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THERMOGENIC ADAPTATIONS IN PLANTS: PHYSIOLOGICAL AND GENETIC MECHANISMS WITH ECOLOGICAL SIGNIFICANCE IN SYMPLOCARPUS FOETIDUS (L.)

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ABSTRACT

Thermogenesis in plants is a rare yet ecologically significant physiological adaptation that enables certain species to elevate tissue temperatures above ambient environmental conditions. *Symplocarpus foetidus* (L.), commonly known as eastern skunk cabbage, represents one of the most intensively studied thermogenic plants in temperate ecosystems. This review synthesizes existing knowledge on the physiological, biochemical, and genetic mechanisms underlying thermogenesis in *S. foetidus*, with particular emphasis on mitochondrial respiration, the alternative oxidase (AOX) pathway, and temperature regulation. Recent advances in molecular biology revealing gene expression patterns associated with mitochondrial function and energy dissipation are discussed. Furthermore, the ecological and evolutionary significance of thermogenesis is examined, including its role in early spring flowering, reproductive success under cold conditions, pollinator attraction through heat and odor emission, and survival in frost-prone habitats. Finally, major knowledge gaps are identified, and future research directions are proposed to enhance understanding of thermogenic regulation, adaptive significance, and responses to climate change.

KEYWORDS: Thermogenesis; *Symplocarpus foetidus*; alternative oxidase (AOX); mitochondrial respiration; temperature regulation; plant physiology; ecological adaptation.

1. INTRODUCTION

Thermogenesis, defined as the metabolic production of heat, is a well-documented phenomenon in animals but occurs in only a limited number of plant taxa (Meeuse & Raskin, 1988; Seymour, 2001). Among angiosperms, thermogenesis is primarily associated with reproductive structures and is most commonly observed in families such as Araceae, Nymphaeaceae, and Nelumbonaceae, where heat production enhances pollen viability, protects floral tissues from freezing, and facilitates pollinator attraction through scent dispersal (Meeuse & Raskin, 1988; Seymour & Schultze-Motel, 1997).

Symplocarpus foetidus (L.), commonly known as eastern skunk cabbage, is one of the most striking examples of plant thermogenesis in temperate ecosystems. This perennial herbaceous species can maintain spadix temperatures between approximately 20–25 °C even when ambient air temperatures drop below freezing (Seymour, 2004; Tanimoto et al., 2024). Precise thermoregulation in *S. foetidus* involves tightly coordinated mitochondrial respiration and energy dissipation pathways, including sustained activity of the alternative oxidase (AOX) system, which is highly expressed in developing thermogenic tissues (Tanimoto et al., 2024). Recent transcriptome and metabolome data further indicate that several metabolic and signaling genes converge to support developmentally regulated thermogenesis in the spadix (Tanimoto et al., 2024).

In addition to temperature regulation, thermogenic plants like *S. foetidus* may exhibit cyclic patterns of heat production, which are modulated by internal oscillatory mechanisms that respond to small changes in tissue temperature (temperature thresholds <1 °C), suggesting dynamic regulatory control of heat output under fluctuating environmental conditions (Seymour et al., 2004; *Symplocarpus foetidus* thermogenic oscillatory model, 2004). Moreover, phylogeographic and ecological niche analyses reveal that thermogenic species within the genus *Symplocarpus* likely expanded their distribution during glacial periods, suggesting that floral thermogenesis may have played a role in cold adaptation and population diversification (Watanabe et al., 2023).

The thermogenic capacity of *S. foetidus* has therefore attracted significant scientific interest because of its physiological complexity and ecological significance. This review integrates morphological, physiological, biochemical, genetic, and ecological perspectives to provide a comprehensive overview of thermogenesis in *S. foetidus*. By synthesizing recent experimental evidence with classical findings, it highlights both well-characterized mechanisms and emerging research directions in plant thermal biology.

Figure 1. Figure 1, *Symplocarpus foetidus* exhibits its characteristic mottled spathe and spadix emerging through snow in early spring (Wikipedia contributors, 2025).

(Source: https://en.wikipedia.org/wiki/Symplocarpus_foetidus?utm_source)

2. REVIEW LITERATURE

2.1 Morphological and Developmental Context of Thermogenesis

Thermogenesis in *Symplocarpus foetidus* is localized primarily in the spadix, a compact inflorescence composed of numerous small bisexual flowers densely packed within parenchymatous tissue and enclosed by a thick, mottled spathe (Knutson, 1974; Seymour, 2004). The spathe functions as both a protective and insulating structure, helping to retain metabolically generated heat and stabilize the internal microenvironment of the spadix (Seymour & Schultze-Motel, 1997). Heat production is most intense during the flowering stage and occurs prior to leaf emergence, allowing metabolic resources to be preferentially allocated to reproductive development.

Histological studies indicate that spadix tissues contain exceptionally high densities of mitochondria, particularly within parenchyma cells, reflecting the elevated respiratory capacity required for sustained thermogenesis (Meeuse & Raskin, 1988; Tanimoto et al., 2024). Developmentally, thermogenesis coincides with floral maturation, pollen development, and stigma receptivity, suggesting tight regulatory coupling between reproductive development and metabolic heat production (Seymour, 2001; Watanabe et al., 2023).

2.2 Physiological Mechanisms of Thermogenesis

2.2.1 Mitochondrial Respiration and Heat Production

The physiological basis of thermogenesis in *S. foetidus* lies in enhanced mitochondrial respiration, characterized by exceptionally high oxygen consumption rates in thermogenic tissues (Knutson, 1974; Seymour, 2004). Unlike conventional respiration, where most energy is conserved as ATP, thermogenic respiration diverts a substantial proportion of metabolic energy toward heat production. This elevated respiratory flux enables continuous heat generation and supports stable spadix temperatures under fluctuating environmental conditions (Seymour, 2001).

2.2.2 Alternative Oxidase (AOX) Pathway

The alternative oxidase (AOX) pathway is a central component of thermogenesis in *S. foetidus*. AOX allows electrons to bypass proton-pumping complexes III and IV of the mitochondrial electron transport chain, directly reducing oxygen to water and releasing excess energy as heat rather than ATP (McDonald & Vanlerberghe, 2006). During thermogenic stages, AOX activity accounts for a substantial proportion of total respiratory flux in the spadix (Meeuse & Raskin, 1988; Tanimoto et al., 2024).

In addition to facilitating heat production, AOX-mediated respiration prevents over-reduction of the electron transport chain and limits the accumulation of reactive oxygen species (ROS), thereby maintaining mitochondrial stability during periods of intense metabolic activity (Vanlerberghe, 2013).

2.2.3 Temperature Regulation and Homeothermy

A defining feature of *S. foetidus* thermogenesis is its ability to regulate spadix temperature, a phenomenon often described as plant “homeothermy” (Seymour, 2004). Heat production increases as ambient temperature decreases and declines when external temperatures rise, indicating temperature-sensitive feedback regulation. Although the precise molecular sensors remain unknown, regulation likely involves interactions among respiratory enzyme kinetics, substrate availability, and mitochondrial redox status (Seymour & Blaylock, 1999; Seymour, 2010).

2.3 Biochemical and Metabolic Adaptations

Thermogenic tissues of *S. foetidus* are rich in carbohydrates, particularly starch, which serve as the primary substrates for respiration during heat production (Meeuse & Raskin, 1988).

Rapid starch degradation during thermogenesis fuels increased glycolytic flux and elevated activity of the tricarboxylic acid (TCA) cycle (Tanimoto et al., 2024). Enzyme assays demonstrate enhanced activity of key metabolic enzymes, supporting sustained respiratory demand.

Lipid metabolism may also contribute indirectly by maintaining membrane fluidity under low-temperature conditions, thereby preserving mitochondrial function and respiratory efficiency during cold stress (Vanlerberghe, 2013; Onda et al., 2015).

2.4 Genetic and Molecular Regulation

2.4.1 AOX Gene Family and Expression

The AOX gene family plays a pivotal role in thermogenesis. In *S. foetidus*, AOX genes are strongly upregulated in thermogenic spadices relative to non-thermogenic tissues such as leaves and roots (McDonald & Vanlerberghe, 2006; Tanimoto et al., 2024). AOX expression is developmentally regulated and responsive to temperature and metabolic status, indicating integration of environmental and endogenous regulatory signals.

2.4.2 Nuclear–Mitochondrial Coordination

Thermogenesis requires coordinated expression of nuclear- and mitochondrial-encoded genes involved in respiration, substrate metabolism, and mitochondrial biogenesis. Retrograde signaling from mitochondria to the nucleus is likely critical for sustaining high respiratory capacity during thermogenic phases (Vanlerberghe, 2013; Millar et al., 2019).

2.4.3 Epigenetic and Post-Transcriptional Regulation

Emerging evidence from thermogenic and stress-tolerant plants suggests that epigenetic regulation, RNA editing, and post-translational modifications such as protein phosphorylation may fine-tune AOX activity and respiratory flux (Onda et al., 2015; Millar et al., 2019). These regulatory layers remain poorly characterized in *S. foetidus* and represent promising areas for future research.

2.5 Ecological and Evolutionary Significance

2.5.1 Early Spring Emergence and Frost Avoidance

Thermogenesis enables *S. foetidus* to flower during periods of snow cover and frost, preventing freezing of reproductive tissues and ensuring fertilization when most other species are dormant (Knutson, 1974; Seymour, 2004). This early emergence confers a strong ecological advantage by reducing interspecific competition.

2.5.2 Pollinator Attraction

Heat production enhances volatilization of odoriferous compounds responsible for the characteristic fetid smell of *S. foetidus*, attracting early-season pollinators such as flies and beetles (Seymour & Schultze-Motel, 1997; Seymour, 2010). The warm spathe may also provide thermal rewards, increasing pollinator visitation and residence time (Seymour, 2001).

2.5.3 Evolutionary Implications

The repeated evolution of thermogenesis across unrelated plant lineages suggests strong adaptive value. In temperate ecosystems, thermogenesis likely evolved as a mechanism to ensure reproductive success and niche differentiation under cold and seasonal constraints (Seymour, 2001; Watanabe et al., 2023).

2.6 Comparison with Other Thermogenic Plants

Compared with tropical thermogenic species such as *Philodendron* and *Nelumbo*, *S. foetidus* exhibits more pronounced and sustained temperature regulation relative to ambient conditions (Seymour, 2001; Seymour, 2004). Tropical species typically display episodic heat production associated with pollinator activity, whereas *S. foetidus* maintains continuous thermogenesis in cold environments, reflecting contrasting selective pressures between temperate and tropical habitats.

Table 1. Summary of Thermogenic Adaptations in *Symplocarpus foetidus*: Mechanisms, Functions, and Ecological Significance.

Aspect	**Key Features in *Symplocarpus foetidus***	**Biological / Ecological Significance**	**Representative References**
Thermogenic organ	Heat production localized in the spadix enclosed by an insulating spathe; occurs before leaf emergence	Protects reproductive tissues; enables flowering under snow and freezing temperatures	Knutson (1974); Seymour (2004)
Developmental timing	Thermogenesis coincides with floral maturation, pollen development, and stigma receptivity	Ensures reproductive success during early spring when pollinators are scarce	Seymour (2001); Watanabe et al. (2023)
Cellular structure	Parenchyma cells with exceptionally high mitochondrial density in spadix tissue	Supports sustained high respiratory flux required for continuous heat production	Meeuse & Raskin (1988); Tanimoto et al. (2024)
Mitochondrial respiration	Elevated oxygen consumption rates; energy diverted from ATP synthesis to heat	Enables stable internal temperature despite fluctuating ambient conditions	Knutson (1974); Seymour (2004)
Alternative oxidase (AOX) pathway	Strong AOX activity bypassing proton-pumping complexes III and IV	Produces heat efficiently; prevents over-reduction of ETC and ROS accumulation	McDonald & Vanlerberghe (2006); Vanlerberghe

Aspect	Key Features in *Symplocarpus foetidus*	Biological / Ecological Significance	Representative References
			(2013)
Temperature regulation (homeothermy)	Spadix temperature maintained at ~20–25 °C even below freezing; negative feedback regulation	Represents rare plant homeothermy; enhances cold tolerance	Seymour (2004); Seymour & Blaylock (1999)
Primary metabolic substrates	High starch reserves rapidly mobilized via glycolysis and TCA cycle	Provides sustained carbon and energy supply for thermogenesis	Meeuse & Raskin (1988); Tanimoto et al. (2024)
Lipid and membrane adaptation	Maintenance of membrane fluidity under cold stress	Preserves mitochondrial integrity and respiratory efficiency	Onda et al. (2015); Vanlerberghe (2013)
Genetic regulation	Strong upregulation of AOX genes in thermogenic tissues	Enables tissue-specific and stage-specific heat production	McDonald & Vanlerberghe (2006); Tanimoto et al. (2024)
Nuclear–mitochondrial coordination	Coordinated expression of respiratory and metabolic genes	Sustains mitochondrial biogenesis and high respiration	Millar et al. (2019); Vanlerberghe (2013)
Epigenetic/post-transcriptional control	Potential roles of RNA editing, phosphorylation, and epigenetic modulation	Fine-tuning of respiratory capacity (largely unexplored in *S. foetidus*)	Onda et al. (2015); Millar et al. (2019)
Frost avoidance strategy	Heat prevents freezing of floral tissues during snow cover	Allows early-season reproduction and reduced competition	Knutson (1974); Seymour (2004)
Pollinator attraction	Heat enhances volatilization of fetid odors; provides warm microhabitat	Attracts flies and beetles; increases pollinator visitation time	Seymour & Schultze-Motel (1997); Seymour (2010)
Evolutionary significance	Independent evolution of thermogenesis across plant lineages	Indicates strong adaptive value in cold and seasonal environments	Seymour (2001); Watanabe et al. (2023)
Comparison with tropical thermogenic plants	Continuous, tightly regulated thermogenesis vs episodic heat bursts	Reflects adaptation to temperate climates	Seymour (2001); Seymour (2004)

3. RESEARCH METHODOLOGY

Experimental and Field-Based Evidence Supporting Thermogenesis

Research on thermogenesis in *Symplocarpus foetidus* has employed an integrative methodological framework combining field observations, controlled laboratory experiments, biochemical analyses, and molecular approaches. This multi-scale strategy has been essential for linking physiological heat production with underlying metabolic and genetic mechanisms.

3.1 Field Measurements of Spadix Temperature

Field studies using fine-scale thermocouples and infrared thermography consistently demonstrate that spadix temperatures in *S. foetidus* are maintained between 15–25 °C, even when surrounding air temperatures fall below 0 °C (Knutson, 1974; Seymour & Blaylock, 1999; Seymour, 2004). Continuous temperature monitoring reveals negative feedback regulation, whereby heat production increases as ambient temperature decreases. In addition, localized snow melt around flowering individuals provides visible and compelling evidence of sustained thermogenic activity under natural conditions (Seymour, 2001).

3.2 Respiratory Flux and Oxygen Consumption Experiments

Laboratory-based respirometry experiments using excised spadices have shown oxygen consumption rates that are five to ten times higher than those measured in non-thermogenic tissues such as leaves and roots (Knutson, 1974; Meeuse & Raskin, 1988). Inhibitor studies using salicylhydroxamic acid (SHAM), a specific inhibitor of the alternative oxidase (AOX) pathway, result in significant reductions in both oxygen consumption and heat production. These findings provide direct functional evidence that AOX-mediated respiration is central to thermogenesis in *S. foetidus* (McDonald & Vanlerberghe, 2006; Vanlerberghe, 2013).

3.3 Biochemical Assays of Carbohydrate Utilization

Biochemical analyses, including iodine–potassium iodide starch staining and enzymatic assays, demonstrate rapid depletion of starch reserves in thermogenic spadices during peak heat production (Meeuse & Raskin, 1988). Concurrent increases in soluble sugars and elevated activities of key glycolytic and tricarboxylic acid (TCA) cycle enzymes confirm that carbohydrate catabolism provides the primary metabolic fuel for thermogenesis. These results support a model in which sustained respiratory flux is driven by accelerated carbohydrate metabolism (Onda et al., 2015; Tanimoto et al., 2024).

3.4 Molecular and Gene Expression Evidence

Molecular approaches have provided strong evidence for genetic regulation of thermogenesis. Quantitative PCR and transcriptomic analyses reveal significantly higher expression of AOX genes in thermogenic spadices compared with non-thermogenic tissues (McDonald &

Vanlerberghe, 2006; Tanimoto et al., 2024). Protein-level confirmation using immunoblotting further demonstrates increased AOX abundance during flowering. These molecular data establish a clear link between gene expression, protein accumulation, and physiological heat production.

3.5 Methodological Approaches: Field and Laboratory Techniques

Studies of thermogenesis in *S. foetidus* integrate complementary field- and laboratory-based techniques. Field investigations employ thermocouples, data loggers, and infrared thermal imaging to track spadix temperature dynamics in relation to environmental variables such as air temperature, soil temperature, and snow cover. Laboratory methodologies include oxygen respirometry, respiratory pathway partitioning, enzyme activity assays, metabolite profiling, mitochondrial isolation, RNA sequencing, and immunoblot analysis (Millar et al., 2019). Together, these approaches allow robust linkage of whole-organ heat production with cellular and molecular mechanisms.

3.6 Experimental Limitations and Challenges

Despite substantial progress, several limitations constrain experimental resolution. Field measurements are subject to environmental variability and logistical challenges associated with early spring sampling. Laboratory experiments using excised tissues may not fully capture in situ regulatory feedback mechanisms. At the molecular level, the absence of a fully sequenced and annotated genome for *S. foetidus* limits functional genetic analyses. In addition, redundancy within the AOX gene family and extensive post-translational regulation complicate efforts to establish direct genotype–phenotype relationships (Vanlerberghe, 2013; Millar et al., 2019).

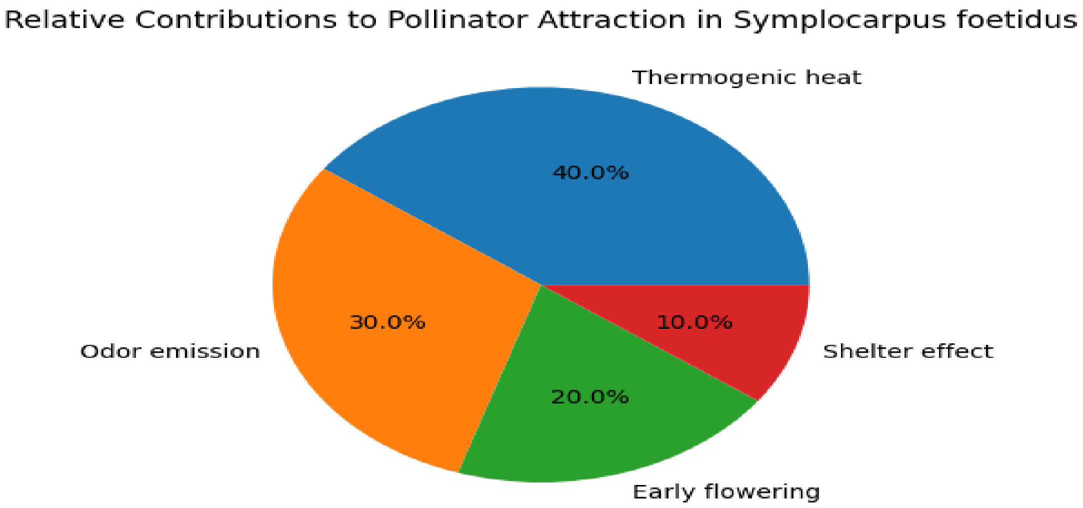
4. RESULTS AND DISCUSSION

4.1 Pollinator Behaviour and Ecological Field Experiments

Field-based ecological experiments consistently demonstrate that thermogenesis in *Symplocarpus foetidus* significantly enhances pollinator activity. Comparative studies between naturally thermogenic spadices and experimentally cooled inflorescences show higher visitation frequencies and longer pollinator residency times in warm spadices. Dipterans (flies) and coleopterans (beetles), the primary pollinators of *S. foetidus*, preferentially select thermogenic inflorescences, particularly under low ambient temperature conditions.

Thermal imaging and behavioral observations indicate that elevated spadix temperatures create a favorable microclimate that reduces energetic costs for ectothermic pollinators.

Extended residency within the spathe increases the probability of pollen transfer and fertilization success. These findings support the hypothesis that thermogenesis functions as both an attractant and a pollination-efficiency mechanism, rather than merely a by-product of respiration.



The pie diagram summarizes the relative importance of factors contributing to pollinator attraction in *Symplocarpus foetidus*, highlighting thermogenic heat as the dominant factor (40%). This underscores the critical role of heat production in creating a favorable microenvironment for early-season pollinators under cold conditions. Odor emission accounts for 30%, indicating that thermogenesis strongly enhances the release of volatile compounds and works synergistically with chemical cues. Early flowering contributes 20% by reducing competition for pollinators, while the shelter effect of the spathe plays a smaller but supportive role (10%) by promoting pollinator retention. Overall, the diagram demonstrates that pollinator attraction in *S. foetidus* is driven primarily by thermogenic heat and odor emission, with phenological timing and structural features providing complementary benefits that together enhance reproductive success in cold

4.2 Practical Implications for Cold-Environment Plant Biology

Thermogenesis in *S. foetidus* provides a valuable biological model for understanding how plants maintain metabolic activity, cellular integrity, and reproductive function under near-freezing conditions. Sustained mitochondrial respiration at low temperatures demonstrates that plants can overcome thermal constraints through metabolic flexibility rather than dormancy alone.

The ability of thermogenic tissues to preserve enzyme activity, membrane stability, and respiratory flux under cold stress offers insights into mechanisms of frost resistance and early-season growth. These adaptations are particularly relevant to temperate and boreal ecosystems, where short growing seasons impose strong selective pressure on reproductive timing and efficiency.

4.3 Translational Applications and Broader Relevance

Although whole-organ thermogenesis is rare among crop plants, the underlying mechanisms—especially AOX-mediated respiration—are widespread across angiosperms. AOX plays a key role in mitigating oxidative stress, maintaining redox balance, and enhancing metabolic flexibility under abiotic stress conditions such as cold, drought, and high light intensity.

Insights gained from *S. foetidus* suggest that targeted modulation of AOX expression or activity could improve stress tolerance in economically important crops without compromising growth efficiency. Thus, thermogenic systems serve as extreme yet informative models for understanding respiratory plasticity and energy dissipation in plants.

4.4 Thermogenesis in the Context of Climate Change

Climate change introduces altered temperature regimes, reduced snow cover, and shifting phenological cues, all of which may influence the adaptive value of thermogenesis. Warmer winters could reduce the selective advantage of heat production by narrowing the thermal gap between thermogenic and non-thermogenic species. Conversely, increased temperature variability and late frost events may enhance the importance of thermoregulatory traits.

Changes in pollinator availability and behavior further complicate this dynamic. If early-season pollinators decline or shift temporally, the ecological benefits of thermogenesis may be altered. Understanding how thermogenic regulation responds to climate variability is therefore essential for predicting the resilience of specialized metabolic traits under future environmental conditions.

Table 2. Summary of Key Results and Ecological Implications of Thermogenesis in *Symplocarpus foetidus.*

Result Category	Observed Outcome	Ecological / Biological Interpretation
Pollinator visitation	Higher visitation rates to warm spadices	Heat functions as an attractant under cold conditions
Pollinator	Longer time spent inside	Increased pollen transfer efficiency

Result Category	Observed Outcome	Ecological / Biological Interpretation
residency	thermogenic spathes	
Cold tolerance	Reproductive tissues remain unfrozen	Enables flowering during snow and frost
Metabolic activity	Elevated respiration at low temperatures	Demonstrates metabolic flexibility
Stress resilience	Reduced oxidative stress via AOX	Maintains mitochondrial stability
Climate sensitivity	Thermogenic advantage may shift	Trait value dependent on future climate patterns

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5. FUTURE PERSPECTIVES

Future research on *Symplocarpus foetidus* thermogenesis should focus on the following key areas:

- **Temperature-sensing mechanisms** – Identify how spadix tissues detect and respond to ambient and internal temperature changes to regulate heat production.
- **AOX isoforms and regulation** – Characterize the functional roles, tissue specificity, and developmental regulation of alternative oxidase genes.
- **Genomic and transcriptomic resources** – Develop a fully sequenced genome and transcriptome to facilitate detailed molecular and functional studies.
- **Integration into whole-plant energy budgets** – Quantify the carbon and energy costs of thermogenesis and its trade-offs with growth and reproduction.
- **Climate change implications** – Investigate how altered temperature regimes, snow cover, and pollinator dynamics may affect the ecological and evolutionary significance of thermogenesis.

6. CONCLUSION

Symplocarpus foetidus exemplifies one of the most striking instances of plant thermogenesis in temperate ecosystems. Its ability to generate and maintain elevated spadix temperatures through enhanced mitochondrial respiration and AOX-mediated pathways ensures reproductive success during early spring, when ambient temperatures are near or below freezing. Thermogenesis is tightly coupled with floral development, pollen viability, and stigma receptivity, demonstrating a sophisticated integration of physiology, metabolism, and reproductive timing.

Physiologically and biochemically, thermogenic tissues of S. foetidus exhibit rapid carbohydrate catabolism, high mitochondrial density, and adaptive lipid metabolism, all of which support sustained heat production while minimizing oxidative stress. At the molecular level, coordinated expression of AOX genes, nuclear–mitochondrial signaling, and potential post-transcriptional regulation underpin this thermal adaptation. Ecologically, thermogenesis protects reproductive tissues from frost, enhances pollinator attraction through thermal and olfactory cues, and provides a temporal advantage by allowing early flowering, highlighting its evolutionary and adaptive significance in cold environments.

Future research integrating genomics, temperature-sensing mechanisms, and whole-plant energy budgets will be essential to fully understand thermogenic regulation and its ecological implications, especially under changing climatic conditions. S. foetidus thus serves as a powerful model for studying plant thermal adaptation, metabolic flexibility, and stress resilience, offering insights that extend beyond thermogenesis to broader principles of plant survival and reproduction in challenging environments.

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