

Thermodynamic Principles in Plant Physiology Under Climate Change and Environmental Stress: A Comprehensive Review

Dr. C. Rama Raju¹, Dr. R. Yadagiri², Dr. Mathe Anil Kumar³,
Gurram Linga Reddy^{4*}

¹Assistant Professor of Botany, Government Degree College, Badangpet. Dist: Ranga Reddy, Osmania University, Telangana.

²Associate Professor of Botany, Government Degree College, Hayath Nagar, Dist: Ranga Reddy, Osmania University, Telangana, India.

³Lecturer, VSR Government Degree College, Movva, Dist: Krishna, Krishna University, Andhra Pradesh, India.

⁴Assistant Professor of Physics, MKR Government Degree College (A), Devarakonda, Dist: Nalgonda, Mahatma Gandhi University, Telangana, India.

*Corresponding Author: Gurram Linga Reddy, botanybdpt@gmail.com

Abstract

Plants function as open thermodynamic systems, continuously exchanging energy and matter with their environment. Rapid climatic changes—including increased temperature, altered precipitation regimes, and expanding drought and salinity—intensify the thermodynamic pressures shaping plant physiology. This review expands on the mechanistic links between free energy, chemical potential, entropy production, and water potential, and their influence on plant survival under stress. It integrates recent findings on water relations, aquaporin-mediated hydraulic conductance, thermodynamic limitations on photosynthesis and respiration, combined stress interactions, and emerging unified models of water-carbon coordination. This paper illustrating water potential gradients, energy flow, and thermodynamic trade-offs. Major themes include how stress alters biochemical feasibility (ΔG), increases metabolic entropy, destabilizes membranes, and shifts plants toward high-cost maintenance modes. The review concludes with implications for climate-resilient agriculture and challenges in applying classical thermodynamics within heterogeneous plant systems.

Keywords: water potential, free energy, entropy, climate change, stress, hydraulics.

1. Introduction

Thermodynamics governs every major process in plant physiology, from transmembrane transport and metabolic reactions to photosynthesis, respiration, and stress adaptation. As open systems, plants rely on gradients of free energy, chemical potential, and water potential to sustain life processes (Kathpalia & Bhatla, 2018). Climate change has increased the frequency, intensity, and overlap of environmental

stressors, revealing the fundamental thermodynamic limits of plant resilience (Dutta et al., 2020). Understanding these limits is essential for predicting responses under future climate scenarios and designing robust agricultural systems.

Plant responses to environmental stress—whether heat-induced membrane instability, drought-driven hydraulic collapse, or salinity-induced osmotic imbalance—are rooted in changes to free energy, entropy, and water potential. This review expands on these core principles, offering a detailed synthesis of current research and theoretical advances.

2. Thermodynamic principles in plant physiology

2.1 Gibbs Free Energy and Chemical Potential

Gibbs free energy (ΔG) determines whether a metabolic process can proceed spontaneously. Environmental stresses affect ΔG by modifying temperature (T), reactant concentration, solute activities, and water availability (Parsegian et al., 2000). For example, drought reduces cytosolic water activity, increasing ΔG for biosynthesis, while heat accelerates kinetic energy and disrupts enzyme-substrate interactions. These changes reduce biochemical efficiency and elevate the metabolic cost of maintaining cellular homeostasis.

Gibbs free energy (ΔG) applies to **biochemical reactions in plants** here's the most appropriate and general one:

$$\Delta G = \Delta G^{\circ'} + RT \ln \frac{\prod a_{\text{products}}}{\prod a_{\text{reactants}}}$$

ΔG → Actual Gibbs free energy change in the plant cell (depends on conditions).

$\Delta G^{\circ'}$ → Standard Gibbs free energy change (measured at pH 7, 25 °C).

R → Gas constant (8.314 J mol⁻¹ K⁻¹).

T → Absolute temperature (Kelvin).

a → Activity (effective concentration) of reactants and products.

In plant metabolism (e.g., photosynthesis, respiration, or osmolyte synthesis), ΔG changes with:

Temperature (T) — affects reaction favorability under heat stress.

Water activity ($a_{\text{H}_2\text{O}}$) — declines under drought, increasing ΔG .

Solute concentrations — shift during stress, modifying reaction direction.

This equation expresses how environmental factors (temperature, water, solute) alter the energetic feasibility of plant metabolic processes.

2.2 Entropy and Plant Structural Organization

Entropy (S), a measure of disorder, increases when plant cells face heat-induced membrane fluidity, protein denaturation, or ROS accumulation (Kumar et al., 2024). Thermodynamic resilience depends on minimizing entropy production while maintaining ordered cellular states. When plants experience heat stress or oxidative stress, the entropy (disorder) within cellular components increases due to membrane lipid phase transitions (increased fluidity), protein unfolding or denaturation, accumulation of reactive oxygen species (ROS) disrupting macromolecular order. To survive, plants must invest metabolic energy (ATP) to restore order — e.g., via heat-shock proteins, lipid remodeling, and antioxidant repair systems.

$\Delta G = \Delta H - T\Delta S$ ⇒ Thermodynamic resilience arises when plants minimize $T\Delta S$ through repair and regulation. This equation elegantly expresses how entropy control underpins plant stress tolerance and structural organization.

ΔG — Gibbs free energy change governing metabolic repair or stabilization.

ΔH — Enthalpy change from energy input (ATP, NADPH, etc.) used for refolding proteins or rebuilding membranes.

3. Thermodynamics of water relations

3.1 Water Potential: The Driving Gradient

Water potential (Ψ) governs water movement across the soil–plant–atmosphere continuum. It sets the thermodynamic gradient that drives root uptake, xylem ascent, and leaf transpiration. Under drought, soil Ψ often becomes more negative than root Ψ , sharply limiting uptake and increasing cavitation risk (Sha et al., 2024).

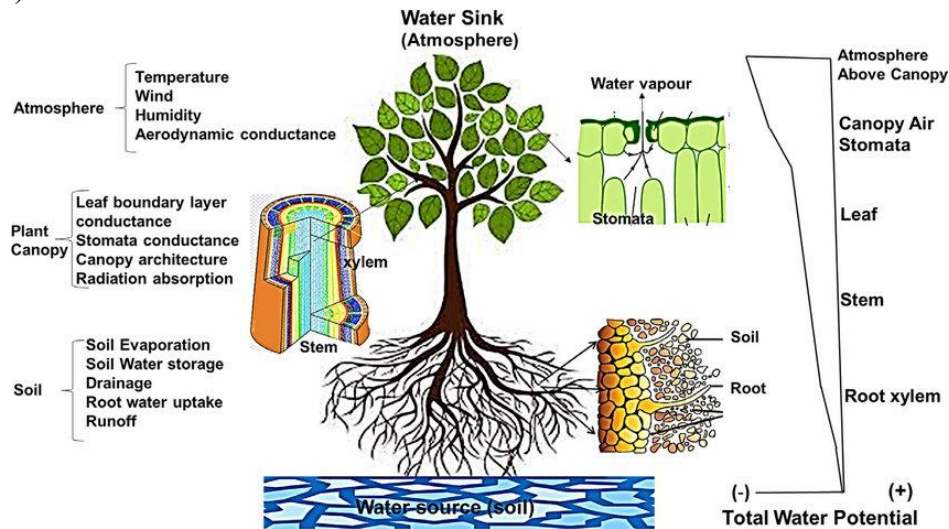


Fig. 1 Soil–Plant–Atmosphere Continuum (SPAC) A conceptual diagram illustrating progressively decreasing Ψ from soil → root → stem → leaf → atmosphere. Water potential (Ψ) is the key thermodynamic variable determining the direction of water movement across soil–plant–atmosphere continuum. Under drought, soil Ψ becomes more negative, often dropping below thresholds required for passive root uptake. Xylem tensions increase, risking cavitation. The plant’s ability to maintain a functional Ψ gradient determines hydraulic survival.

$Soil \Psi \rightarrow Root \Psi \rightarrow Stem \Psi \rightarrow Leaf \Psi \rightarrow Air \Psi$

3.2 Aquaporins and Membrane Water Transport

Aquaporins regulate membrane-level hydraulic conductivity. Stress-induced phosphorylation, gating, or downregulation of AQP’s reduces water loss but also restricts hydraulic flow. Thermodynamically, AQP’s reduce resistance to water flow, lowering the energy required to maintain hydration (Tamma et al., 2018).

3.3 Osmotic Adjustment and Energetic Trade-Offs

Plants synthesize or accumulate solutes—proline, sugars, ions—to reduce osmotic potential during drought or salinity (Singh et al., 2015). While this helps maintain turgor, solute production requires ATP, representing an energy-costly survival strategy. Maintaining low water potential internally increases stress tolerance but constrains growth.

4. Thermodynamic Constraints on Photosynthesis and Respiration

4.1 Photosynthesis under Heat and Drought Stress

Photosynthetic efficiency is strongly constrained by thermodynamic stability within the chloroplast. Heat stress disrupts thylakoid membrane structure, increases entropy, and reduces Rubisco specificity for CO₂ (Hu et al., 2020). Drought limits CO₂ diffusion, forcing plants into energy-inefficient photorespiration (Dusenge et al., 2019).

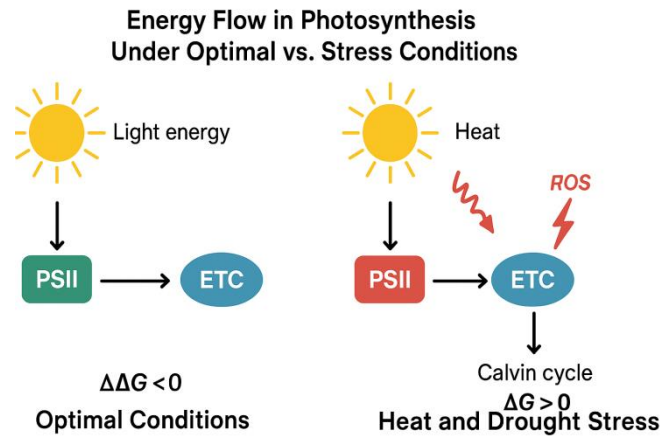


Fig. 2 Energy Flow in Photosynthesis under Optimal vs. Stress Conditions

Light energy → PSII → ETC → Calvin cycle; and disruptions under heat/drought.)

Photosynthesis is energetically limited and susceptible to thermodynamic disruption. Heat stress weakens thylakoid membrane stability, reducing quantum efficiency and increasing non-photochemical quenching. Drought restricts CO₂ diffusion, leading to elevated photorespiration, which consumes ATP and releases CO₂ without producing sugars.

4.2 Respiration and Metabolic Maintenance

Stress increases mitochondrial leakiness, ROS production, and repair demands. Respiration rates often rise to maintain ion homeostasis and repair membranes, even when photosynthesis declines—leading to carbon starvation in prolonged stress (Imtiaz et al., 2023).

5. Integrated Thermodynamics of Hydraulics and Carbon Assimilation

5.1 Unified Hydraulic–Photosynthetic Models

Recent models unify carbon gain and water loss through a thermodynamic lens, considering stomatal optimization, hydraulic risk, and energy use efficiency. These frameworks show that stomatal responses reflect optimization of free energy (CO₂ uptake) vs. entropy and energy loss or transpiration (Katul et al., 2010).

5.2 Trade-Offs in Plant Strategy

Drought-adapted species increase investment in hydraulic safety (thicker xylem walls, narrower vessels), while fast-growing species prioritize carbon gain—reflecting evolutionary thermodynamic strategies (Xu, 2024).

6. Thermodynamic Interactions under Combined Stress

6.1 Heat–Drought Synergy

Heat and drought interactions produce supra-additive thermodynamic stress. Heat accelerates transpirational demand, steepening Ψ gradients, while drought reduces soil water availability—together elevating entropy, ROS formation, and membrane instability (Murmu et al., 2025). These stresses reduce photosynthesis and increase metabolic maintenance costs.

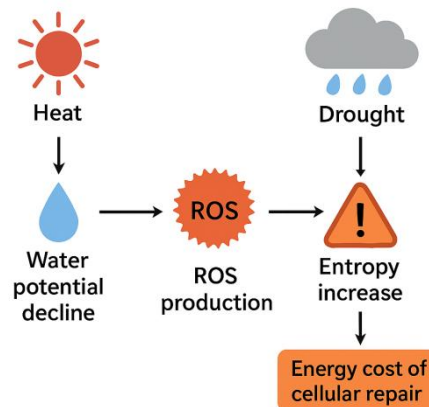


Figure 3. Thermodynamic Consequences of Combined Heat–Drought Stress

Conceptual diagram showing interactions among water potential decline, ROS production, entropy increase, and energy cost of cellular repair. Combined heat and drought amplify thermodynamic disturbances: heat accelerates evaporative water loss, steepening Ψ gradients; drought reduces hydraulic conductivity; together they elevate entropy and impair biochemical stability.

6.2 Salinity and Heat Interactions

Salinity increases osmotic stress and ion toxicity, while heat further destabilizes membranes—raising the energy cost of maintaining ion gradients and cellular integrity. Elevated salinity disrupts metabolic enzyme activity, impairs nutrient uptake, and causes excessive accumulation of Na^+ and Cl^- in the cytoplasm, leading to ionic imbalance (Awais et al., 2023). Concurrently, heat stress accelerates reactive oxygen species (ROS) formation, resulting in oxidative damage to proteins, lipids, and nucleic acids. Together, these stresses compromise photosynthetic efficiency, reduce water use efficiency, and inhibit cellular homeostasis, ultimately constraining plant growth and productivity.

7. Applications for Climate-Resilient Agriculture

7.1 Thermodynamic Traits for Breeding

Climate-resilient breeding can strategically target multiple physiological and biochemical traits that enhance plant tolerance to combined abiotic stresses. Improved aquaporin regulation enhances cellular water transport and maintains optimal tissue hydration under osmotic and heat stress conditions, supporting sustained transpiration and nutrient mobility. Membrane thermostability ensures the integrity and functionality of cellular and organelle membranes at elevated temperatures, thereby safeguarding ion homeostasis and photosynthetic apparatus stability. Enhancing antioxidant enzyme efficiency, such as superoxide dismutase, catalase, and peroxidases, mitigates oxidative stress by scavenging reactive oxygen species (ROS) generated under salinity and heat stress (Rao et al., 2025). Strengthening hydraulic safety margins through adaptive xylem structure and stomatal control prevents hydraulic failure and supports steady water flow during drought or salinity exposure. Furthermore, reducing photorespiratory cost via breeding or genetic modification improves carbon-use efficiency and energy balance, allowing plants to maintain higher photosynthetic productivity under thermal and osmotic stress. Collectively, these traits represent a multi-tiered approach to fortifying crops against the escalating impacts of climate change.

7.2 Thermodynamics-Informed Agronomy

Strategies to enhance plant resilience under combined heat and salinity stress include Ψ -based irrigation scheduling, mulching, microclimate cooling, and soil amendments — each of which optimizes plant–wa

water relations and reduces metabolic entropy.

By managing ΔH (energy input from metabolism and environment) and minimizing $T\Delta S$ (entropy-related energy loss), these practices ensure:

$\Delta G < 0 \Rightarrow$ Spontaneous and energetically efficient plant processes.

Thus, thermodynamics-informed agronomy enhances resilience, photosynthetic stability, and yield sustainability under climate stress (Singh & O'Neill, 2022).

8. Challenges and Theoretical Limitations

Classical thermodynamics, by design, operates under the assumption of homogeneous and closed systems in equilibrium. However, plant tissues are highly heterogeneous and compartmentalized, comprising distinct domains such as the symplast, apoplast, and vacuole, each with unique ionic compositions, redox potentials, and osmotic gradients. This structural complexity violates the equilibrium assumption and introduces non-equilibrium thermodynamic behaviors that are difficult to quantify experimentally.

Accurate measurement of *in vivo* Gibbs free energy changes (ΔG), chemical potential (μ), or entropy (S) in living tissues remains a formidable challenge. The dynamic exchange of water, solutes, and ions between compartments occurs under continuous flux, making it nearly impossible to isolate variables without perturbing the system. Additionally, temperature and salinity gradients at the cellular and tissue level generate local non-equilibrium steady states, where ΔG and ΔS cannot be easily inferred from bulk measurements.

Modern techniques such as microcalorimetry, isothermal titration calorimetry (ITC), and fluorescent thermosensing provide partial insights but are limited by spatial resolution and calibration uncertainties. Moreover, reaction kinetics, membrane transport, and metabolic regulation introduce time-dependent variables that classical equilibrium thermodynamics does not fully address. Despite these limitations, thermodynamic frameworks remain indispensable because they provide a quantitative and conceptual foundation for interpreting energy conversion, water relations, and metabolic efficiency under abiotic stress. Emerging approaches in non-equilibrium thermodynamics and entropy production analysis are gradually bridging this gap, enabling more realistic modeling of plant-environment interactions.

9. Conclusion

Thermodynamic principles—free energy (ΔG), entropy (ΔS), chemical potential (μ), and water potential (Ψ)—offer a unifying language to describe how plants sense, respond to, and adapt under climate-induced stressors such as drought, salinity, and heat. Variations in these parameters govern essential physiological processes: osmotic adjustment, ion transport, membrane stability, and metabolic regulation.

By integrating thermodynamic theory with empirical plant physiology and process-based modeling, researchers can derive predictive insights into stress thresholds, energy budgets, and adaptive capacity. For example, modeling ΔG of ATP hydrolysis and Ψ gradients across membranes can quantify the energetic cost of stress acclimation. Similarly, entropy-based indices can describe metabolic disorder or inefficiency under prolonged stress conditions.

Such integration transforms thermodynamics from a descriptive to a predictive framework—capable of informing climate-resilient breeding, irrigation optimization, and crop simulation models under global change. In essence, thermodynamics does not merely explain stress responses; it provides a quantitative

blueprint for resilience engineering, linking molecular energetics to whole-plant performance in dynamic environments.

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