LR-5609
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REVIEW ARTICLE Legume Research- An International Journal

Thermal Sensitivity of Legume-rhizobium Interactions: Root Morphogenesis and Variability: A Review

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10.18805/LR-5609

ABSTRACT

Legumes are vital to food and nutritional security, often referred to as the “poor man’s meat” because of their high protein content. Their role in sustainable agriculture is anchored in Biological Nitrogen Fixation (BNF), a symbiotic process involving rhizobia that is highly sensitive to fluctuation in soil temperature. Soil temperature governs root system architecture (RSA), microbial colonization and enzymatic activity and is a critical determinant of legume productivity. Extreme soil temperatures impair root activity, microbial symbiosis and nitrogen fixation. This synthesis drew from over 91 out of 124 peer-reviewed studies spanning molecular biology, microbial ecology and agronomic interventions. It examines temperature thresholds affecting nodulation kinetics, RSA traits and symbiotic gene expression, including heat shock proteins (HSPs), cold responsive genes (*e.g.*, GmFRI-1) and hormonal signalling pathways. RSA traits such as root elongation, branching, biomass and vascular development are temperature sensitive, with optimal performance between 20-30°C. Cold stress delays nodulation and reduces nitrogenase activity (~60% at 4°C), while heat stress damages root tip and reduces nitrogenase reductase (~42%). Molecular responses include disrupted auxin transport and HSP induction. Thermotolerant rhizobial strains, Nod factors and inoculation strategies support symbiosis. Agronomic practices such as mulching, conservation tillage and strategic sowing buffer soil thermal regimes and enhance microbial activity. Managing the thermal sensitivity of the legume-rhizobium system through integrated genetic, microbial and agronomic strategies are vital for climate resilient legume cultivation and sustained productivity under variable soil temperature regimes.

Key words: Legume crops, Management, Rhizobium, Root nodules, Soil temperature, Symbiosis.

Legumes play a pivotal role in food and nutritional security, especially in low-income and vegetarian populations, earning the moniker *“poor man’s meat”* due to their protein, essential amino acids and affordability. Rich in micronutrients like iron, zinc and folate, contribute to balanced diets and combat hidden hunger. Agronomically, legumes sustain farming systems through biological nitrogen fixation (BNF), wherein symbiotic rhizobia convert atmospheric nitrogen into plant-available forms, reducing fertilizer dependency and enhancing soil fertility (Wissal *et al.,* 2020; Owaresat *et al.,* 2023). Their dual roles in nutrition and agro-ecological resilience makes legumes central to climate-smart agriculture and inclusive food systems.

Global and regional legume crops in food security

Legumes have diverse global centres of origin, reflecting their ancient domestication across continents. Chickpea and Lentil were domesticated in the Fertile Crescent (Zohary *et al.,* 2012). Peas traces its roots to the Mediterranean Basin and Central Asia. Soybean originated in northeastern China (Hymowitz and Shurtleff, 2005). The common bean has dual centres in Mesoamerica and the Andean region of South America (Bellucci *et al.,* 2013), while Faba bean originated in the Near East, although its wild progenitor remains unidentified (Caracuta *et al*., 2016). Groundnut is native to South America, particularly Brazil and Peru (Krapovickas, 2017). Cowpea emerged from Sub-Saharan Africa, adapted to arid climates and low-input systems (Boukar *et al.,* 2019). Grass pea, known for its drought tolerance, is native to the Mediterranean and South Asia (Gonçalves *et al.,* 2024). India is a major centre of origin for several tropical legumes such as pigeon pea, black gram, green

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How to cite this article: Panchulakshmi, M., Ga., D., Sathyamoorthy, N.K, Jegadeeswari, D., Arthirani, B., Dhasarathan, M. and Kumar, S.M. (2026). Thermal Sensitivity of Legume-rhizobium Interactions: Root Morphogenesis and Variability: A Review. *Legume Research.* 1-10. doi: 10.18805/LR-5609.

Submitted: 24-11-2025 **Accepted:** 13-02-2026 **Online:** 05-03-2026

gram, Horse Gram, Lablab Bean and Moth Bean are native to the Indian subcontinent, where they have long supported rainfed subsistence farming and protein nutrition (Srivastava *et al.,* 2025). These origins underscore the ecological and cultural significance of legumes in shaping resilient food systems across agro climatic zones in India.

Leguminosae crops addresses global food and nutritional security challenges, particularly in regions with protein-deficient diets (Salaria *et al.,* 2022; Amel *et al.,* 2018), being rich in protein (20-35%) (Grdeñ and Jakubczyk, 2023), essential amino acids, fibre, vitamins and minerals (Çakir *et al.,* 2019). Legumes offer a nutritionally balanced alternative to animal protein (Rajput *et al.,* 2024), make them especially valuable in vegetarian populations in India, where pulses are dietary stables. Globally, rising demand for plant-based proteins reflects health and sustainability concerns (Aschemann-Witzel *et al.,* 2021).

Legumes like lentils, chickpeas, mung beans and soybeans are recognized as “future-smart foods” for their nutritional and ecological resilience (Sharma *et al.,* 2024). In India, pulses contribute significantly to protein intake and are culturally embedded in rural traditional food systems (Singh *et al.,* 2017; Sonika *et al.,* 2020). Beyond human nutrition, legumes also support sustainable diets by reducing reliance on resource-intensive animal agriculture (Röös *et al.,* 2020). Their inclusion in cropping systems enhances food system diversity and resilience, align with the UN Sustainable Development Goals (SDGs), particularly SDG 2 (Zero Hunger) and SDG 13 (Climate Action) (Unicef, 2022).

Despite their benefits, legume production is constrained by low yields, biotic and abiotic stresses and limited policy support. Breeding, biofortification and value addition are key to enhancing their role in global food and nutritional security worldwide.

Objective and scope of the review

This review synthesizes current knowledge on soil temperature effects on legume rhizobium interactions, with emphasis on root morphogenesis and nitrogen dynamics across physiological, molecular, microbial and agronomic dimensions relevant to climate resilient cultivation. The process is illustrated in the graphical abstract (Fig 1) and PRISMA flow diagram (Fig 2).

From an initial 162 publications retrieved via Scopus, Web of Science, Google Scholar, PubMed and CAB Abstracts using targeted keywords, 124 were shortlisted after screening and 91 peer-reviewed studies were retained for final synthesis, based on rigor and relevance.

Thematic organization focused on temperature thresholds influencing nodulation, root system architecture (RSA) and symbiotic gene expression. Key regulators included heat shock proteins, cold responsive genes (*e.g.*, GmFRI-1) and hormonal pathways modulating auxin-cytokinin dynamics. Integrated analysis covered physiological traits (root elongation, branching, biomass), microbial adaptations (strain tolerance, inoculant formulations) and agronomic practices (mulching, conservation tillage, co-inoculation) that shape symbiotic efficiency under variable soil temperatures.

Soil temperature and crop production

Soil temperature is a fundamental environmental variable regulating biological, chemical and physical processes in agriculture. It directly influences seed germination, root development, microbial activity, nutrient mineralization and water uptake, making it a critical determinant of crop productivity (Hatfield and Prueger, 2015). Optimal soil temperatures for tropical and subtropical crops are typically 20-30°C, varying by species and growth stage. Deviations from this range due to seasonal or climate induced shifts can disrupt enzymatic activity and hormonal signalling, impairing seed imbibition, radicle emergence and root

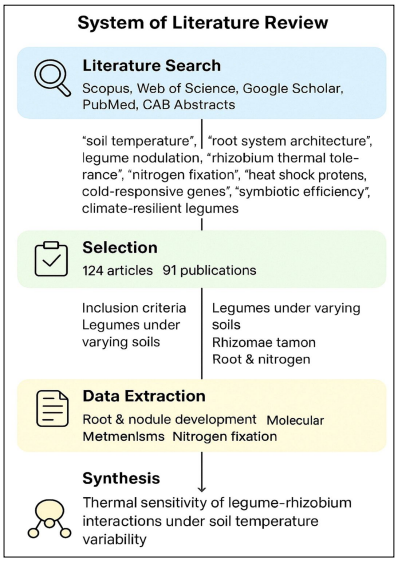


Fig 1: System of literature review process adopted in this review article.

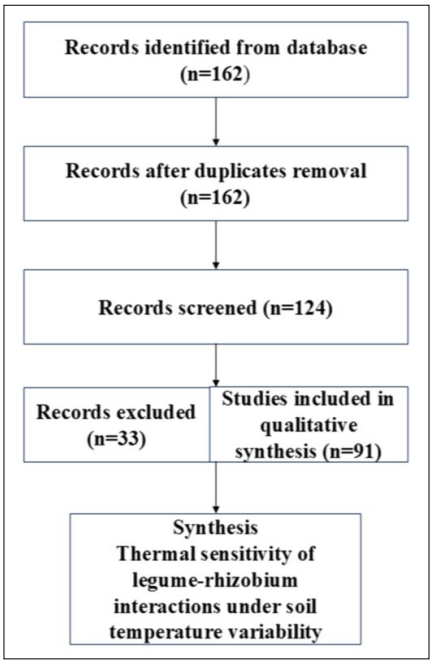


Fig 2: PRISMA flow diagram.

elongation. (Yanjun *et al.,* 2005). Cold soils delay germination and weaken seedling vigour, while excessive warmth accelerates metabolism but impairs root integrity and water balance. Nutrient solubility and uptake is also affected, with phosphorus availability reduced in cooler soils due to limited microbial activity (Blackwell *et al.,* 2010). Microbial processes like decomposition, nitrification and symbiosis are highly temperature sensitive, shaping microbial biomass, diversity and nutrient cycling.

Conservation practices such as mulching, cover cropping and residue management help maintain optimal thermal regimes for microbial health and crop resilience (Lal, 2020). Moreover, soil temperature interacts with moisture dynamics, influencing evapotranspiration, root water uptake and drought tolerance. Recent studies highlight its role in regulating enzymatic activity, membrane fluidity and hormonal signalling, affecting germination, root growth and biomass accumulation (Yeremko *et al.,* 2025).

Understanding soil temperature dynamics is crucial for optimizing legume productivity, guiding sowing windows, varietal choice and inoculant strategies for climate resilient agriculture. While warmer soils may extend temperate growing seasons but also intensify heat stress and disrupt root–microbe interactions in tropical zones. A nuanced grasp of these dynamics is essential for designing adaptive agronomic practices, selecting thermotolerant cultivars and refining sowing schedules under variable climates.

Root system architecture under soil temperature stress

The rhizosphere is highly sensitive to temperature fluctuations, especially in legumes where root-microbe interactions drive productivity. Soil temperature shapes root system architecture (RSA), influencing elongation, branching and biomass (Luo *et al.,* 2020). RSA governs water and nutrient uptake, microbial colonization and stress resilience. A dual fertilizing layer at the 30/ cm crest buffers soil temperature, enhancing root geometry through shallower angles, lateral proliferation, increased diameter and vertical expansion (Kang *et al.,* 2025). Conversely, cooler root zones (7-13°C) restrict root growth and reduce vascular duct size, impairing mineral uptake and translocation (Miao *et al.,* 2023).

Root elongation

Highly temperature sensitive, elongation in soybean peaks near 30°C, while drops by 70% at 12°C (de Moraes and Gusmao, 2021). Near-zero temperatures halted root extension in cereals like wheat and maize (Morandage *et al.,* 2021), while cooler soils reduce root length density in spring cereals, limiting soil exploration (Qin *et al.,* 2018). Most legumes elongate optimally 20-28°C; below 15°C, cell division slows, while above 35°C root tips are damaged, reducing elongation and lateral root formation.

Lateral root formation

Moderate soil warmth promoting auxin-mediated lateral root development, while excessive heat disrupts hormonal signalling, producing sparse roots. Tripathi *et al.* (2024) reported that legumes exposed to fluctuating soil temperatures exhibited altered branching patterns and reduced adventitious root density, impairing nodulation and nitrogen fixation.

Biomass accumulation

Root biomass peaks under optimal soil temperature and moisture. Legumes showed higher root biomass cooler temperatures (19-20°C), due to improved water retention and reduced thermal stress (Tchapga *et al.,* 2023). Elevated temperatures accelerate decomposition but reduce biomass *via* increased respiration and lower carbon allocation. In maize, root dry weight was highest under 30/ 22°C and 35/27°C regimes (Walne and Reddy, 2022), while warming 4-6°C above ambient deteriorated fine roots and reduce absorptive root biomass (Parts *et al.,* 2019). In cold ecosystems, warming increased root, fungal and fungivore biomass, though bacterial and archaeal levels remained stable (Salazar *et al.,* 2020).

Thermal sensitivity of rhizobial function

Rhizobial activity and colonization under soil temperature stress

Soil temperature is a critical determinant of rhizobial activity, colonization efficiency and legume-rhizobium symbiosis. Rhizobia exhibit optimal metabolic activity and BNF between 20-30°C (Bordeleau and Prévost, 1994), while below 15°C or above 35°C impair bacterial viability, signal exchange and symbiotic function. Low temperatures slow rhizobial metabolism, reduce Nod factor synthesis and delay colonization (Liu *et al.,* 2019). Cold stress also alters gene expression in rhizobia and host roots, affecting early signalling and nodule initiation. In contrast, elevated temperatures may boost root growth but disrupt rhizobial membrane integrity, enzymatic stability and signalling molecule production (Kumar *et al.,* 2023; Caruso *et al.,* 2014).

Soil temperature strongly influences rhizobial motility, chemotaxis and attachment to root hairs, critical steps for colonization. Moderate warmth enhances these processes and boosts nodule biomass, while temperatures outside the optimal (20-30°C) delay colonization (Zhang *et al.,* 2020). Optimal temperatures (20-30°C) favour rhizobial colonization, nodule development and nitrogenase efficiency. Conversely, temperatures below 15°C or above 30°C can hinder nodulation and reduce nitrogen fixation rates (Aranjuelo *et al.,* 2007; Mohammadi *et al.,* 2012). Importantly, rhizobial strains vary in thermal tolerance, with some maintaining symbiotic efficiency under heat stress, making their selection vital for legume cultivation in warming climates (Asadi Rahmani *et al.,* 2009; Alexandre and Oliveira, 2011).

Rhizobial inoculant formulation and delivery systems

The efficacy of rhizobial inoculants under temperature stress depends on both strain selection and formulation. Carrier-based inoculants using peat, lignite, or charcoal help buffer rhizobia against desiccation and thermal

fluctuations, extending shelf life and field viability (Bashan *et al.,* 2014). Liquid inoculants enriched with protective polymers and osmolytes enhance thermal tolerance and rapid colonization, especially in high-temperature environments (Tittabutr *et al.,* 2007). Encapsulation in alginate beads or biochar matrices creates protective microenvironments that moderate temperature and moisture stress (Schoebitz and López Belchí, 2016). Precision placement of inoculants near the rhizosphere, particularly in mulched or conservation tillage systems, enhances nodulation. Combining thermotolerant strains with optimized formulations and targeted delivery sustains symbiosis under climate variability.

Molecular mechanisms of nodule initiation

Nodule formation begins with molecular dialogue between host roots and compatible rhizobia. Within nodules, rhizobia differentiate into nitrogen-fixing Bacteroides (Ledermann *et al.,* 2021), supported by spatially and temporally regulated signalling networks. Nodules create a microaerobic niche for nutrient exchange and nitrogenase activity. Soil temperature influences nodule development and rhizobial strain competitiveness, for instance, B. diazoefficiens USDA 110/122 perform best at 28/23°C, while B. japonicum USDA 123 prefers cooler conditions (Shiro *et al.,* 2016). Maintaining optimal soil temperatures and using thermotolerant strains with suitable soil management enhances symbiotic efficiency and legume productivity.

Thermal sensitivity of rhizobial function

Soil temperature on nodule formation

Rhizobia form a symbiotic association with legumes, enabling atmospheric nitrogen fixation through nodule formation (Masson-Boivin and Sachs, 2018; Raza *et al.,* 2020). The process begins with root-exuded flavonoids that attract compatible rhizobia and induce Nod factor synthesis (Abd-Alla *et al.,* 2023). These signals recognized by root surface receptors, triggering root hair curling and infection thread formation (Krönauer and Radutoiu, 2021; Ghantasala and Roy Choudhury, 2022). Soil temperature critically influences rhizobial strain competitiveness and nodule occupancy. For example, B. diazoefficiens USDA 110/122 nodulated optimally at 28/23°C, while B. japonicum USDA 123 prefers cooler conditions, highlighting the importance of temperature-specific strain selection (Shiro *et al.,* 2016).

Temperature effects on nodule development

Optimal root-zone temperatures for nodule development are species-specific: 25°C for tropical beans, 20°C for peas and 15°C for lentils (Junior *et al.,* 2005). Deviations delay nodule initiation and reduce size, number and growth rate. Rhizobial colonization also varies with temperature, rhizosphere populations rise between 20-30°C, while endophytic movement in chickpea peaks at 25°C (Landa *et al.,* 2004). Co-inoculation with Bradyrhizobium and *Azospirillum brasilense* enhances nodulation in soybean under 20-30°C, with peak efficiency at 76% soil water retention and 112 nodules per plant (Deak *et al.,* 2019). In contrast, low temperatures (15°C) reduce clover productivity and delay nodulation (Janczarek *et al.,* 2024), while high temperatures (>40°C) can cause nodulation failure and genetic stress in rhizobia (Hungria and Vargas, 2000).

Role of heat shock proteins in nodule development

In legumes, Heat shock proteins (HSPs) are essential for symbiosis during nodule development, preventing protein aggregation and maintaining cellular homeostasis (Ogden *et al.,* 2017; Flynn *et al.,* 2024). Small HSPs like GmHSP17.9 inhibit thermal aggregation of malate dehydrogenase at 45°C and support early signalling and differentiation (Yang *et al.,* 2022). HSPs also safeguard nitrogenase enzymes from heat-induced denaturation and oxidative stress, preserving nitrogen fixation (Rajaram and Apte, 2008). Heat-tolerant rhizobial strains such as CIAT899 upregulate specific HSPs (*e.g.*, 21/ kDa) under 40-45°C, enhancing thermotolerance (Michiels *et al.,* 1994). Their stress-induced expression makes HSPs valuable biomarkers and breeding targets for heat-resilient legumes, supporting symbiotic efficiency under climate stress (Aranjuelo *et al.,* 2015).

Cold responsive genes and their impact on nodulation

Cold responsive genes enable legumes to sustain symbiosis under low-temperature stress by encoding proteins such as C-repeat binding factors (CBFs), antifreeze proteins and Osmo protectant enzymes that preserve cellular homeostasis (Thomashow, 2010). Active rhizobial symbiosis enhances cold tolerance in alfalfa by boosting antioxidant defences and modulating cold-response genes (Liu *et al.,* 2019). Cold stress disrupts hormonal signalling, cytokinin is pivotal for Nod factor transduction and nodule organogenesis (Dolgikh *et al.,* 2016), while low temperatures suppress auxin transporters (PIN1-PIN7), impairing root elongation and gravitropism (Tiwari *et al.,* 2023). Nitrogenase activity is highly cold-sensitive, declining by 60% in Bradyrhizobium japonicum nodules within 24 hours at 4°C (Zhang *et al.,* 2014). However, genes like GmFRI-1 help maintain nodulation under cold stress, its overexpression enhances soyabean nodule formation at 4°C, while RNAi silencing inhibits it (Zhang *et al.,* 2025).

Nodule senescence under temperature stress

Root nodule senescence is an orchestrated process involving the programmed death of bacteroids and plant cells, which results in a gradual decline in nitrogen fixation (Tsyganova *et al.,* 2023). Temperature strongly shapes senescence, at 28°C, wild-type SGE nodules senesced centrally after three days, while mutant lines SGEFix"-3 and SGEFix"-7 showed rapid apex and basal senescence within one day (Serova *et al.,* 2023a). Heat-induced senescence is also governed by hormonal pathways, with upregulation of GA deactivation (PsGA2ox1), ethylene (PsACS2, PsACO1), jasmonic acid (PsLoxN1) and ABA synthesis genes (PsNCED2, PsAO3), alongside downregulation of GA biosynthesis gene PsGA20ox1-collectively promsoting nodule aging (Serova *et al.,* 2023b).

Nitrogen fixation dynamics under soil temperature variability

Biological nitrogen fixation (BNF) is highly soil temperature-sensitive with extremes threaten symbiotic efficiency and crop productivity (Flynn *et al.,* 2024; Kajić *et al.,* 2016). Conservation tillage enhances nodulation and BNF by improving moisture retention, moderating temperature and boosting microbial biomass (Torabian *et al.,* 2019). Root-zone temperature (RZT) is critical, nitrogen fixation in grass pea halts below 10°C, temperate rhizobia peak at 25°C and cold-adapted strains at 15°C (Mahdavi *et al.,* 2010). This highlights the importance of matching rhizobial thermal adaptation to local soil conditions. In Arctic soils, BNF peaks below 14°C with adequate moisture, suggesting vulnerability of cold-adapted diazotrophs to warming (Rousk *et al*., 2018). In temperate zones, BNF rates rise with temperature, peaking at 35°C under moderate moisture (Li *et al.,* 2018). In chickpea, nitrogenase and nitrate reductase activities peak during flowering but decline at ~39°C, with nitrogenase reductase dropping by 40.12% and nitrogenase by 20.21% (Jain *et al*., 2014). Ammonium assimilation enzymes GS and GOGAT are even more sensitive to heat stress (Hungria and Kaschuk, 2014). These findings highlight the critical need for temperature resilient symbiotic systems to sustain BNF under climate stress. The interactions between soil temperature and key activities in legume-rhizobium systems are summarized in Table 1 and a graphical abstract (Fig 3).

Agronomic and microbial interventions for soil temperature management

Soil temperature regulates seed germination, root development, microbial activity and nutrient cycling, making its management vital under climate variability. Mulching with straw, leaf litter, or green manures, buffers temperature, conserves moisture and promotes microbial health. In Indian natural farming, mulching synergizes with inputs

Table 1: Optimal soil temperature for the key activities in legume-rhizobium systems.

Activity	Optimal soil temperature range	Effect of low temperature (<15°C)	Effect of high temperature (>35°C)	Remarks / Citations
Seed germination	20-30°C	Delayed imbibition, poor viguor	Accelerated metabolism, reduced viability	(Hatfield and Prueger, 2015) and (Yeremko *et al*., 2025)
Root elongation	20-28°C	70% reduction in soybean at 12°C	Tip damage, inhibited elongation and branching	(de Moraes and Gusmao, 2021) and (Tripathi *et al*., 2024)
Lateral root Formation	22-30°C	Sparse branching, hormonal disruption	Auxin imbalance, reduced adventitious roots	(Tripathi *et al*., 2024)
Root biomass accumulation	19–30°C	Reduced cell division, poor vascular development	Increased respiration, reduced carbon allocation	(Tchapga *et al*., 2023) and (Walne and Reddy, 2022)
Rhizobial colonization	20-30°C	Delayed Nod factor synthesis, impaired infection threads	Membrane instability, reduced signaling	(Liu *et al*., 2019) and (Mohammadi et al., 2012)
Nodule initiation	Species-specific (15-25°C)	Delayed primordia formation, reduced nodule number	Genetic stress, nodulation failure	(Junior *et al*., 2005) and (Hungria and Vargas, 2000)
Nitrogenase activity	25-30°C	60% decline at 4°C in B. japonicum nodules	40% reduction at ~39°C in chickpea	(Zhang *et al*., 2014) and (Jain *et al*., 2014)
Heat shock protein expression	>40°C	Not induced	Upregulated to protect nitrogenase and inhibit thermal aggregation of MDH	(Yang *et al*., 2022) and (Michiels *et al*., 1994)
Cold-responsive Gene expression	<15°C	Upregulated (*e.g.*, GmFRI-1, CBFs)	Suppressed	(Zhang *et al*., 2025) and (Thomashow, 2010)
Agronomic Interventions (Mulching)	All ranges	Buffers cold stress, improves microbial activity	Reduces evapotrans-piration, stabilizes root zone	(Lakhani and Bodar, 2025) and (Demo and Asefa Bogale, 2024)
Microbial inoculant Selection	20-30°C	Thermotolerant strains underperform	Cold-adapted strains underperform	(Asadi Rahmani *et al*., 2009) and (Alexandre and Oliveira, 2011)
Sowing window Optimization	Region-specific	Avoid early sowing in cold soils	Avoid peak heat periods	(Zhang *et al*., 2019)

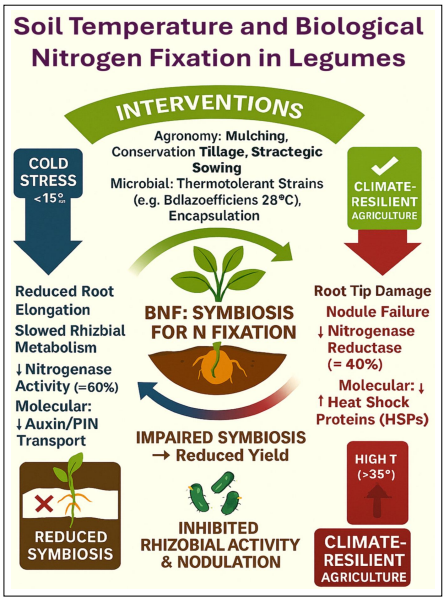


Fig 3: Graphical abstract of soil temperature and legume-rhizobium symbiosis.

like Jeevamrit and Bijamrut to enhance nutrient cycling and nitrogen fixation (Lakhani and Bodar, 2025). Mulching also suppresses weeds, reduces evapotranspiration and cold stress, making it especially valuable in dryland and semi-arid regions (Demo and Asefa Bogale, 2024).

Thermotolerant strains of *Rhizobium*, *Azospirillum* and phosphate-solubilizing bacteria improve nodulation and nutrient uptake. Inoculants applied with organic carriers and placed near the root zone, often alongside mulching enhance microbial efficacy (Abro *et al.,* 2011). Region-specific formulations are increasingly recommended to match local soils and cropping systems. Sowing window optimization-based on soil temperature thresholds improves germination and seedling vigour. Aligning sowing with seasonal rainfall and temperature patterns boosts yields (Zhang *et al.,* 2019). Longterm Agrometeorological data and crop-weather calendars guide ideal sowing periods for rainfed crops.

Together, these interventions form a low-cost, synergistic framework for climate-resilient agriculture across diverse agro-climatic zones. Integrated with conservation agriculture and ICT-based advisories, they strengthen soil health, microbial diversity and crop productivity under temperature stress.

Way forward

To enhance legume productivity and nitrogen fixation under variable soil temperatures, integrated agronomic management strategies are essential to improve resilience. Advanced inoculant technologies, including encapsulated and polymer-enriched formulations may strengthen the nodulation process. Molecular insights into heat shock proteins, cold-responsive genes and hormonal pathways provide breeding targets. Embedding these approaches in extension programs, policies and farmer training ensures scalable adoption across diverse agro-climatic zones.

CONCLUSION

Soil temperature critically shapes root architecture and legume-rhizobium symbiosis, influencing water uptake, nutrient acquisition and nitrogen fixation. Extreme heat or cold impair root development and symbiotic efficiency. Integrating thermotolerant rhizobial strains, optimized inoculants, mulching and conservation tillage helps buffer temperature stress. Strategic sowing windows and root-zone management further enhance nodulation in rainfed systems. Molecular insights into heat shock proteins and cold-responsive genes offer new breeding targets for thermal resilience. Coupled with ICT-based advisories and region-specific agrometeorological data, these interventions can boost legume productivity and soil health. A systems approach, linking genetic, microbial and agronomic innovations is essential for sustaining biological nitrogen fixation and advancing climate-smart agriculture.

ACKNOWLEDGEMENT

The authors gratefully acknowledge the Ministry of Social Justice and Empowerment and the University Grants Commission (UGC), Government of India, for the student fellowship and sincerely thank the scientists of the DST–Centre of Excellence on Disaster and Climate Resilient Agriculture, Agro Climate Research Centre, TNAU, Coimbatore, for valuable support in collecting review materials.

Disclaimers

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Informed consent

No animal used during the research.

Conflict of interest

The authors declare no conflict of interest.

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