



## Influence of drought and heat stresses in fodder legumes productivity and nutritive value

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### Article info

Article history:

Received 28/02/2023

Accepted 19/05/2023

Keywords: Fodder legumes, drought, heat stress, productivity, nutritive value



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**Conflict of Interest:** The authors declare no conflict of interest.

### Abstract

Plants are often subjected to several environmental constraints in the field, often simultaneously, which significantly affect their productivity. Among these constraints, water deficit and heat stress are the main constraints limiting plant yield in the arid regions of the Mediterranean basin. Both of these abiotic factors are exacerbated by climate change. Fodder legumes provide a rich resource of plant nutrition to human diets, and are vital for food security and sustainable cropping. Numerous biochemical, molecular, and physiological responses are evoked by drought and heat stresses, influencing the fodder crop yield and nutritional value. When plants are water stressed, they are unable to maintain good growth and produce high yields. Drought also reduces the protein content of the plants, which can lead to a decrease in forage quality. Heat can negatively affect the productivity of forage legumes. High temperatures can cause heat stress which can lead to decreased photosynthesis and reduced productivity. In addition, high temperatures can result in decreased forage quality and increased nutrient losses. Exposure to combined water stress and heat can reduce the protein, fiber and mineral content of forage legumes and can also reduce their digestibility. This review summarizes the current status of the effects of drought and heat stresses on forage crops productivity and fodder quality.

## 1. INTRODUCTION

According to UN estimates, the global human population will reach 9 billion by 2050, leading to an unprecedented rise in demand for animal-based food (National Research Council, 2015). As a result, the demand for food items like meat and vegetables is growing at the same time. Grain and forage legumes make up about 15% of the world's cultivable land and are one of the most important sources of protein for human consumption and animal feed (Vance et al., 2000). Changes in centralizations of carbon dioxide and other ozone depleting substances have made worldwide surface air temperatures climb by around 0.8°C throughout the past 100 years (IPCC, 2022). Variation in temperature levels and water

shortage events, will be more important in future climates. Climate change and weather variability pose a threat to food security, which necessitates immediate consideration, particularly in geographical regions where agriculture is heavily dependent on rainfall (Khanal and Mishra, 2017). According to Wheeler and Von Braun (2013), recent climate changes pose a global threat to the availability of sufficient food for both humans and animals. Therefore, it is essential to evaluate forage crops yields and nutritive values in light of the inevitability of climate change. Livestock provides human nutrition and food security and contributes approximately 40% of global agricultural production value (Smith et al.,

2008). Cereal crops have been utilized as ruminant animal feed for many centuries due to their high dry matter production. However, due to their low protein content, they are frequently regarded as low-quality forage sources. Forage legume crops, on the other hand, provide livestock with high-quality nutrition and fodder for animals.

Alfalfa (*Medicago sativa* L.), a perennial legume, is currently the most common and commercially grown source of forage and feed in many countries. It is grown worldwide in dry tropical and temperate regions (Yadav et al., 2021), when it yields the most in its second year of cultivation. The most important traits in alfalfa improvement are thought to be forage quality and yield, lodging resistance, and early spring vigor (McCord et al., 2014). Additionally, alfalfa plants can fix up to 350 kg N ha<sup>-1</sup> (Carlsson and Huss-Danell, 2003). Other vegetable harvests, like Austrian winter pea (*Pisum sativum* subsp. *Arvense*, *Trifolium repens* L.'s white clover, *Melilotus albus* L.'s sweet clover, and *Arvense* L.'s arvense) have all been popular in various parts of the world.

The annual legume soybean, on the other hand, is domesticated primarily for its high oil and seed protein content (Patil et al., 2017). Soybean (*Glycine max* (L.) Merr.) has a long history of being developed as a scrounge crop (Blount et al., 2009). The first-time soybean acreage for grain in the United States exceeded soybean acreage for forage was in 1941 due to the rising demand for soybean meal and oil (Nielsen et al., 2011). However, soybean cultivation as a forage crop has gained popularity over the past three decades. It has many advantages as a forage crop, including a high protein content at the seed-filling stage, a wide range of harvestable growth stages, effective cover to reduce soil erosion, and a wide range of adaptability to various climate zones (Asekova et al., 2016). Soybean is estimated to fix 79 kg N ha<sup>-1</sup> on average (Salvagiotti et al., 2008). Soybean forage harvested at R5 (seed development) and R7 (beginning of maturity) growth stages which has the best combination of high protein, low fiber, and more digestible energy, has been deemed ideal for animal feed (Asekova et al., 2016).

To meet global food and feed requirements in light of current climate change scenarios, it is essential to have a comprehensive understanding of how plants respond and adjust their metabolism when there is less water available (Anjum et al., 2017; Abdelrahman et al., 2018).

Stressors in the environment like drought and extreme temperatures have a negative impact on plant productivity. To adapt to these stresses, tolerant plants use a variety of morpho-physiological and molecular processes (Ullah et al., 2018). Plants transcriptome, proteome, and metabolome are all altered due to these changes, which affect cellular biosynthesis and degradation. Thus, plants trigger under environmental constraints, various pathways such as secondary metabolite synthesis, phytohormones and ROS signaling, (Tardieu et al., 2014; Jogawat et al., 2021; Yadav et al., 2021).

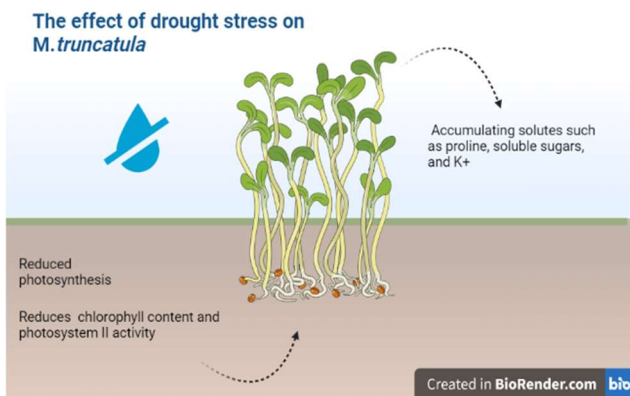
## 2. BIODIVERSITY OF FORAGE LEGUMES RESPONSES TO DROUGHT STRESS

Drought is an environmental stressor that has a global impact on crop yield and can result in a 50%–70% decrease in crop productivity (Verma et al., 2014). To ensure food supply in the event of future climate change, it is necessary to understand the physiological responses of plants to stress. The quantitative and qualitative aspects of growth, production, and crop yield are severely impacted by drought stress. Reduced nutrient supply and cellular toxicity, affects the crop's normal physiological function (Ullah et al., 2018). When soil and atmospheric humidity are low and the surrounding air temperature is high, drought stress occurs. According to Lipiec et al. (2013), this state is the outcome of an imbalance between evapotranspiration flux and soil water intake.

When selecting suitable forage legumes for agronomic productions under conditions of anticipated climate change, it appears that the effect of brief drought on the nutritive value of legumes is less important than other properties (Das et al., 2016). Changes in the pool of sugars used for signaling cellular processes or as substrates for biopolymers like cellulose, starch, and proteins are another effect of a lack of water on carbon metabolism (Liu et al., 2013).

A severe drought resulted in an increase in water soluble carbohydrates (WSC) concentrations and a decrease in fiber concentrations, which may have made the herbage easier to digest. Additionally, the proportion of crude protein (CP) to WSC, a pointer for N use, was more modest under a dry spell and which could subsequently improve the ruminal N maintenance and diminish the N excess in ruminates (Küchenmeister et al., 2013). Even in stressful conditions, secondary metabolisms can be a useful tool for preserving the health and productivity of food crops while minimizing losses. Badri et al. (2016), showed high variation within and among *M. truncatula*

natural populations under water deficit. Drought stress dramatically lowers the *M. truncatula* plants leaf water potential and stomatal closure, which inhibits photosynthesis and limits plant growth (Luo et al., 2016). *M. truncatula* plants have developed a range of responses to drought stress, including modifications to tissue structures and gene expression patterns. In addition, regulation of stomatal conductance (Nunes et al., 2008) and epidermal wax accumulation (Zhang et al., 2005) is an effective way for *M. truncatula* plants to cope with drought stress. Furthermore, osmotic and oxidative regulation are also essential in the response of this species to drought stress (Luo et al., 2016). For instance, *M. truncatula* populations adapt to drought tolerance by accumulating solutes such as proline, soluble sugars, and K<sup>+</sup> (Yousfi et al., 2010) (Fig. 1). Soybean is the most widely produced high-value legume crop, meeting a substantial portion of the world's increasing demand for protein and oil. Drought stress has been identified as a factor restricting soybean yield in various places of the world (Luo et al., 2019). As a result, breeding soybean for drought tolerance is critical to avoiding yield losses (Arya et al., 2021). Drought stress causes a variety of physiological, biochemical, and molecular changes in plants, including decreased



**Fig. 1.** The physiological effect of drought stress on *M. truncatula*. This figure is created with BioRender.com.

photosynthesis (Wang et al., 2018), oxidative stress caused by the accumulation of reactive oxygen species (ROS) (Ahmad et al., 2014), changes in enzyme and other cellular compound metabolism (Kapoor et al., 2021), and transcriptional changes (Jorge et al., 2020). These alterations are reflected in crop performance traits such as reduced stem development and plant height, leaf withering and senescence, altered root growth, and decreased yield (Ye et al., 2018).

### 3. VARIATION OF FORAGE LEGUMES PRODUCTIVITY UNDER HEAT STRESS

Heat stress, similar to drought, harms the vegetative stages of plant growth, which may result in significant yield losses for forage crops. Heat stress-related incidents are becoming a significant issue in light of global climate change and may pose a significant threat to the world's food security (Bitá and Gerats, 2013). Among the changes expected in the new climate, all prediction models consensually forecast a 2–4°C increase in temperature over the next century (Tadross et al., 2007). Plants may exhibit morphological and physiological changes that differ in response to salt and drought stresses, but similar responses may be seen. Heat stress challenges key physiological, biochemical, and other essential metabolic processes in plants, resulting in substantial yield losses (Jha et al., 2017). Under drought stress, photosynthesis inhibition by the closure of stomata causes the unbalance between the Calvin cycle and light reaction leading to less diffusion of CO<sub>2</sub> into the leaves (Chaves et al., 2008). On the other hand, heat stress decreases photosynthesis by affecting biochemical reactions within plant tissues (Allakhverdiev et al., 2003). According to Mahoney (1991), peas usually grow at a temperature of 15–20°C, and the intensity, duration, and timing of the heat exposure influence the plant's response to heat stress. Moreover, the heat stress in peas can be divided into two stages: the vegetative stage and the reproductive stage. At the cellular level, heat stress causes membrane protein denaturation, enzyme activation in mitochondria and chloroplasts, changes in membrane permeability and integrity, resulting in reduced ion flux, electrolyte leakage, changes in relative water content (RWC), toxic compound production, and a general disruption of homeostasis that reduces cell viability (Nijabat et al., 2020). Heat stress imposes oxidative stress to plant and provoke higher generation of ROS, including free radicals (O<sub>2</sub><sup>•-</sup> and OH<sup>•</sup>) and non-radicals (H<sub>2</sub>O<sub>2</sub> and <sup>1</sup>O<sub>2</sub>) mainly localized in the mitochondria, chloroplast and peroxisomes, with secondary sites in endoplasmic reticulum, cell wall, cell membrane and apoplast (Armenta-Medina et al., 2021). It is well-known that heat shock proteins (HSPs) play a vital role in plant heat tolerance by maintaining the function of proteins and integrity of various bio-membranes under heat stress (Ohama et al., 2016). Different legumes are significantly affected by heat stress, which results in reduced shoot

growth, root number and diameter, reduced stomatal conductance and leaf water content, leaf curling, wilting, and yellowing (Sehgal et al., 2017).

For vegetable pea growers, heat stress phase is more difficult during the vegetative. They choose short-duration picking varieties of peas, ideally in September and October (with a predominant temperature >30-32°C) in most Asian nations.

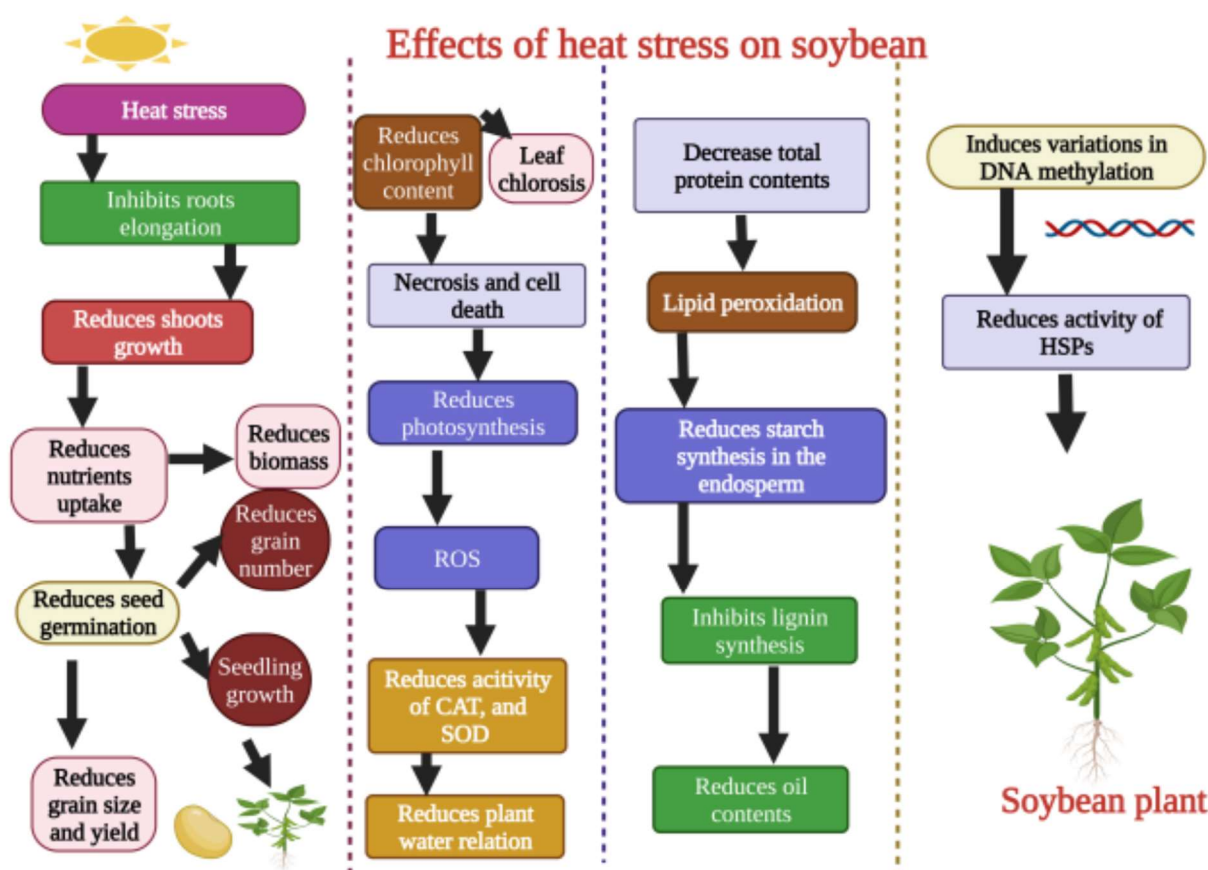
Cowpea [*Vigna unguiculata* (L.) Walp] is a crucial protein-rich nutritional crop that is planted extensively throughout Africa, Southeast Asia, and Latin America. Heat stress has a severe negative impact on cowpea development and yield in the main cowpea growing regions (Jha et al., 2017). In a RIL population, Lucas et al., (2012) revealed five genetic loci that accounted for 11.5-28.1% of the phenotypic variation governing cowpea heat tolerance. These genomic areas are syntenic with the soybean genome, according to a comparative genome analysis, and they contain genes for HSPs, heat-shock transcription factors,

and proline transporters, all of which improve cowpeas' ability to withstand heat.

On the other hand, many studies have observed yield loss when soybean was exposed to short-term and long-term heat waves (Hatfield and Dold, 2019; Zandalinas et al., 2020) and season-long warming (Ruiz-Vera et al., 2013). Heat stress significantly decreased the germination of soybean seeds and affects its root growth, alters morphology, and restricts elongation (de Moraes and Gusmao, 2021) (Fig. 2). Additionally, it decreases the ability of the plants to absorb carbon, damages membranes and causes stomatal closure (Farooq et al., 2009). Heat stress impairs the metabolic pathways which results in altered plant growth (Liu et al., 2014).

#### 4. DIVERSITY OF FORAGE LEGUMES RESPONSES UNDER COMBINED EFFECTS OF DROUGHT AND HEAT STRESS

The effects of a combination of different stress factors on the functioning traits of plants result in distinct responses as a result of a synergistic or



**Fig. 1.** Effects of heat stress on morphological, physiological, biochemical, and molecular level of soybean. Heat stress affects the shoot growth, root growth, reduces seed germination, produces reactive oxygen species (ROS), decreases the activity of antioxidant enzymes, and total protein contents. Heat stress causes changes in DNA methylation and gene's function (Jianing et al., 2022). This Figure is created with BioRender.com.

antagonistic effect of both stress factors (Bansal et al., 2013). Particularly in tropical and subtropical locations, plant development and performance rapidly deteriorate under field conditions when water shortage and high temperature coexist (Zandalinas et al., 2017). Plant adaptation to the stress combination is governed by the interaction of the two stresses and controlled by distinct signaling pathways that may interact, inhibit one another, or be prioritized differently by the plant when two stresses co-occur (Zandalinas et al., 2017).

It is imperative to investigate forage crop responses to combined heat and drought stresses (Zandalinas et al., 2017) given the possibility of an increase in the frequency of drought and heat stress (IPCC, 2022).

Xu et al. (2020) studied the combined effect of drought and heat stress on photosynthesis, pigments, and xanthophyll cycle particularly in two *M. sativa* varieties ('Deqin' and 'Algonguin'). Results revealed that the values of the net photosynthetic rate demonstrated a significant decrease under stresses. The combined effects of both the stresses were found to be much stronger than their individual effects (Dreesen et al., 2012; Rollins et al., 2013). Nelimor et al. (2019) found a highly positive correlation between grain yield of maize under heat and combined drought and heat stresses, which indicated that heat-tolerant genotypes would most likely tolerate combined drought and stress. Plant responses could be different under individual and combined stresses (Chen et al., 2012; Prasch and Sonnewald 2013). According to Rashmi et al. (2014) Chickpea (*Cicer arietinum* L) under individual and combined stress damaged membranes, and decreased cellular oxidising ability, stomatal conductance, PSII function and leaf chlorophyll content; damage was greater under combined stress. Leaf rubisco activity increased with heat stress, decreased with drought stress and decreased severely with combined stress. Sucrose and starch concentrations decreased in all seeds through reductions in biosynthetic enzymes; reductions were greater under combined stress.

## 5. INFLUENCE OF DROUGHT AND HEAT STRESS ON FORAGE QUALITY

Legumes are crucial for the development of forage due to their high nutritional content, particularly their proteins and minerals (Ca<sup>2+</sup> and Mg<sup>2+</sup>). Climate change has a significant impact not only on the yield and nutritive value of forage but also on the health of livestock (Craine et al., 2010; Baumgard et al., 2012). Forage crops may be

subjected to various abiotic stresses as a result of the adverse climate, which could have an impact on forage quality. The chemical composition and digestibility of forage crops grown in various parts of the world have been the subject of a number of studies that have looked at how environmental factors like light, temperature, drought, and soil nutrients affect these aspects (Hopkins and Del Prado, 2007). Heat and drought stress impair the plant's photosynthetic ability, resulting in altered sugar production and translocation. Changes in sugar and mineral remobilization alter reproductive development, resulting in a shorter grain-filling time (Sehgal et al., 2018). The combined effect of heat and drought stress has been found to aggravate the condition, increases the harmful effects on growth and severely limits maize yield (Kebede et al., 2012). Each degree rises in temperature above 30°C resulted in 1% reduction in maize yield under optimal growth conditions, 1.7% under the water deficit and up to 40% or more under the combined stresses (Lobell et al., 2011). Finally, changes in photosynthesis, hormone levels, assimilated reserves and remobilization, and grain-filling length all have an impact on the physical and nutritional composition of mature grains. Drought and heat are the most important constraints to chickpea production globally. It is estimated that drought and heat stresses together account for about 50% of the yield losses caused by abiotic stresses. The economic value of these losses is estimated at US\$ 1.28 billion (Zandalinas et al., 2017). Chickpea is a dry and cool season crop, largely grown rainfed on residual soil moisture after the rainy season. The progressively receding soil moisture conditions often lead to moisture stress towards end of the crop season (terminal drought) causing heavy yield losses. Development of cultivars that can escape (early maturity) or avoid/tolerate (greater extraction of water from the soil, enhanced water use efficiency) terminal drought has been a major objective in chickpea breeding program. Drought and heat stress, when combined, reduce leaf water content more severely. This results in early leaf wilting, acute chlorosis, and membrane damage (Awasthi et al., 2014). Various studies, for example, in chickpea (Awasthi et al., 2014); lentil (Sita et al., 2017); and barley (Sehgal et al., 2017) corroborate these results. Though the impact of each of these stresses on plants varies depending on their strength and duration, some frequent signs include a reduction in vegetative biomass, reproductive growth, and yield-traits. When

applied separately, the effects of heat and drought stress may differ; for example, heat stress during seed filling may accelerate or even suppress the seed filling process, reducing the duration of filling to inhibit the accumulation of various reserves (Chakraborty *et al.*, 2013). As shown in wheat (Shah and Paulsen, 2003; Farooq *et al.*, 2017), chickpea (Awasthi *et al.*, 2014), and lentil (Awasthi *et al.*, 2014), cumulative shocks reduce seed-filling length more than individual treatments (Sehgal *et al.*, 2017). Both constraints can occur concurrently after anthesis, limiting seed-filling length and resulting in poor-quality grains (Sehgal *et al.*, 2017), leading to a significant drop in seed dry weight, seed numbers, and starch content (Balla *et al.*, 2011). In response to combined heat and drought stress, the rate of transport of non-structural carbohydrates in endosperm tissue falls (Kebede *et al.*, 2012). Starch accumulation is severely reduced due to combined stressors applied during seed filling, which has been ascribed to more dramatic inhibition of starch synthesizing enzymes, as seen in chickpea (Awasthi *et al.*, 2014) and lentil (Sehgal *et al.*, 2017), and seeds become wrinkled as a result. Heat and drought stress can reduce the nitrogen pool by lowering free amino acids, which contain numerous transfer chemicals associated to nitrogen metabolism and other osmotic molecules (Prasad *et al.*, 2008; Awasthi *et al.*, 2014). The reaction to dual stress is crop specific; for example, seeds from soybean plants treated to dual stress had higher protein contents but lower oil contents than controls/individual stresses (Dornbos and Mullen, 1992). Since heat and drought stress often occur simultaneously and pose a significant risk to grain crops in the future, additional research is needed to assess the effects of these two stresses on processes at different organizational levels that affect seed production and quality in different crops.

## 6. CONCLUSION

As seen in this review, drought and heat stresses have significant effects on legume forage productivity and nutritional value. Further work is needed to select new varieties of forage legumes with high tolerance to both combined stresses.

## ACKNOWLEDGEMENTS

This study was financially supported by the Tunisian Ministry of Higher Education and Scientific Research (LR15 CBBC02).

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