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Review Article

Hemp response to drought, heat stresses and their mitigation strategies

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Abstract

Hemp species are increasingly cultivated for industrial, nutritional and pharmaceutical applications across diverse agroecological zones. However, productivity and quality are highly sensitive to drought and heat stress. The objectives of this review are to synthesize current knowledge on the adaptive mechanisms and management strategies that enable hemp to withstand climatic extremes. The inherent hardiness of hemp, highlighting it's morphological and physiological traits from seed to maturity such as deep rooting, stomatal regulation, water use efficiency, antioxidant defence, proline accumulation, and photosynthetic resilience were explored. The review examines stress impacts across developmental stages including germination, seedling establishment, vegetative growth, flowering, and seed/flower quality, culminating in overall yield outcomes. Genetic insights into heat and drought tolerance mechanisms are discussed, with emphasis on cultivar-specific responses and molecular control in *C. sativa.* Finally, we evaluate practical management interventions such as shade netting, mulching, irrigation scheduling, soil amendments, seed priming, and genotype selection alongside emerging tools for stress monitoring and diagnostics. This comprehensive review aims to inform breeding programs, agronomic planning, and climate-resilient hemp production systems

Keywords: Alkaloids, Cannabis *spp.*, Cannabinoid, Climate change, Genetic resistance

Introduction

Cannabis can be classified according to legislative purposes which are drug-type and fiber-type (hemp). Their difference lies in the concentration of the psychoactive compound delta-9-tetrahydrocannabinol (THC). The drug-type cannabis is characterized by a high THC content of above 0.3% to 1%, while fiber-type cannabis contains low THC levels of less than 0.3% to 1%. Hemp has got many uses and benefits which includes, efficient carbon sink, capable of sequestering up to 22 tonnes of CO_2 per hectare annually (Visković *et al.,* 2023; Muttil *et al.,* 2024) These attributes are important and are synonymous with climate smart agriculture. Its fibre is used in textiles, paper, bioplastics, and construction materials such as hempcrete (Crini *et al.,* 2020). Whereas its seeds rich in protein and omega fatty acids are utilized in food products, cosmetics, and animal feed (Apetroaei *et al.,* 2024). Accordingly, hemp cultivation aligns with sustainable development goals by promoting food security, rural economic growth, and environmental stewardship (Maluleke & Thobejane, 2025). In recent years, *Cannabis sativa* has gained attention for its potential resilience to abiotic stressors, particularly heat and drought, which are becoming increasingly prevalent due to climate change. Several studies have investigated hemp's physiological, morphological and biochemical responses to these stresses, highlighting its adaptability and potential for sustainable cultivation (Gill *et al.,* 2022; Mateva *et al.,* 2024).

Heat and drought stress individually and in combination can severely impair crop performance, leading to reduced yields and economic losses (Choudhury *et al.,* 2017; Ndlovu *et al.,* 2021). As global temperatures continue to rise and heatwaves become more prolonged, agricultural productivity faces mounting challenges (Hoegh-Guldberg *et al.,* 2018). Drought, driven by erratic rainfall patterns, is expected to intensify in frequency and severity necessitating the development and use of drought resilient crops (Gill *et al.,* 2022). Hemp has demonstrated remarkable drought tolerance, capable of surviving in soils with gravimetric moisture content as low as 5% a threshold at which most crops fail (Gill *et al.,* 2023). This resilience is largely attributed to its deep rooting system, extending up to 2 meters and a robust taproot that can access subsurface water reserves (Amaducci *et al.,* 2002). However, the effectiveness of this trait depends on soil depth and compaction, as shallow or degraded soils may limit root penetration and reduce drought tolerance (Amaducci *et al.,* 2002). Physiologically, temperature stress in hemp leads to reduced germination rates, impaired photosynthesis, stunted growth, and diminished seed production (Payment & Cvetkovska, 2023). Therefore, the aim of this review is to synthesize current state of knowledge on the physiological, morphological, and biochemical responses of hemp to drought, heat and combined drought and heat stress. In addition, the review explores management strategies for mitigating these stresses and examines the genetic mechanisms underlying hemp's adaptive responses, with particular emphasis on molecular control pathways, stress-responsive gene networks, and emerging insights from functional genomics to support future breeding and crop improvement efforts.

Seed and seedling attributes that make hemp hardy

Hemp's hardiness begins at the seed and seedling stages, where several key traits contribute to its resilience. High-quality seeds exhibit strong germination rates and genetic stability, which are essential for resistance to environmental stressors such as drought and heat (Du *et al.,* 2022). Feminized seeds, commonly used for CBD

production, tend to produce uniform, vigorous plants due to their stable genetic profiles and reduced male contamination. As seedlings, hemp develops rapid root systems especially deep taproots that anchor the plant and efficiently draw moisture from lower soil layers, a trait linked to drought adaptation in genotypes like *Cannabis sativa ZB* and *Cannabis indica MP* (Mateva *et al.,* 2024). Early leaf formation enables quick photosynthesis, while adaptability to varied light conditions supports steady growth across different environments. Hemp seedlings also demonstrate efficient water use, avoiding overhydration, and with proper airflow and moisture control, they resist common fungal threats such as damping off (Du *et al.,* 2022). These combined attributes make hemp a robust crop capable of thriving in diverse and challenging environments.

Morphological responses to heat and drought stress

Hemp exhibits several morphological adaptations that make it withstand drought and heat stress. One of the most critical traits is leaf morphology plasticity, which allows the plant to regulate water loss and thermal load. Herppich *et al.* (2020) observed that hemp cultivars exposed to combined drought and heat stress adjusted their leaf area and structure, developing smaller, thicker leaves with reduced surface area. These changes minimize transpiration and improve thermal regulation, allowing the plant to maintain photosynthetic activity under extreme conditions. A study by Yavas *et al.* (2023) reviewed drought induced changes in leaf anatomy across various crops and noted that epidermal thickening, cuticle deposition, and reduced leaf angle are common responses that limit water loss. In hemp, similar structural modifications such as increased leaf tissue density and reduced leaf expansion are likely to contribute to its drought resilience. Additionally, Akhter Ansari *et al.* (2019) emphasized that leaf rolling, reduced leaf number, and altered stomatal positioning are key morphological responses to drought stress. These traits help conserve water by reducing transpiration and shielding photosynthetic tissues from direct sunlight. Together, these morphological changes reflect hemp's phenotypic plasticity, enabling it to adapt to fluctuating environmental conditions and maintain productivity in water limited regions.

Stem elongation, chemical profile and biomass

Heat stress significantly reshapes hemp seed composition and biochemical profiles, particularly in *Cannabis indica*, where chemical traits such as cannabinoid content are economically and therapeutically vital. Elevated temperatures disrupt metabolic pathways, leading to reduced carbohydrate and lipid accumulation in seeds, which in turn affects nutritional value and germination performance (Du *et al.,* 2022). In indica-dominant cultivars, heat stress has been shown to alter the biosynthesis of key secondary metabolites including THC, CBD, and terpenes. For example, under heat stress at 45-50 °C, CBD concentrations dropped from 1182 μg/g to 297 μg/g, and THC levels declined from 3927 μg/g to 580 μg/g a reduction of over 80% in some cases (Park *et al.,* 2022). These shifts not only lower potency but may also change the cannabinoid ratio, affecting therapeutic applications.

Studies also show that fatty acid methyl esters (FAMEs), which are critical for membrane fluidity and seed viability, decline under high-temperature regimes, while amino acid levels may rise, indicating stress-induced protein turnover and metabolic reprogramming (Hahm *et al.,* 2025). These biochemical changes are genotype-specific, meaning some indica strains exhibit greater vulnerability than others depending on their genetic expression of biosynthetic enzymes such as THCAS and CBDAS.

Furthermore, high temperatures during flowering and seed maturation impair trichome development, which directly affects resin yield and cannabinoid concentration. Fibre yield is also compromised, with stem elongation and biomass significantly reduced under heat stress. Musio *et al.* (2018) reported a 25-40% reduction in stem height and dry biomass in heat-stressed fibre hemp cultivars, while Basak and Packirisamy (2025) observed similar declines in indica strains grown under elevated temperatures. These findings underscore the dual challenge of maintaining both structural and chemical integrity in hemp cultivation under climate stress.

Cannabis indica and *Cannabis sativa* demonstrate varied responses to heat stress, with genotypic differences playing a crucial role in adaptation. While some varieties exhibit strong physiological resilience, others suffer from growth limitation. Heat stress can lead to reduced stem elongation and overall biomass production, affecting fibre yield. Basak and Packirisamy (2025) noted that environmental stressors like heat and drought can negatively impact hemp growth, including reductions in stem elongation and biomass accumulation, both critical for fibre yield potential. Additionally, the study by Musio *et al.* (2018) highlights that harvesting hemp under suboptimal conditions, such as high temperatures, can compromise fibre quality and yield due to altered plant development and reduced stem growth. Understanding these responses can aid in breeding programs and cultivation strategies to enhance hemp's heat tolerance.

Physiological responses to drought and heat stress

Photosynthesis reduction

In hemp photosynthesis is not adversely affected by increase in temperatures up to 35 °C. Varietal differences were noted in temperature tolerance with some being more plastic than others (Herppich *et al.,* 2020). Some varieties have been reported to survive at temperature approaching 40 °C, a known threshold for photosynthetic inhibition. Cultivars bred for Central-Northern Europe showed less photosynthetic reduction and better yield stability than those grown in Southern Europe, even under irrigation at high temperatures. This suggests that genetic adaptation to local climates may buffer photosynthetic machinery against combined heat and drought stress. In contrast, the cultivar

'Futura 75' showed a 20% reduction in dry mass and 30% shorter stem length under drought (25% ETm), highlighting how photosynthetic decline under water stress can directly impact biomass accumulation. The study implies that photosynthetic reduction under drought and heat is not uniform across cultivars. While stomatal regulation and leaf morphology play roles, genotype-specific resilience especially in CO_2 uptake and water-use efficiency determines how well hemp maintains photosynthesis and yield under stress.

Water use efficiency and stomatal regulation

Water use efficiency (WUE) in hemp is a key adaptive trait under heat and drought stress, shaped largely by stomatal regulation. Research shows that hemp cultivars respond to elevated temperatures by adjusting stomatal conductance to balance water conservation with carbon assimilation, though this trade-off can reduce photosynthetic productivity (dos Santos *et al.,* 2022). Studies by Herppich *et al.* (2020) demonstrates that WUE varies significantly across cultivars, with some fibre and floral types maintaining higher efficiency under stress through tighter stomatal control and reduced transpiration. Tang *et al.* (2022) quantified canopy-level WUE values between 4.0 and 7.5 mmol CO_2 mol^{-1} H_2O, placing hemp among moderately efficient C_3 crops. However, prolonged stress can lead to leaf senescence and reduced leaf area, further limiting CO_2 uptake and biomass accumulation. These findings highlight the importance of selecting genotypes with optimized stomatal behaviour and integrating irrigation and nutrient strategies to sustain WUE under increasingly variable climatic conditions.

Antioxidant defence, ROS and proline accumulation

Antioxidant defence mechanisms play a central role in hemp's resilience to heat and drought stress, primarily through the regulation of reactive oxygen species (ROS). According to Ndlovu *et al.* (2021), plants under abiotic stress enhance their antioxidant capacity to neutralize ROS and their byproducts, thereby minimizing oxidative damage and preserving cellular integrity. Hemp responds similarly, with Apetroaei *et al.* (2024) reporting that hempseed contains bioactive compounds such as tocopherols, flavonoids, and polyphenols that contribute to ROS scavenging and membrane stabilization under elevated temperatures. Dos Santos *et al.* (2022) observed that heat stress significantly increases ROS production in hemp tissues, triggering upregulation of key antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD), which collectively mitigate oxidative stress and prevent lipid peroxidation. In addition to enzymatic defences, hemp synthesizes proline, a multifunctional osmoprotectant that accumulates in response to thermal stress. Proline not only stabilizes proteins and membranes but also acts as a molecular chaperone and ROS scavenger, contributing to redox homeostasis and osmotic balance. Elevated proline levels have been correlated with improved stress tolerance in both fibre and floral hemp cultivars, suggesting its role as a biochemical marker for resilience. These coordinated antioxidants and osmoprotective responses enable hemp to maintain metabolic function and cellular stability under extreme environmental conditions, reinforcing its reputation as a hardy and adaptable crop.

Cannabinoid production

Heat and drought stress are major abiotic factors that influence cannabinoid biosynthesis in hemp particularly during flowering when secondary metabolite production peaks. In the study by Park *et al.* (2022), short-term exposure to 45-50 °C and water deprivation in the cultivar 'Green-Thunder' led to significant shifts in cannabinoid profiles. Heat stress alone reduced levels of cannabigerolic acid (CBGA) and cannabigerol (CBG), suggesting impaired upstream biosynthesis, while drought caused a 40% increase in CBG and a 75% decrease in CBD, alongside elevated THC levels. These changes reflect stress-induced reallocation of metabolic flux, likely driven by altered enzyme activity and oxidative pressure. While CBD, THC and CBG are the most studied cannabinoids, hemp produces over 100 others including cannabichromene (CBC), cannabinol (CBN), and cannabidivarin (CBDV) whose synthesis may also be sensitive to environmental stressors. The increase in THC under drought may result from enhanced THCA synthase activity or reduced degradation into CBN, a process influenced by reactive oxygen species (ROS) and cellular redox status.

Hemp biochemical attributes

Photosynthesis: efficiency & adaptability

Hemp is classified as a C_3 plant that it uses the Calvin-Benson cycle for carbon fixation, with 3-phosphoglycerate as the first stable product and Rubisco as the key enzyme. While C_3 plants are generally less efficient under heat and drought due to photorespiration, hemp demonstrates exceptional photosynthetic adaptability for a C_3 species. According to Tang *et al.* (2022), hemp maintains a high light-saturated net photosynthesis rate (Amax), reaching up to 31.2 μmol CO_2 m^{-2} s^{-1} at 25 °C, supported by robust Rubisco activity and elevated mesophyll conductance (gm), which enhances internal CO_2 diffusion. Its carboxylation capacity (Vcmax) enables strong carbon assimilation even under low nitrogen availability, with photosynthetic performance remaining stable between 25-35 °C, only declining significantly above 35 °C. These traits contrast with C_4 crops like sorghum, which use PEP carboxylase and Kranz anatomy to avoid photorespiration and maintain high photosynthetic rates under stress (Sage & Zhu, 2011). Sorghum thrives in arid environments due to its efficient carbon fixation and water-use strategies, making it a benchmark for drought-hardy crops. Although hemp lacks the anatomical advantages of C_4 species, its biochemical flexibility, nutrient-use efficiency, and temperature resilience position it as one of the most robust C_3 fiber crops for cultivation in semi-arid and nutrient-poor regions (Herppich *et al.,* 2020; Tang *et al.,* 2022).

Respiration: energy balance & stress tolerance

Compared to other crops, particularly sorghum (*Sorghum bicolor*), hemp (*Cannabis sativa*) exhibits a distinct set of biochemical strategies for coping with environmental stress, especially heat and drought. Hemp's resilience is rooted in its efficient respiration system, including balanced day respiration (Rd) and triose phosphate utilization (Tp), which help maintain energy balance and carbon flow through the Calvin cycle even under suboptimal conditions (Ndlovu *et al.,* 2021). Its high water-use efficiency (WUE), especially in cultivars like 'Ivory', is driven by strong stomatal regulation, allowing the plant to conserve water while maintaining gas exchange (Herppich *et al.,* 2020; Gill *et al.,* 2022). Hemp also employs photoprotective mechanisms such as non-photochemical quenching (NPQ) and chlorophyll fluorescence modulation, which protect its photosystems from damage under intense light and heat stress (Ruban & Wilson, 2021).

Hemp shares several stress-adaptive traits with sorghum but differs in the extent and mechanisms of their expression. Like sorghum, hemp exhibits osmotic adjustment and membrane stability under drought and heat stress, supported by proline accumulation and antioxidant enzyme activity that help maintain cellular integrity and reduce oxidative damage (Ndlovu *et al.,* 2021; dos Santos *et al.,* 2022). Hemp also demonstrates moderate antioxidative capacity through elevated levels of superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD), which mitigate reactive oxygen species (ROS) accumulation during stress events. High-temperature stress is a major abiotic constraint limiting plant growth and agricultural productivity. While its adverse effects are well documented, most studies have examined individual species or isolated physiological mechanisms. This review provides a comprehensive comparative analysis of heat stress responses across four major crops - barley (*Hordeum vulgare*), rice (*Oryza sativa*), maize (*Zea mays*), and tomato (*Solanum lycopersicum*), alongside the model plant Arabidopsis thaliana, focusing on their morphological, physiological, and biochemical adaptations as well as current mitigation strategies. Morphological assessments reveal that root traits are more heat-sensitive than shoot length, biomass, or germination rate. Physiologically, all species exhibit reduced photosynthetic rate and PSII efficiency (Fv/Fm), though stomatal conductance and transpiration responses vary. Biochemically, the accumulation of reactive oxygen species (ROS) and antioxidant activity exhibit species- and stress-dependent regulation, with both upregulation and downregulation observed. Among mitigation approaches, seed priming emerges as a cost-effective strategy, while miRNA-mediated regulation shows strong potential for developing heat-tolerant cultivars. This synthesis highlights critical knowledge gaps and outlines future directions for enhancing crop resilience in the face of rising temperatures. However, unlike sorghum, hemp lacks a well-defined "stay-green" trait. While some cultivars maintain photosynthetic activity under stress, this persistence is not genetically fixed or as pronounced as in sorghum, which uses delayed senescence and cooler canopy temperatures to sustain productivity (Ndlovu *et al.,* 2021).

In terms of morphological adaptations, hemp does not exhibit leaf rolling key water-saving trait in sorghum but instead relies on deep taproot systems and stomatal regulation to manage water loss. Genetic responses to stress in hemp are less extensively characterized than in sorghum, though emerging transcriptomic studies suggest that hemp does undergo changes in gene expression related to secondary metabolite biosynthesis, stress signalling, and cell metabolism under drought and heat conditions (Park *et al.,* 2022). For instance, stress-induced shifts in cannabinoid profiles such as increased THC and altered CBD/CBG ratios are linked to differential expression of synthase genes like THCA synthase and CBDA synthase. While sorghum's stress response is more thoroughly mapped at the genomic level, hemp shows promising but underexplored genetic plasticity that warrants further investigation, particularly in the context of climate resilience and phytochemical stability.

While hemp excels in biochemical flexibility and metabolic efficiency, sorghum's strength lies in its integrated structural and genetic resilience, making both crops highly adaptable but through fundamentally different mechanisms. Hemp's C_3-based photosynthetic system is unusually efficient for a fiber crop, whereas sorghum's C_4 pathway and robust physiological traits make it a model for drought-hardy cereals. Together, they offer complementary strategies for climate-resilient agriculture in semi-arid regions.

Effects of drought and temperature at different hemp growth stages

Drought and heat stress can significantly impact hemp at every stage of its development from seed to harvest. Below is a breakdown of how these stresses affect each growth phase:

Germination

Seed germination is highly sensitive to heat and serves as an important indicator of heat stress in plants. Temperatures above optimal levels disrupt germination, with rates dropping significantly above 30 °C and potentially stopping entirely beyond 45 °C (Samat *et al.,* 2025). The impact varies by species and genotype, some crops like barley and rice experience drastic reductions, while certain maize varieties show greater heat tolerance. Temperature is an important environmental factor that influences germination through breaking dormancy, imbibition and the mobilization of storage reserves and, ultimately, modifying germination percentage and rate (Langa *et al.,* 2024). Hemp is generally known to germinate well between temperature that ranges from 19 to 30 °C (Geneve *et al.,* 2022). However, temperature for germination in hemp is dependent of the genetics and geographical location. In a study by Herppich *et al.* (2020) two hemp varieties responded differently to temperature and drought during germination. Variety 'Santhica 2' showed higher germination success under hot and dry conditions and an early vigour which contributed to higher overall yield as compared to variety 'Ivory'. 'Ivory'

had a lower germination rate which led to its limited overall productivity. Moreover, Langa *et al.* (2024) in their study reported that varieties 'Georgina', 'Victoria' and Northern European hemp varieties thrive in temperatures up to 30 degrees whilst variety 'Bama' and Canadian cultivars could not germinate above 25 degrees Celsius. Drought affects germination as moisture is very important for germination to take place. However, the intensity of drought determines the effects that can be caused during germination. Extreme drought may cause germination failure whilst moderate drought can delay germination. In a study by Du *et al.* (2022) hemp seed germination was sensitive to drought stress, as the germination indices (germination rate and germination potential) decreased significantly.

Seedling stage

The study by Du *et al.* (2022) simulates drought induction using 20% PEG-6000, a method that creates osmotic stress by limiting water availability to seedlings without causing direct toxicity. Under these conditions, seedling growth specifically hypocotyl and radicle elongation are significantly impeded, as water deficit restricts root expansion and shoot development, ultimately reducing nutrient uptake and photosynthetic capacity. When combined with heat stress, which accelerates transpiration and leads to leaf wilting, chlorosis, and cellular damage, the impact intensifies, often resulting in complete seedling collapse within three days even with partial irrigation. This highlights the vulnerability of early growth stages to environmental stress. Herppich *et al.* (2020) further illustrate this by comparing hemp cultivars, where 'Santhica 27' showed better seedling establishment under drought and heat than Ivory, which, despite having a larger leaf area, suffered from poor early vigor and lower yield. These findings underscore that drought induction models like PEG-6000 are critical for understanding stress responses and that managing heat and water availability during establishment is essential for achieving a strong crop stand. Environmental control and timely supplementary irrigation during this phase can significantly influence long-term productivity.

Vegetative stage

During the vegetative stage, drought and heat stress can cause a decline in photosynthesis. These stresses reduce CO_2 assimilation and stomatal conductance, limiting energy production and growth. Drought and heat reduce CO_2 uptake and transpiration, thereby restricting biomass accumulation (Zheng *et al.,* 2021). In addition, leaf area can shrink as plants reduce leaf size to conserve water, which also limits light capture. Water-use efficiency may be affected; however, it varies across genotypes. Some adapt by improving intrinsic water-use efficiency through stomatal regulation. For example, in a study by Mateva *et al.* (2024) genotypes like 'MP' (*indica*) and 'AQ' (*sativa*) adapted by regulating stomata and increasing proline accumulation for osmotic balance. In the same study, a Zimbabwean variety was found to exhibit high non-photochemical quenching (NPQ) and chlorophyll fluorescence changes to protect photosystems under heat and drought. High temperatures above 35 °C can accelerate transpiration and risk heat-induced cellular damage, impair enzyme activity, and destabilize membranes, reducing vegetative vigor. Conversely, low temperatures below 15 °C can slow metabolic processes and delay vegetative expansion, especially in non-adapted cultivars. Mateva *et al.* (2024) further elaborated that drought stress at 40% field capacity may trigger adaptive responses without major yield loss, whereas severe drought at 0% field capacity leads to leaf senescence, reduced biomass, and impaired nutrient uptake.

Flowering stage

Drought stress during early flowering significantly disrupts cannabinoid production. These alkaloids are the most critical biochemical compounds in both industrial and medicinal hemp that give the crop its value. Drought during early flowering caused a 70-80% drop in cannabidiol (CBD) and delta-9 tetrahydrocannabinol (THC), while increasing CBG by 40% whilst heat stress (45-50 degrees Celsius) reduced CBGA and CBG production (Park *et al.,* 2022). Therefore, it is critical for medicinal hemp producers to manage temperature so that the quality of crop is not compromised. Furthermore, Hahm *et al.* (2025) exposed hemp cultivars to heat stress at 45 °C and found significant changes in CBD and CBN levels, indicating disrupted cannabinoid biosynthesis and increased expression of THCAS and CBDAS genes, which are key to cannabinoid production. A correlation between high temperature and altered trichome-related gene activity, suggesting potential impacts on trichome density and resin yield.

Seed and flower quality

Heat and drought stress during flowering can dramatically alter the chemical profile of hemp flowers. One of the most concerning effects is the reduction in cannabinoid content, particularly CBD and CBG, which are key for medicinal and industrial applications. Park *et al.* (2022) observed that under severe drought (0% field capacity), CBD levels dropped significantly, and flower biomass was reduced by up to 40%. Stress also affects terpene synthesis, which influences aroma and therapeutic properties. Drought can shift the balance between monoterpenes and sesquiterpenes, leading to a less desirable scent profile and reduced market value. Perhaps most critically, stress can trigger a spike in THC levels, sometimes pushing them above the legal threshold of 0.3% for industrial hemp. This is particularly problematic for cultivars that already hover near the compliance limit. Morgan's study documented cases where drought-induced stress led to THC levels exceeding legal limits, complicating harvest decisions and regulatory compliance.

Economic yield

Hemp exhibits yield reductions under prolonged drought and heat stress, though moderate levels of either stress may have minimal impact depending on cultivar and timing. Fibre hemp typically suffers biomass losses due

to reduced photosynthetic activity and impaired carbon assimilation, while floral hemp experiences decline in flower weight and cannabinoid concentration, with severe stress occasionally pushing THC levels above legal thresholds. Cultivars such as 'Cherry Mom' and 'MP' have demonstrated greater resilience under drought through physiological traits like proline accumulation, enhanced photoprotection, and stable carbon assimilation, as reported by Mateva *et al.* (2024). Strategic irrigation during the vegetative and early flowering stages has been shown to mitigate most yield losses, emphasizing the importance of genotype selection and targeted water management in maintaining productivity and compliance under climate stress.

Genetics of heat and temperature resistance (mechanisms and control)

Cannabis spp. response to heat stress at the genetic level

The three cannabis species respond differently to heat stress at the genetic level due to their distinct evolutionary backgrounds and adaptations. A breakdown of how each subspecies copes with high temperatures, focusing on their genetic responses and physiological traits will be synthesised:

AQ1 **Table 1:** Summary of hemp physiological, phenological and morphological attribute conferring resistance to drought and heat stresses

Physiological	Stomatal regulation
	Proline accumulation
	Photosynthetic reduction
	Water use efficiency
	Antioxidant defence
	Oxidative stress management
	Increase in cannabinoid production
Phenological	Rapid germination under moderate water stress
	Strong hypocotyl and radicle growth under mild drought (e.g., 40% FC)
	Early flowering in some cultivars- Timing avoids peak drought periods
	Short-duration varieties escape late-season drought
Morphological	Quick seedling emergence
	Deep taproot system

Cannabis sativa, having originated from tropical and equatorial regions, is genetically predisposed to tolerate high-temperature environments. This heat resilience is supported by several physiological and molecular traits. Sativa varieties often express genes that regulate heat shock proteins (HSPs), which function as molecular chaperones to stabilize proteins and prevent denaturation under thermal stress. These varieties also enhance the activity of reactive oxygen species (ROS)-scavenging enzymes such as superoxide dismutase (SOD) and catalase (CAT), which mitigate oxidative damage and maintain cellular homeostasis (Driedonks *et al.,* 2015).

One of the key molecular responses to heat stress in *C. sativa* involves the upregulation of stress-responsive transcription factors, notably Heat Shock Factors (HSFs) and Dehydration-Responsive Element Binding proteins (DREBs). HSFs activate the transcription of HSPs and other protective genes, while DREBs regulate genes involved in osmotic balance, antioxidant defence and stress signalling. These transcription factors have also been identified in other heat-adapted crops such as sorghum, rice, and Arabidopsis, where they play similar roles in orchestrating stress responses. In hemp, emerging transcriptomic studies such as those by Park *et al.* (2022) suggest that HSFs and DREBs are upregulated during heat and drought stress, contributing to enhanced thermotolerance and metabolic adjustment.

Additionally, *C. sativa* exhibits enhanced abscisic acid (ABA) signalling under heat stress, which promotes stomatal closure and conserves water. This hormonal regulation is crucial for maintaining turgor pressure and reducing transpiration water loss. Morphologically, sativa varieties tend to have narrower leaves, which reduce surface area and limit overheating an adaptation also seen in other xerophytic species. While hemp does not possess a defined "stay-green" trait like sorghum, some genotypes maintain photosynthetic activity longer under stress, suggesting partial functional analogues.

Overall, the tropical lineage of *C. sativa* has endowed it with robust genetic mechanisms for managing oxidative stress, regulating water use, and sustaining photosynthesis under heat stress. These traits make sativa varieties particularly suitable for cultivation in warm and arid

AQ1 **Table 2:** Summary of drought, heat and combined stresses effects on hemp at different crop stages

Growth Stage	Drought Stress	Heat Stress	Combined Stress (Drought + Heat)
Seed & Seedling	Slow seed imbibition Reduced germination Hypocotyl and radicle length Limits root expansion Limits shoot emergence Reduced nutrient uptake Reduced photosynthetic capacity	Accelerates transpiration Can lead to wilting Chlorosis Cellular damage	Complete seedling collapse within three days Poor early vigour can lead to low yield
Vegetative	Impaired nutrient uptake Reduced biomass Can lead to leaf senescence	Impaired enzyme activity & membrane stability Accelerates transpiration	Reduced CBGA & CBG synthesis Reduced CO_2 assimilation, water-use efficiency & photosynthesis
Flowering + Maturity	Reduced cannabinoid production Reduced THC & CBD Increased CBG	Early flowering Reduced yield	Reduced CBGA & CBG synthesis

climates, although further genomic studies are needed to fully characterize and harness these adaptive responses.

Cannabis indica

Cannabis indica, particularly landraces from hot, arid regions such as Afghanistan, India, and parts of the Middle East, shows evidence of genetic adaptation to elevated temperatures. Genomic studies indicate the presence of upregulated heat-responsive genes, including small heat shock proteins (e.g., Hsp20 family), heat shock transcription factors (HSFs), and ROS-scavenging enzymes such as superoxide dismutase (SOD) and catalase (CAT) under heat and drought stress (Rahman *et al.,* 2022). These genes protect cellular proteins and membranes from denaturation and oxidative damage during thermal stress. Morphologically, *indica* varieties often exhibit broad leaves with thick cuticles, dense trichomes, and waxy layers, traits linked to genes involved in cuticle biosynthesis and lipid metabolism (Danziger & Bernstein, 2022). These features contribute to reduced transpiration and increased tolerance to solar radiation. Furthermore, under elevated temperatures, some *indica* genotypes maintain stable cannabinoid production and reproductive function, suggesting a level of metabolic plasticity under heat stress (Wellington *et al.,* 2022). These traits make *indica* a promising genetic reservoir for breeding heat-resilient cannabis varieties.

Cannabis ruderalis is known for its adaptation to harsh and variable climates, primarily through its unique auto-flowering trait, which enables it to complete its life cycle independently of photoperiod. This trait likely evolved as a survival mechanism in environments with short summers and erratic temperature shifts, such as Central and Eastern Europe and Siberia (Groom, 2014; Clarke & Merlin, 2016). Although *C. ruderalis* shows general resilience to environmental stress, direct genetic evidence of specialized heat resistance remains limited. The auto-flowering trait itself, controlled by a set of loci including the FLOWERING LOCUS T (FT) homologs, contributes more to heat avoidance (by accelerating phenology) than active physiological tolerance (Zhang *et al.,* 2021). There is a lack of specific studies showing enhanced expression of heat shock proteins (HSPs), antioxidant enzymes, or membrane-stabilizing genes in *C. ruderalis* under thermal stress. However, its small leaf surface area and reduced biomass may passively contribute to reduced heat load and water loss (Russo, 2018). Overall, while *C. ruderalis* is robust, its genetic contribution to heat resistance likely centres on developmental timing rather than direct cellular defence mechanisms.

Managing heat and drought stress in hemp production

Temperature management strategies

One of the temperature management strategies is to grow hemp in environments with temperature ranging from 24°C to 30°C which is its optimal range. Controlled rooms or greenhouse with controlled temperatures can be used for hemp production. This temperature, supports robust vegetative growth, flower development, and cannabinoid biosynthesis. Temperatures exceeding 31 °C can impair flower formation and reduce the concentration of key cannabinoids like CBD and THC. Bok *et al.* (2023) found that flower biomass and cannabinoid content were highest under controlled conditions at 27:21 °C (day: night), indicating that even slight deviations from the optimal range can significantly affect yield and quality.

The use of shade netting and row covers is equally important for both industrial (fibre) and medicinal (floral) hemp, though the specific benefits may differ slightly based on the production goal. For fibre hemp, maintaining optimal canopy temperature and relative leaf water content is crucial for maximizing vegetative biomass, which directly influences fibre yield and quality. Excessive heat and transpiration can lead to premature leaf senescence, reduced stem elongation, and lower cellulose content key parameters for industrial applications. By moderating light intensity and temperature, shade netting helps sustain photosynthetic activity and structural integrity during critical growth phases. In medicinal hemp, the stakes are even higher. Floral hemp is highly sensitive to environmental stress, and elevated temperatures or UV exposure can disrupt cannabinoid biosynthesis, alter terpene profiles, and reduce flower biomass. Moreover, heat stress has been linked to spikes in THC concentration, which can push levels beyond legal limits for hemp compliance. Shade netting mitigates these risks by creating a buffered microclimate that stabilizes flower development and chemical composition. Studies in other crops, such as the (İkinci, 2025) work by on pomegranate, reinforce the value of shade netting in heat-sensitive species. While direct data on hemp is still emerging, the physiological parallels suggest that both fibre and floral hemp benefit substantially from this intervention. Ultimately, integrating shade netting into hemp production systems offers a low-cost, scalable solution to climate stress supporting yield, quality, and regulatory compliance across production types.

Mulching

Mulching is a widely used technique to regulate soil temperature, retain moisture, and reduce evaporation. Organic mulches like straw, compost, and wood chips insulate the soil, keeping it cooler during hot periods and warmer during cold spells. El-Beltagi *et al.* (2022) emphasized that mulching can reduce soil temperature fluctuations, improve water retention, and enhance seedling establishment critical factors for hemp grown in arid regions.

Heat tolerant cultivars

Selecting heat tolerant hemp cultivars is essential for maintaining productivity under rising temperatures. Mateva *et al.* (2024) identified cultivars like 'MP' (*Cannabis indica*) and 'ZB' (*Cannabis sativa*) as resilient under heat and drought stress. These genotypes maintained

high photosynthetic efficiency, exhibited strong non photochemical quenching (NPQ) for photoprotection, and accumulated proline, an Osmo protectant that stabilizes cellular functions under thermal stress.

Drought mitigation techniques

Natural plant survival strategies

Drought reduces water availability, causing loss of turgor, reduced photosynthesis, and impaired transport in plants. Severe drought leads to cellular dehydration, damaging membranes and proteins, which can result in cell death (Sato *et al.,* 2024). To counter drought, plants in general develop mechanisms for survival under drought stress conditions. These strategies include: drought escape (altering life cycles), drought avoidance (reducing water loss, e.g., via stomatal control), and drought tolerance (surviving low water conditions). Drought tolerance involves mechanisms such as scavenging reactive oxygen species, producing compatible solutes, and accumulating protective molecules.

Human interference on mitigation measures

Irrigation type and scheduling

To mitigate drought stress in hemp cultivation, precision irrigation techniques are essential. One of the most effective methods is drip irrigation, which delivers water directly to the root zone, minimizing evaporation and runoff (Yang *et al.,* 2023).This targeted approach can reduce water usage by up to 50% compared to conventional methods. Drip irrigation promotes healthier root development, improves nutrient uptake, and reduces the risk of foliar diseases associated with overhead watering. Timing matters: According to Shortridge and Porter (2021), watering during the early morning or late evening helps reduce evaporative losses and prevents heat stress on plants. Soil moisture monitoring using sensors or manual testing ensures irrigation is applied only when needed, avoiding overwatering and conserving resources. Mulching around the base of hemp plants further enhances moisture retention and reduces surface evaporation.

Soil amendments

To improve drought resilience in hemp cultivation, soil amendments play a critical role in enhancing water retention, nutrient availability, and soil structure. Organic matter (e.g., compost, vermicompost, manure) increases soil porosity, promotes aggregate formation, and improves water-holding capacity. It also supports microbial activity, which enhances nutrient cycling and root health. Subberwal *et al.* (2025) found that organic amendments significantly improve water retention and nutrient mobilization in various soil types. Mateva *et al.* (2024) and Subberwal *et al.* (2025) emphasized that organic matter boosts microbial diversity and soil resilience under drought stress. Hydrogels (e.g., sodium polyacrylate) are water-absorbing polymers that can retain large amounts of moisture and release it slowly to plant roots. Sun *et al.* (2023) demonstrated that hydrogel-amended soils showed improved water retention and enhanced wheat growth under water deficit conditions. Biochar, a carbon-rich product of biomass pyrolysis, has a porous structure that improves soil aeration, moisture retention, and nutrient retention. Veazie *et al.* (2023) showed that biochar decreased bulk density and increased microporosity and available water content in tropical sandy soils. Wei *et al.* (2023) found that biochar improved water retention most significantly in coarse-textured soils, increasing field capacity by up to 23.8%. These amendments not only help hemp withstand drought but also contribute to long-term soil health and sustainability.

Seed priming

One of the most powerful ways to prepare hemp for drought stress begins before the plant even emerges from the soil. Seed priming, a pre-sowing technique that activates metabolic processes by treating seeds with water or chemical solutions, has proven to enhance germination and early vigour under challenging conditions (Ingale & Pathak, 2023). Among the various priming agents, gibberellic acid (GA_3) stands out for its effectiveness. As a plant growth regulator, GA_3 boosts germination rate, seedling vigour, and stress tolerance by stimulating cell division and elongation, which promotes robust root and shoot development (Zhang *et al.,* 2021; Rahman *et al.,* 2022). It also enhances osmotic adjustment through the accumulation of soluble sugars and proline, activates antioxidant defence systems, and reduces oxidative damage during water stress (Hasanuzzaman *et al.,* 2020). Furthermore, GA_3 priming helps preserve chloroplast integrity and cellular ultrastructure, especially in sensitive tissues like root tips and leaf mesophyll, which are critical for photosynthesis and nutrient uptake under drought conditions (Zhang *et al.,* 2021). According to Cornea-Cipcigan *et al.* (2020), optimal results are achieved with GA_3 concentrations between 50-100 mg/L, significantly improving germination and early seedling growth in water-limited environments.

Genotype selection

Genotype selection is a cornerstone of drought mitigation in hemp cultivation, as different cultivars exhibit distinct physiological and biochemical responses to water stress. Mateva *et al.* (2024) conducted a comprehensive study on three CBD flower hemp genotypes and their findings revealed that 'MP' variety maintained high assimilation rates and superior photosynthetic performance, while 'ZB' variety showed elevated proline accumulation during drought recovery, indicating optimized resource allocation and osmotic adjustment. Both cultivars demonstrated effective stomatal regulation and high non-photochemical quenching (NPQ), a photoprotective mechanism that helps dissipate excess light energy and protect photosystems under stress (Mateva *et al.,* 2024). These traits, proline accumulation, stomatal control, and NPQ activity are critical for maintaining cellular integrity, reducing oxidative damage, and improving water-use efficiency under drought conditions. Their presence in

specific genotypes provides a strong foundation for breeding programs aimed at developing resilient hemp varieties suited to arid and semi-arid environments.

Monitoring and diagnostics

Effective drought mitigation in hemp cultivation requires early detection and precise monitoring of physiological stress. Two advanced tools which are Raman spectroscopy and carbon isotope analysis ($\delta^{13}C$) offer powerful, non-invasive insights into plant water status and biochemical responses. Raman spectroscopy is a cutting-edge, non-destructive technique that detects biochemical changes in hemp leaves caused by drought and heat stress. It can differentiate between stress types with up to 100% accuracy, based on shifts in carotenoid, cellulose, and protein vibrational bands. Steczkowski *et al.* (2023) demonstrated that handheld Raman devices accurately identified drought, heat, and light stress in hemp cultivars, making it a valuable field diagnostic tool. Payne and Kurouski (2021) reviewed Raman-based diagnostics for abiotic stress in plants, highlighting its precision and portability.

Carbon isotope analysis ($\delta^{13}C$) provides a long-term measure of water-use efficiency (WUE) by tracking the ratio of intercellular to atmospheric CO_2 during photosynthesis. Seibt *et al.* (2008) explained that $\delta^{13}C$ signatures reflect intrinsic WUE and can be used to assess drought adaptation across species and environments. Jiang *et al.* (2021) applied $\delta_{13}C$ analysis to evaluate WUE in plants along altitudinal gradients, confirming its utility in ecological and agronomic research.

Conclusion and future perspectives

Hemp demonstrates considerable resilience to drought and heat stress through a combination of morphological, physiological, and biochemical adaptations. Its deep rooting system, dynamic leaf morphology, efficient stomatal regulation, and robust photoprotective mechanisms enable it to maintain metabolic stability under environmental extremes. Stress responses vary across growth stages, with the flowering phase being particularly vulnerable to temperature and water deficits that can impair flower development and cannabinoid biosynthesis. Effective management strategies such as genotype selection, seed priming with gibberellic acid, precision irrigation, soil amendments, and microclimate control have shown promise in enhancing hemp's tolerance to abiotic stress. Advanced monitoring tools like Raman spectroscopy and carbon isotope analysis further support early detection and adaptive management. As climate challenges intensify, hemp's hardiness and adaptability position it as a valuable crop for sustainable cultivation in arid and semi-arid regions, warranting continued research into its stress physiology and genetic improvement. More research needs to be done to understand.

Author contributions

Thembilihle Mhlahlayazi: Author wrote the original draft, Visualisation, Conceptualisation, Methodology, Formal analysis. Mcebisi Maphosa: Supervision, Reviewing and Editing. Rutendo Zishiri: Proof reading and document formatting; Mhuru Emmanuel: Reviewing and editing. All authors agreed to the final draft of the manuscript.

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