spp., represents a promising strategy to restore these functional interactions (Pang *et al*., 2021; Compant *et al*., 2019) [8, 36]. Such microbes can modulate ethylene levels, enhance phosphorus availability, and activate secondary metabolic pathways, effectively reconstituting the plant as a functional holobiont rather than a microbe-depleted individual (Trivedi *et al*., 2020; Berg *et al*., 2020) [3, 49].

Low and inconsistent seed germination remains a critical barrier to both cultivation and restoration of *C. teeta*. Seed priming treatments using osmotic agents (e.g., polyethylene glycol) or plant growth regulators such as gibberellic acid (GA_3) partially activate metabolic pathways prior to germination, enhancing enzyme activity, membrane repair, and antioxidant defenses (Paparella *et al*., 2015; Lutts *et al*., 2016) [37]. As a result, primed seeds exhibit faster and more synchronized emergence, improved early vigor, and higher establishment success under suboptimal field conditions (Farooq *et al*., 2019) [13]. For endangered species with slow life cycles, such improvements at early developmental stages can have disproportionately large effects on long-term population viability.

Future Directions and Conclusion

1. Research Gaps: Unexplored Frontiers in Proteomics, Epigenetics, and Field Ecology

Despite growing insights from transcriptomic and physiological studies, our understanding of stress adaptation in *C. teeta* remains incomplete. Several critical research gaps must be addressed to move from correlative evidence toward mechanistic and predictive conservation science.

Proteomics: Bridging the mRNA-Function Gap

Most molecular insights into stress tolerance in *C. teeta* are currently derived from transcript-level analyses. However, mRNA abundance does not always correlate with protein abundance or enzymatic activity due to post-transcriptional regulation, protein turnover, and post-translational modifications (Vogel and Marcotte, 2012) [54]. For example, while elevated transcript levels of antioxidant genes such as ascorbate peroxidase (APX) suggest enhanced oxidative stress defense, it remains unclear whether these transcriptional responses translate into sustained increases in enzyme activity under field conditions. Targeted and quantitative proteomic approaches (e.g., LC-MS/MS, iTRAQ, SWATH-MS) are therefore essential to validate whether stress-responsive transcripts are functionally expressed and biologically effective in situ (Kosová *et al*., 2011) [24].

Epigenetics: Stress Memory and Transgenerational Resilience

An emerging but largely unexplored question is whether exposure to abiotic stress induces a form of epigenetic memory in *C. teeta*. In many plant species, environmental stress has been shown to generate stable DNA methylation patterns or histone modifications that prime future stress responses, sometimes persisting across generations (Walter *et al*., 2011; Lämke and Bäurle, 2017) [26]. Investigating whether drought or heat stress leaves heritable epigenetic marks in *C. teeta* could fundamentally alter conservation strategies, enabling the selection or induction of “pre-adapted” lineages for restoration and cultivation programs.

Field Trial and Ecologial Realism

A major limitation of current knowledge is the heavy reliance on controlled-environment experiments. While invaluable for mechanistic clarity, such studies often fail to capture the complexity of natural forest ecosystems, where plants experience fluctuating stressors, microbial interactions, and microclimatic heterogeneity. Long-term field-based trials comparing wild and cultivated populations-particularly with respect to microbiome composition, stress physiology, and alkaloid yield-are urgently needed to assess ecological validity and long-term sustainability (Poorter *et al*., 2012; Trivedi *et al*., 2020) [39, 49].

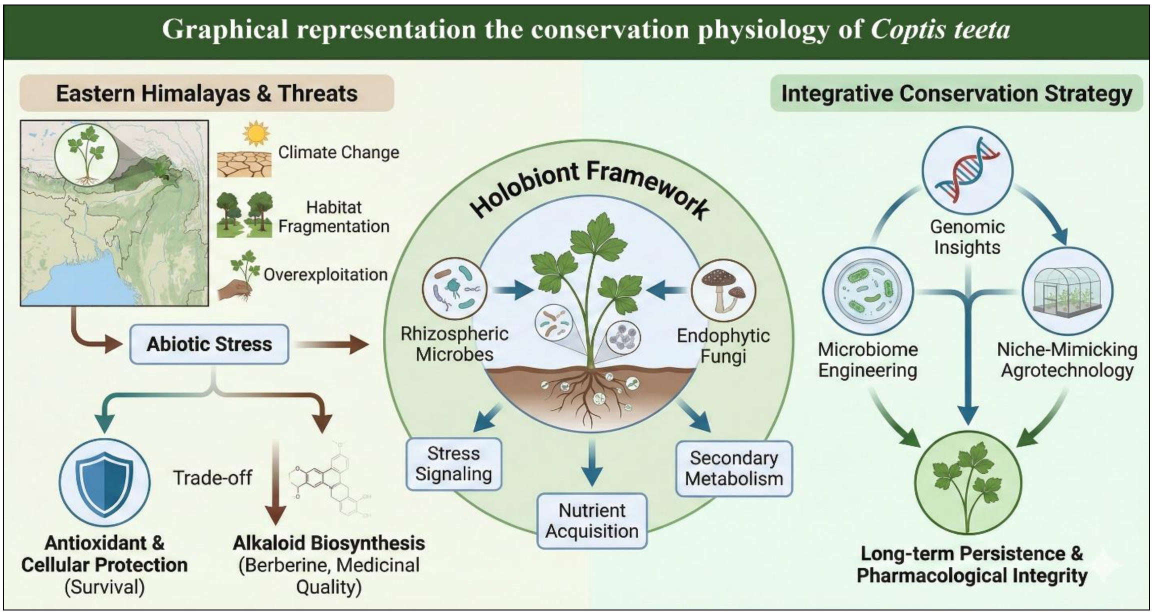

Fig 1: Graphical representation the conservation physiology of *Coptis teeta*

The Eastern Himalayan Endemic *C. teeta* faces pressures from climate change and habitat fragmentation (top). Abiotic stress triggers a physiological trade-off, prioritizing antioxidant defense over the biosynthesis of medicinal isoquinoline alkaloids like berberine (bottom left). The holobiont framework highlights the critical role of rhizospheric and endophytic microbes in modulating these stress responses (bottom right). An integrative conservation strategy (bottom) combines genomic tools, microbiome engineering, and niche-mimicking agrotechnology to ensure species survival and pharmacological integrity.

2. Conclusion

Integrating Genomics, Ecology, and Physiology for Sustainable Conservation

Coptis teeta represents a biological jewel of the Eastern Himalayas, embodying a rare convergence of evolutionary antiquity, ecological specialization, and pharmacological significance. Yet, this synthesis reveals that the species is currently subjected to a pronounced “physiological squeeze,” arising from the interaction between its rigid K-selected life-history strategy and the unprecedented pace of Anthropocene-driven environmental change (Sih *et al*., 2011; Urban *et al*., 2016) [46, 51].

At the molecular level, *C. teeta* exhibits clear signatures of stress-induced reprogramming, including the upregulation of antioxidant systems, molecular chaperones, and transcriptional regulators associated with abiotic stress tolerance. While these responses enhance short-term survival by detoxifying reactive oxygen species and preserving cellular integrity, they appear to divert metabolic resources away from secondary metabolite biosynthesis, potentially explaining the reduced berberine content observed under stress conditions. Thus, stress resilience and medicinal potency may represent competing physiological priorities rather than synergistic outcomes.

The path forward lies in embracing a holistic Conservation Physiology framework, wherein molecular insights are directly translated into management action. This includes integrating genomic information (e.g., selection of genotypes with elevated DREB, HSF, or antioxidant capacity), ecological engineering (restoration of native microbiomes through targeted inoculation), and precision agrotechnology (microclimate manipulation, shade regulation, and soil conditioning). Such a multidimensional strategy recognizes *C. teeta* not merely as an isolated organism, but as a dynamic component of a forest holobiont whose survival depends on finely balanced interactions across biological scales (Madliger *et al*., 2018; Berg *et al*., 2020) [3, 29].

Only through this integrative approach can Ccontinue to thrive in the mist-laden forests of the Eastern Himalayas-preserving not only its genetic lineage, but also its ecological role and enduring medicinal legacy for future generations.

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