The Impact Of Climate Change-Induced Abiotic Stresses on the Nutritional Quality of Legume Seeds

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Highlight

Herein, we analyse the impact of drought, heat and elevated CO_2 on the nutritional quality (protein, amino acids, minerals, carbohydrates, lipids, and bioactive compounds) of multiple legume crops.

Abstract

Legumes are integral to agricultural sustainability, offering multifaceted benefits ranging from enhanced yields to companion crops to improved soil health. Despite their recognized advantages, challenges such as technological lock-ins, limited breeding resources, and adverse environmental conditions pose threats to their cultivation. Herein, the complex interaction between climate change stressors — specifically drought, high temperatures, and elevated CO_2 levels — and their individual and combined impacts on the nutritional quality of legumes will be discussed. This topic has not been reviewed very often for multiple legume crops, despite its importance under climate change. This review critically examines the impact of environmental stresses on the nutritional quality of legume seeds and explores the underlying regulatory mechanisms, encompassing protein, amino acids, minerals, carbohydrates, lipids, and bioactive compounds. Key insights indicate a general need to shift legume cultivation practices, and the necessity of field studies beyond controlled environments for results that are more readily translated to the target population of environments for legume cultivation.

Introduction

At the agricultural level, the introduction of legumes in cropping practices positively impacts the production of calories and important micro and macronutrients, the gross value of crop sales and food access at lower environmental cost, since their cultivation requires fewer inputs, improves soil quality, and reduces environmental degradation compared to other crops (Poore and Nemecek, 2018; Saget et al., 2020; Costa et al., 2021). For example, legumes can fix atmospheric nitrogen (N) in symbiosis with the soil bacteria rhizobia and increase soil carbon (C) content, consequently increasing the yield of subsequent crops and reducing the need for chemical fertilisers (Soares et al., 2019a). Another economic advantage of including legumes in the rotation cycle is their effect on reducing the incidence of pests. Protein crops break the cycles of soil-borne diseases of cereals, so fewer inputs (pesticides) are needed on the following crop (Jalli et al., 2021). Despite all of the evidence supporting the beneficial role of legumes in the agri-food chains several factors have led to the abandonment of legume production in Europe (Balázs et al., 2021). These factors include technological lock-ins (such as lack of specialised machinery or specific biocontrol agents), difficulties in quantifying the value of ecosystem services (ES), limited breeding material, low policy support, and a loss of empirical and technical knowledge on legume cultivation (Mamine and Farès, 2020). The area dedicated to grain legumes in Europe has declined from 5.8 million hectares (4.7% of the arable area) in 1961 to approximately 1.5 million hectares (1.2% of the arable area) in 2021 (FAO, 2023). A major driver of this shift is the comparative advantage of producing starch-rich cereals over protein-rich grain legumes, influenced by policy support and industrialized agriculture practices. However, contexts are changing, and the new Common Agricultural Policy (CAP) reform for 2023-2027, a key policy of the European Union, is set to support farmers in crop diversification. It evidences the urgency of providing good jobs in the primary sector while fostering sustainable agricultural practices with legumes being key to achieving these goals.

Legume seeds hold great health benefits, serving as a rich source of essential nutrients including protein, carbohydrates, dietary fibre, vitamins and minerals (Kumar et al., 2022). Specifically, legumes are particularly dense in certain vitamins and minerals, specifically, folate (vitamin B9), thiamine (vitamin B1) and niacin (vitamin B3) (Kamboj and Nanda, 2018; Andac-Ozturk et al., 2022); and iron, zinc, magnesium, potassium, phosphorus and calcium (Margier et al., 2018). Additionally, bioactive peptides isolated from legumes' protein have a remarkable potential in pharmacological applications, and these short sequences have been identified in lupin, soybean, chickpea, pea, cowpea and bean (Kamran and Reddy, 2018; Serventi and Dsouza, 2020). Legumes are also rich in other bioactive compounds, oftentimes considered as antinutrients due to their potential to cause adverse effects when consumed in excess (Salim et al.,

2023). These include the potential to affect the integrity of intestinal epithelial cells, reduce the absorption of nutrients, or impair protein and starch digestion (Nath et al., 2022). However, when ingested within recommended intake levels and following proper processing, they have been shown to possess beneficial health properties (Shi et al., 2004; Singh et al., 2017; Ferreira et al., 2021; Geraldo et al., 2022; Duarte et al., 2024). Specifically, lectins and saponins have the potential to act as anticarcinogenic agents and have immune modulatory activity (Salim et al., 2023), while phytates and phenolics are potent antioxidant agents, with the potential to chelate toxic metals and prevent harmful Fenton reactions (Petroski and Minich, 2020). Additionally, there are some compounds which don't possess any health benefits, such as tannins. These polyphenolic compounds form protein complexes, reducing protein digestibility and inactivating digestive enzymes (Zhang et al., 2023).

Europe's plant-based food industry is growing, and the demand for legume-based products is increasing, as they are affordable protein sources (Moreira et al., 2022). Despite being generally well-adapted to different edaphoclimatic conditions, legumes are very sensitive to climatic extremes, suffering major impacts at the production and productivity levels (Sennhenn et al., 2017; Habib-ur-Rahman et al., 2022; Kudapa et al., 2023). Unpredictable heatwaves or extreme droughts are currently major challenges to farmers (Churchill et al., 2022). **Drought** stands out as a primary constraint restricting the production of food legumes. The adverse effects of drought are particularly critical during grain development stages, resulting from impaired germination and a decrease in photosynthetic activity, along with reduced assimilate translocation and carbon (C) fixation, and leading to substantial yield losses (Smith et al., 2019; Sachdeva et al., 2022). In addition to drought, both heat and cold exert significant influence on the phenology and growth dynamics of crops (Bhandari et al., 2019). Among these factors, **extreme temperatures** pose one of the most severe environmental risks to crop production, with detrimental effects on legume yield, leading to decreased pod production, smaller seed sizes, and lower harvest indices (Balko et al., 2023; Burroughs et al., 2023). Notably, the accumulation of greenhouse gases is rapidly raising global temperatures, as evidenced by future climatic projections that highlight a pronounced correlation between elevated temperatures and increased atmospheric CO_2 levels (Roy et al., 2024; Shah et al., 2024). Consequently, elevated CO2 (**eCO_2**) is acknowledged as the primary driver of global climate change. While eCO_2 levels appear to have a beneficial impact on legume productivity by enhancing plant photosynthetic rate, growth, and yield (Ainsworth and Long, 2021), their interactive effects with other stressors are intricate and can lead to unpredictable outcomes. Furthermore, the combined effect of heat and drought can severely impair crop growth and development (Cohen et al., 2021). It is also crucial to recognize the dependency of these responses on genetic variability and the

ability of each genotype to form symbiotic relationships with rhizobia strains (Quirós-Vargas et al., 2021; Soares et al., 2021; Bellido et al., 2023). Therefore, rather than solely focusing on the individual effects of each stressor, there is a growing urgency to investigate their combined impact, albeit research efforts often lag behind the accelerated pace of climate change (Köhler et al., 2019).

Regrettably, adverse environmental conditions not only disrupt plant physiology and reduce productivity but also alter the nutritional profile of crops, as these traits are closely linked. Seed morphological characteristics, such as seed size, are interconnected with seed quality and further influenced by environmental factors (Mašková and Herben, 2018). Hence, while the scientific community has traditionally emphasized the impact of climate change on crop production, recent attention has shifted towards understanding the nutritional composition of crops, including legume seeds. For instance, studies under elevated eCO_2 conditions have extensively explored the impact on seed protein, noting a general decrease, but the mechanisms behind this effect are yet to be fully defined (Palacios et al., 2019). These alterations may lead to fluctuations in nutrient availability, thereby affecting the adequacy and diversity of diets, particularly among vulnerable populations. Moreover, fluctuations in legume quality could disrupt food systems, exacerbating existing challenges related to food access, affordability, and nutritional adequacy (Losa et al., 2022). Current production systems will soon become inadequate to cultivation due to some areas becoming less viable for production. The adjustment of the range and location of cultivation of legumes is a possible mitigation mechanism to the upcoming scenarios (Hummel et al., 2018). However, comprehensive research efforts are imperative to gather the necessary data on the multifaceted impacts of climate change on legume seeds nutritional quality.

Protein

Legumes play a crucial role as a protein source owing to their significant protein content, ranging between 19-35% of the dry matter (Margier et al., 2018; Kiersnowska and Jakubczyk, 2022; Grdeń and Jakubczyk, 2023). For this reason, they hold a promising solution to the pressing challenge of delivering high-quality, plant-based, dietary protein to the expanding global population, especially in the global south (Singh et al., 2022). Since the nutritional quality and functionality of legume proteins are influenced by their solubility, they are traditionally classified according to this property: albumins dissolve in water, globulins are soluble in saltwater solutions, and prolamins dissolve in ethanol/water solutions (Rubio et al., 2014). The solubility of proteins often correlates with their digestibility, which refers to the amount of digested proteins available for absorption (Sá et al., 2020). Water-soluble proteins (e.g., albumins) are generally more digestible compared to fibrous or insoluble proteins (e.g., collagen), which are more resistant to

digestion. However, other factors other than solubility can also affect protein digestibility, including, the above mentioned antinutritional factors and processing methods (Arnal et al., 2025).

Nonetheless, the decline in protein during drought stress appears linked to hindered protein biosynthesis due to constraints on nitrogen (N) partitioning and fixation in water-scarce environments (Farooq et al., 2016). In Table 1, studies concerning the effect of different levels of drought stress on protein content of grain legumes are discriminated. Several authors have observed decreased seed nitrogen and protein content across various legume species, including **common bean** (Ghanbari et al., 2013), **soybean** (Nakagawa et al., 2018), **mung bean** (Yagoob and Yagoob, 2014), **lupin** (Khalil et al., 2010), **faba bean** (Al-Suhaibani, 2009), and **chickpea** (Ashrafi et al., 2015), following drought stress. In **soybean** seeds, the decrease in protein content under drought stress is correlated with the downregulation of protein storage proteins encoded by the *Gy1*, *Gy2*, *Gy4*, and *Gy5*, which belong to the globulin family and by β-conglycinin, regulated especially by abscisic acid. It also correlates with the upregulation of genes involved in protein degradation, specifically *CysP1* and *CysP2* that encode cysteine protease proteins, as well as cysteine and aspartate proteinases that target proteins stored in vacuoles, converting them into usable nutrients (Nakagawa et al., 2018; Sheteiwy et al., 2021). This regulation was observed when drought stress was applied during the critical seed-filling stage, as observed both when two soybean genotypes were tested in controlled glasshouse conditions by maintaining soil moisture at 50% of the pot's water-holding capacity (Nakagawa et al., 2018) as well as when one genotype was grown under field conditions with irrigation withheld for two weeks at seed development (90 days from sowing) (Sheteiwy et al., 2021). Accordingly, Medeiros et al. (2024) found no significant changes in protein content when testing two **chickpea** cultivars (Desi and Kabuli) under different water supplies (90% to 25% field capacity) from 15 days after germination. In contrast, Ashrafi et al. (2015) reported increased protein content in two chickpea cultivars (Azad and Bivanji) under severe drought stress, though genotype itself was not a significant factor in either study. These variations suggest that drought severity, also plays a critical role in determining protein content under stress conditions, adding complexity to our understanding of how legumes regulate protein content under drought. Similarly, contrasting findings regarding **common bean** have been reported, with certain cultivars exhibiting higher protein content under water deficit, being hypothesized that this could be due to the *de novo* synthesis of drought-related proteins as part of the plants' defence mechanism (González de Mejía et al., 2003).

Heat stress also induces significant alterations in seed protein content across various legume crops, including **chickpea** (Benali et al., 2023), **lentil** (Sita et al., 2018), **pea** (Mession et al., 2013), **mung bean**

(Batra et al., 2023), **common bean** (Hummel et al., 2018) and **soybean** (Krishnan et al., 2020). As shown in Table 1, from 32 ºC to 42 ºC (day temperature) severe reductions are generally observed, which can be attributed to a declined rate of protein synthesis and increased protein degradation (Batra et al., 2023). Furthermore, high temperatures not only reduce protein content but also affect its quality, though reports vary. Specifically, in Batra et al. (2023), 13 **mung bean** genotypes were exposed to temperatures of 34°C to 36°C and 38°C to 40°C, with high temperatures leading todecreased albumins and globulins and increased glutelins and prolamins. Sensitive genotypes showed a notable decline in protein content, whereas tolerant genotypes were less affected (Batra et al., 2023). On the other hand, Priya et al. (2023) examined two mung bean genotypes, one heat-sensitive and one heat-tolerant, under day/night temperatures of 42°C/30°C compared to control conditions of 35°C/25°C, finding significant reductions in all storage proteins. Similar adverse trends in storage protein patterns have been observed in **lentils**, where two genotypes exposed to heat stress (33°C/28°C vs 28°C/23°C) during the seed-filling stage experienced significant protein reductions. The extent of protein loss differed between genotypes, with one genotype showing a more pronounced decline (Sita et al., 2018). Additionally, in two **soybean** genotypes with contrasting tolerance to high growth temperatures, heat stress has been found to reduce the levels of lipoxygenase, the β-subunit of β-conglycinin, and sucrose binding protein (Krishnan et al., 2020). The simultaneous occurrence of heat and drought stress further exacerbates protein declines in **lentil** and **chickpea** by disrupting protein biosynthetic pathways and/or reducing precursors availability (Awasthi et al., 2014; Sehgal et al., 2019; Choukri et al., 2020; El Haddad et al., 2021; Samineni et al., 2022). Overall, heat stress negatively impacts protein content and quality across legume species, with varying effects based on genotype and stress interactions.

Concomitantly, eCO_2 (600-800 ppm, Table 1) appears to impair N metabolism, protein content, and production quality in legumes, but significant genotypic variability exists (Xu et al., 2016; Lamichaney et al., 2021, 2022). This phenomenon has been attributed to the dilution effect brought about by carbohydrate enrichment at the expense of the N pool, coupled with increased protease activity in seeds (Saha et al., 2015). However, some studies report conflicting results, with protein content increasing or remaining unaffected under eCO_2 conditions in certain varieties of **soybean**, **common bean**, **pea**, and **faba bean** (Soares et al., 2019b; Garmendia et al., 2022; Deuchande and Vasconcelos, 2024).

Amino acids

Legumes are characterised by a high content of the essential amino acids, leucine, lysine and valine, but also with satisfactory amounts of phenylalanine, histidine, isoleucine, threonine, and tryptophan (Margier et al., 2018; Wang et al., 2024). Methionine and cysteine are sulfur-containing amino acids, and their levels are usually low in grain legumes, however, they have an important role in the nutritional quality of some species, such as common bean, given their positive correlation with protein quality and seed storage (López-Pedrouso et al., 2014; Viscarra-Torrico et al., 2021).

As adverse environmental conditions can lead to alterations in the composition of protein fractions, they impact amino acid concentrations, exacerbating concerns regarding human nutrition in challenging environments. In Table 2, the effect of different drought levels, of heat stress (33 ºC during daytime) and of eCO_2 (550 ppm) on legume's amino acid profile is summarised. These studies refer both to free and protein-bound amino acids, where free amino acids are those that exist in a soluble form and protein-bound amino acids are those that are incorporated into proteins and peptides (Peace and Gilani, 2005).

For instance, Smith et al. (2019) investigated 12 **bush bean** genotypes, including drought-tolerant and commercial checks, in a field trail under irrigated and rainfed conditions to induce terminal drought. Drought was imposed by suspending furrow irrigation after four initial irrigations, leading to water limitation from flowering to maturity, with the drought-stressed plants exhibiting increased concentrations of protein-bound amino acids such as glutamine, aspartic acid, leucine, and glycine. Similarly, both kabuli and desi **chickpeas** showed significant increases in the free amino acids fraction like arginine, glutamic acid, glycine, isoleucine, leucine, and proline under drought conditions (withholding water for 14 days at the pod-setting stage, when the plants had developed 7 to 9 pods per plant). However, the concentration of phenylalanine, tyrosine, tryptophan, valine, alanine, and histidine was decreased, with desi varieties experiencing more pronounced declines compared to kabuli (Nayyar et al., 2006), suggesting potential differences in adaptive strategies among **chickpea** cultivars. Nevertheless, kabuli seeds had significantly higher levels of arginine, glutamic acid, glycine, and proline compared to the desi type (Nayyar et al., 2006), highlighting the diverse nutritional profiles between **chickpea** varieties.

Heat stress also impacts amino acid concentrations in legume grains, with changes influenced by genotypic variability. One heat-tolerant **lentil** genotype (FLIP 2009) demonstrated increases in the free fraction of alanine, glycine, isoleucine, leucine, lysine, and proline under heat stress (33/28 ºC) compared to control conditions (28/23 ºC), whereas the heat-sensitive genotype (IG4242) exhibited decreases in all amino acids (Sita et al., 2018). Additionally, two **lentil** genotypes - a drought-tolerant genotype (DPL 53)

and a drought-sensitive genotype (LL699) – grown under drought stress (maintaining soil at 50% field capacity), heat stress (33/28 °C), and combined drought and heat stress, exhibited reductions in nearly all free amino acids that typically increase under heat stress alone, especially in the drought-sensitive genotype (Sehgal et al., 2019).

Similarly, eCO_2 can lead to a reduction in the amino acid content of legume seeds. For instance, studies have demonstrated a decrease in seed amino acid content in mature **soybean** plants under eCO_2 conditions (550 ± 30 ppm), when four genotypes were compared (Li et al., 2018). These responses varied depending on the genotype, with significant reductions observed in the free amino acid concentration of asparagine, arginine, phenylalanine, leucine, serine and proline (Singh et al., 2016; Li et al., 2018).

Across all legumes, improving the resilience of protein content and essential amino acids is a critical priority (Jha et al., 2022). This includes increasing the stability of proteins and amino acids, particularly lysine, threonine, and tryptophan (Wu et al., 2024).

Minerals

Legumes stand out as rich sources of essential minerals like iron (Fe), zinc (Zn), magnesium (Mg), and calcium (Ca), playing pivotal roles in fundamental bodily functions such as enzyme activity, bone health, and immune function. In Europe, the recommended dietary allowance of these minerals are as follows: 8-18 mg/day of Fe, 8-11 mg/day of Zn, 310-420 mg/day of Mg and 1000-1200 mg/day of Ca (European Food Safety Authority, 2017). Notably, beans, lentils, and chickpeas, among others, are known for their high Fe and other minerals content, being able to provide between 10-30% of the recommended daily values of these compounds for adults (Didinger and Thompson, 2021). Unfortunately, drought, heat and eCO_2 can lead to a decrease in seed mineral concentrations due to various factors, including: (i) poor nutrient mobility in the soil and reduced mineral uptake resulting from impaired root growth and decreased soil moisture (Samarhah et al., 2004), (ii) reduced mineralization and limitations in the mass flow of nutrients from the soil to the rhizosphere and the xylem flow from roots to shoots (He and Dijkstra, 2014), and (iii) compromised remobilization from vegetative to reproductive tissues (Etienne et al., 2018). Table 3 highlights the main changes registered in legumes' mineral composition due to these conditions.

For instance, in a study comparing 20 newly introduced **chickpea** genotypes for drought tolerance under rainfed and irrigated conditions, six were selected (three drought resistant: Azad, ILC.482 and ILC.1799; three drought susceptible: Hashim, X96, TH62K2 and FLIP.97-219) and all of themexhibited decreased levels of Ca, potassium (K), and sodium (Na) in their grains when exposed to drought conditions. However,

the drought-susceptible experienced greater declines compared to the drought-resistant ones (Rozrokh et al., 2012). Similarly, in the same crop, when testing two **chickpea** cultivars (Desi and Kabuli) under different water supplies (90% to 25% field capacity from 15 days after germination), limited water supply did not affect concentrations of K, Ca, Mg, Zn, manganese (Mn), and boron (B), but it did lead to lower phosphorus (P) concentration (Medeiros et al., 2024). Additionally, eight **common beans** genotypes, including white beans (WA4502-1 and WA4531-17), red beans (Akhtar, D81083 and AND1007) and Chitti beans (KS21486, MCD4011 and COS16), subjected to drought under two irrigation levels (irrigation after 55-60 and 100-110 mm evaporation) showed a reduction in grain P, Fe, and Zn (Ghanbari et al., 2013). On the other hand, Mutari et al. (2023) who investigated the impact of drought stress on navy beans (110 lines) under both drought-stressed and well-watered field conditions in Zimbabwe dry season, when rainfall was minimal, observed an increase in Fe concentration but a decrease in Zn. The mineral increases observed in **chickpea** and **common bean** under drought stress have been linked to their redistribution among different plant organs (Foster et al., 1995; Davies et al., 2000). However, the extent of this effect is not solely determined by genetic factors and the severity of drought stress, as suggested by Mutari et al. (2023), as the specific environmental conditions at the growing site also play a crucial role. For instance, Smith et al. (2019) found that while field drought conditions - induced by irrigating the plants only until flowering and limiting water availability during critical growth stages - reduced the yield of twelve **bush bean genotypes**, they did not significantly affect seed mineral concentrations. This suggests that the response of seed mineral content to drought stress can vary depending on specific environmental factors such as soil type, temperature, and humidity levels.

Besides drought, elevated temperatures have been associated with reduced root nutrient uptake, characterized by decreased root biomass and metabolic rate, or direct damage to roots (Heckathorn, 2013; Huang et al., 2012). For instance, **chickpeas** exposed to high temperatures - both in field studies during the reproductive stage with critical temperatures exceeding 35ºC (Samineni et al., 2022) and in controlled greenhouse conditions (25/15 ºC for control plants vs 32/20 ºC for heat-stressed plants from pod set until maturity; Devi et al., 2023) - showed decreased grain concentrations of P, Ca, Fe and Zn, even among heat-tolerant genotypes. Similarly, **mung beans** (heat-tolerant EC 693369 and heat-sensitive KPS1) experienced significant reductions in P, K, Mg, and Zn when subjected to high-temperatures applied from the beginning of pod set until maturity, with plants grown at day/night temperatures of 42°C/30°C compared to control conditions of 35°C/25°C (Priya et al., 2023). Although the impact of heat stress alone (33/28 ºC day/night, fully irrigated) on **lentil** grain quality in both the drought-tolerant (DPL 53) and drought-sensitive (LL699) genotypes was less pronounced than that of drought stress alone (28/23 ºC,

50% field capacity), concurrent exposure to both stresses intensified reductions in P, K, Mg, Ca, Fe, and Zn content in grains, particularly in the drought-sensitive genotype. This combined stress likely disrupted leaf water relations, inhibiting mineral translocation into developing seeds (Sehgal et al., 2019). Choukri et al. (2020) supported this finding, demonstrating that combined heat and drought stress (late planting without irrigation during the reproductive phase) led to a significant reduction in Fe and Zn concentration across 100 **lentil** genotypes, with the combined stress exerting a more severe effect than heat stress alone. However, recent research by Benali et al. (2023) provided contrasting findings, showing that **chickpea** grain mineral profiles exhibited significant increases in average concentrations of Mg, Mn and Na when subjected to heat (32 ºC) and combined heat-drought stresses (32ºC with no irrigation from the flower initiation phase onward, corresponding to less than 5 mm of rainfall during the reproductive stage). In contrast, no significant effects were observed for K, Ca, Fe, Zn, selenium (Se), and copper (Cu).

Alike heat stress, the impact of eCO_2 on mineral content in different legumes appears to be multifaceted, with varying outcomes observed across studies. For instance, in **pea**, minerals such as P, K, Ca, Mg, Fe, Mn, Zn, Cu, B, and Na remained unaffected by eCO_2, while in **faba bean**, both P and Fe increased, under greenhouse conditions (Garmendia et al., 2022). Conversely, in one **chickpea**, decreases in K and Ca were observed under eCO_2 conditions applied through free air ozone and carbon dioxide enrichment (FACE) rings (Bhatia et al., 2021). Similarly, eCO_2 did not influence P, Ca or Zn concentrations in **common bean** seeds of plants grown in controlled conditions, but it led to decreased concentrations of K, Fe, and Mn, while Mg increased (Soares et al., 2019b). The observed differences are likely attributed to interactions between CO_2 levels and plant genotypes, with certain common bean cultivars showing higher tolerance to mineral impairments induced by eCO_2 and also due to the different methods of CO_2 enrichment (Garmendia et al., 2022; Deuchande and Vasconcelos, 2024).

In **soybean** seeds, exposure to eCO_2 also resulted in dissimilar mineral accumulation patterns among studies, likely influenced by differences in plant genotypes and eCO_2 levels. For example, in a study under Open-Top Chamber conditions, at 550 ppm, Mg, Ca, and sulphur (S) increased, while P and K remained unaffected, and Fe and Zn decreased (Li et al., 2018). However, at 800 ppm, eCO_2 did not influence P, Mg, Zn or Fe concentrations, while K and Mn decreased, and Ca increased, under controlled environment (Soares et al., 2019b). Importantly, the response of soybean mineral concentrations to eCO_2 varied between genotypes, with specific cultivars exhibiting higher concentrations of Fe and Zn compared to ambient CO_2 conditions. However, subsequent FACE studies revealed detrimental effects of eCO_2 on several minerals in **soybean**, including those previously deemed unaffected (Soares et al., 2021). Notably,

minerals such as P, Mg, Fe, or Zn were adversely impacted, while Ca exhibited an increase (Soares et al., 2021). The shift in outcomes observed between controlled and field conditions underscores the need for comprehensive research across diverse environments to fully grasp the complexities of eCO_2 and its interactions with other environmental factors in legume seeds. The few studies on this issue have shown that the combination of eCO_2 with elevated temperature generally restores Fe and Zn concentrations in **soybean** seeds to levels obtained under ambient CO_2 and temperature conditions (Köhler et al., 2021). Some studies have explored genetic markers and gene expression patterns, offering insights into potential approaches for supporting mineral content in legumes amid varying stressors, but such research remains notably limited, hindering the possibility to develop breeding strategies aimed at enhancing the mineral composition of legume crops under adverse environmental conditions. For instance, specific genetic markers have been associated with grain Fe and Zn content in **chickpeas** under drought stress (Samineni et al., 2022), while the upregulation of specific genes encoding ferritins, ferrochelatases, and Fe transporters like *IRT1*, *FER*, and *FRO* have been documented in **chickpeas** and **soybeans** under eCO_2 conditions (Bencke-Malato et al., 2019; Palit et al., 2020; Soares et al., 2021, 2022; Deuchande and Vasconcelos, 2024). On another point of view, studies indicate that Fe and Zn levels in legume crops, such as cowpea and common bean, can be enhanced through agronomic biofortification (Manzeke et al., 2017; 2019; 2020; Huertas et al., 2022). These studies advocate for integrated nutrient management approaches that focus not only in improving the nutritional quality of the seeds but also on enhancing their resilience to environmental stressors.

Given the results collected and presented in the tables, mineral content in legumes shows both crop-specific and mineral-specific responses. Across eCO_2, drought, and heat conditions, there is a consistent trend of mineral reduction, particularly for Ca, P, K, and Mg. While Fe and Zn show more variable responses, they often increase under terminal drought (as in common bean) but decrease under heat stress, particularly in lentil and chickpea. These trends likely stem from reduced transpiration, disrupted root function, altered photosynthetic demand, and impaired transport protein function under stress conditions.

Carbohydrates

Legumes are good sources of complex carbohydrates, including dietary fibre. Among the different starch categories, resistant starch - considered a type of dietary fibre - has high potential in health and functional foods development (Sempio et al., 2024). The recommended intake of resistant starch is of at least 25 grams/day (Baptista et al., 2024) and, on average, legumes contain about 65-72% total carbohydrates by

weight on a dry basis, of which 85% is composed of starch, while dietary fibre constitutes anywhere from 10-20% (Keskin et al., 2022). However, unfavourable environmental conditions have the potential to disrupt carbohydrate metabolism in legumes, leading to changes in seed accumulation of starch, fibre, and sugars (Table 4). In two **common bean** cultivars, Pinto Saltillo and Rarámuri, which are adapted to the erratic rainfall conditions of semiarid regions and exhibit distinct levels of drought tolerance, changes in carbohydrate composition were observed under drought stress. The plants were subjected to either no irrigation during the reproductive stage (terminal drought) or restricted irrigation throughout the growth cycle, maintaining soil moisture at 40% field capacity after seedling emergence. Under restricted irrigation, total carbohydrate content decreased, while dietary fibre levels increased, with significant differences between the two cultivars. (Herrera et al., 2021).

Regarding non-digestible carbohydrates, both common bean cultivars showed elevated levels of resistant starch and raffinose family oligosaccharides (RFOs) such as raffinose, stachyose, and verbascose when subjected to restricted irrigation (Herrera et al., 2021). However, under terminal drought conditions, one cultivar (Rarámuri) demonstrated a reduction in resistant starch and RFO concentrations, whereas the other cultivar (Pinti Saltillo) showed a moderate increase, though not as pronounced as under restricted irrigation (Herrera et al., 2021). Previously, Herrera et al. (2019) showed that for the cultivar Pinto Durango, raffinose levels increased regardless of whether stress occurred throughout the growth cycle or at flowering, while stachyose and verbascose levels raised only under restricted irrigation, declining under terminal drought conditions (Herrera et al., 2019). It is important to note that RFOs play a complex role, as they act as anti-nutritional factors and may contribute to unfavourable symptoms after legumes consumption, but they also have health-promoting properties in humans and contribute to the above-mentioned drought stress tolerance in plants (Elango et al., 2022; Sanyal et al., 2023).

In addition to this, in the drought-sensitive common bean cultivar Brown Speckled, seed sucrose contents decreased, while the drought-resistant line SEA 15 exhibited an increase when drought stress was imposed at the early pod-fill stage by withholding water to maintain the soil moisture level at approximately 30% of the maximum water-holding capacity (Gebeyehu et al., 2010). Similar responses have been observed in other legume species, such as **purple french beans** grown under drought conditions, where stress was applied by reducing irrigation from twice a week in control plants to once a week in stressed plants, based on tensiometer readings that were in the range of 10–15% for the control treatment and 50–60% for the water deficit treatments. The plants presented increased concentrations of total free sugars in pods, particularly glucose and sucrose, while fructose decreased (Fernandes et al., 2021).

Molecular studies have revealed that the accumulation of sugars in legume seeds under water stress is a result of adjusting seed sink strength and altering sugar-related gene expression during different developmental stages. In **soybean**, this process involves the up-regulation followed by down-regulation of various genes related to sucrose transport (*SUC2*, *SWEET12*, *SWEET21*), synthesis (*SPS1*, *SPS2*, *SPS3*, *SPS4*, *Susy1*, *Susy2*), and metabolism (*A-INV*, *C-INV*), although specific responses may vary among genes and developmental stages (Nakagawa et al., 2018; Du et al., 2020). In **pea**, increased soluble sugars under water stress mostly result from sucrose accumulation in seeds, which is regulated by the downregulation of invertase-encoding genes (*CINV1.1*, *CWINV1.2*, and *VINV1.1*), alongside the upregulation of sugar transporters (*TMT2.2* and *ESL2.1*) (Corbineau et al., 2000; Morin et al., 2022). The authors propose that sucrose accumulation in **peas** at the expense of glucose and fructose results from the intracellular reorganization of sugar reserves to uphold cell turgescence under drought conditions (Corbineau, 2000; Morin et al., 2022).

Overall, in legumes such as **common bean** and **soybean**, carbohydrates not only serve their nutritive function but also play essential roles in osmoprotection, with compounds like glucose, fructose, and starch being negatively impacted by drought conditions (Bailly et al., 2001; Bellaloui et al., 2013; Nakagawa et al., 2018; Sheteiwy et al., 2021). Decreased sucrose content under drought stress is related to lower activity of sucrose phosphate synthases being associated with a reduction in seed starch content (Stein and Granot, 2019). Starch hydrolysis resulting from water stress is generally associated with susceptibility rather than tolerance and has been observed in **common bean** (Gebeyehu et al., 2011), **chickpea** (Awasthi et al., 2014), **lentil** (Sehgal et al., 2017), **pigeon pea** (Keller and Ludlow, 1993), and **soybean** (Liu et al., 2004). Overall, these results show the contribution of RFOs and sucrose to seed quality changes under drought conditions, and the relevance of understanding further sugar and starch metabolism under restricted access to water (Kavar et al., 2008; dos Santos et al., 2011; Du et al., 2020).

In **lentils**, heat stress (33/28 °C day/night temperature) applied at the start of the seed filling seems to enhance the activity of enzymes responsible for starch and sucrose breakdown, resulting in elevated levels of soluble sugars, particularly glucose and fructose, while reducing starch content (Sehgal et al., 2019). Moreover, when combined with drought stress (33/28 ºC, 50% field capacity), it exacerbates the inhibition of cellular metabolism involving sugar synthesis and utilization (Sehgal et al., 2019). However, the impact of heat stress at 33/28 ºC (day/night) on carbohydrate content in **lentils** appears to vary by genotype sensitivity, with the heat-sensitive genotype IG4242 showing a marked decrease in sugars, an effect that was less pronounced in the heat-tolerant FLIP 2009 genotype (Sita et al., 2018). Similar disruptions in carbohydrate metabolism under heat stress have been observed in other legume crops such as **mung bean**

(Priya et al., 2023), **chickpea** (Kaushal et al., 2013), and **common bean** (Soltani et al., 2019). In **chickpea**, decreased starch under heat stress (35 ºC) resulted from the downregulation of various sucrose and starch metabolism genes, including *UGP*, *SPS2*, and *CWIN3x2* (Chandel and Sharma, 2023). The upregulation of *BAM1* (encoding a β-amylase) and minimal changes in *ISA3* (isoamylase 3) expression putatively indicated to maltose accumulation during prolonged heat stress, and may be considered a protective mechanism against heat stress, supporting seed quality and yield under high-temperature conditions (Devi et al., 2023). Additionally, genes encoding glucose-6-phosphate/phosphate translocators (GPTs) play a crucial role in glucose-6-phosphate transport between cellular compartments, essential for starch biosynthesis (Weise et al., 2019). Notably, in a targeted study focused in finding GPT sequences in **chickpea**, *GPT2* was overexpressed in a heat-tolerant variety ICC 15614 but downregulated in the susceptible one (ICC 10685), suggesting its association with heat tolerance, and implicating it as a potential candidate gene for heat tolerance in legumes (Chandel et al., 2020).

Regarding the impact of eCO_2, varying effects on seed composition across different legume species have been documented across legumes species. In **chickpea** and **mung bean**, eCO_2 (600 ppm) resulted in increased starch content and decreased protein and soluble sugars (Saha et al., 2015; Lamichaney et al., 2021, 2022). In **soybean** both starch and soluble sugars increased under eCO_2 conditions (600 ppm) (Soares et al., 2021). Interestingly, **pea**, **faba bean**, and **common bean** seeds maintained consistent levels of soluble sugars and starch regardless of CO_2 exposure, but common bean seeds displayed a reduction in total carbohydrates under eCO_2 conditions (700 ppm) (Garmendia et al., 2022). These findings underscore the species-specific responses to eCO_2 and highlight the complex interactions between atmospheric CO_2 levels and seed composition in leguminous plants. The limited research available suggests a resemblance between the molecular mechanisms governing sugar and starch metabolism under eCO_2 conditions and those involved in drought responses. In three **chickpea** genotypes exposed to eCO_2, several genes encoding key enzymes in glycolysis/gluconeogenesis, the galactose metabolism pathway, starch and sucrose metabolic pathways, and carbohydrate transmembrane transport were found to be differentially expressed (Palit et al., 2020; Bhatia et al., 2021). Notably, *BAM9*, which encodes β-amylase crucial in starch and sucrose metabolism, was downregulated, while *GOLS1*, involved in the biosynthesis of RFOs, exhibited upregulation (Palit et al., 2020; Bhatia et al., 2021).

Lipids

Lipids may range from 2-6% of legumes dry matter (Baptista et al., 2017; Margier et al., 2018; Zhao et al., 2021). Despite not being a dietary source of fat, the lipid profile in legumes has a functional role, as it comprises a diverse group of molecules, including fats, oils, phospholipids, and sterols (Bulut et al., 2023). For instance, lipid concentration decreased in **purple French bean** exposed to drought stress, where

irrigation frequency was lowered from twice weekly in the control to once weekly for stressed plants (Fernandes et al., 2021). In contrast, lipid concentration increased in two **common bean** cultivars, Pinto Saltillo and Rarámuri, which were subjected to terminal drought (no irrigation during the reproductive phase) or limited irrigation throughout the growing period (Herrera et al., 2021). For **soybean**, variations in the relative abundance of oil fractions have been described: while oleic and palmitic acids increased, linoleic, linolenic, and stearic acids decreased when drought-stressed plants were maintained between −90 and −100 kPa, compared to well-watered control plants held between −15 and −20 kPa (Bellaloui et al., 2013). Decreased oil in soybeans has been associated with the downregulation of genes involved in lipid biosynthesis (*PK*, *BCCP2*, and *KAS1*) and the upregulation of genes involved in lipid degradation (*ACX2*, *MS*, and *PEPCK*) (Nakagawa et al., 2018; Sheteiwy et al., 2021). In this regard, it was recently demonstrated that the ectopic expression of the At*SINA2* gene, a member of the RING E3 ligase family, enhances shoot biomass and grain yield in soybean, while also enhancing seed oil content and drought tolerance compared to wild-type plants (Yang et al., 2023). Therefore, At*SINA2* could serve as a promising candidate gene for the genetic modification of new legume varieties, offering enhancements in yield, nutritional composition, and resilience to drought stress.

Concomitantly, heat stress (32/20 °C day/night) has been shown to reduce the fat content in two sensitive and two tolerant **chickpea** genotypes, with a greater decrease observed in the sensitive genotypes, likely due to the decline in acetyl-CoA content resulting from inhibited photosynthetic activity (Devi et al., 2023). A similar reduction in lipid content was reported in one cultivar of **red kidney beans** grown from emergence to maturity under elevated temperatures (34/24 ºC vs 28/18ºC for control plants) (Thomas et al., 2009). Likewise, **soybean** exposed to elevated temperatures (36/32 ºC vs 28/24ºC for control plants) during seed filling, showed lower lipid and oil contents, with decreases in unsaturated fatty acids such as linoleic and linolenic acids, but an increase in oleic acid (Dornbos and Mullen, 1992; Xu et al., 2016). In general, lipid remodelling is described as a mechanism of heat tolerance (Liu et al., 2019; Sharma et al., 2023), and it has been shown in **soybean** (Narayanan et al., 2020) and **peanut** (Spivey et al., 2023) genotypes. This phenomenon is likely associated to the impairment of fatty acid desaturases (FAD) and oil and fatty acid accumulation rates (Carvalho et al., 2005; Bellaloui et al., 2013; Nakagawa et al., 2018; Sheteiwy et al., 2021), with the downregulation of several FAD genes, including *FAD3A* and *FAD3B*, which are responsible for converting 18:2 lipids to 18:3 (Narayanan et al., 2020; Spivey et al., 2024). However, other studies have shown inverse responses, with several phospholipids, oil, and free fatty acids increasing in **soybean** seeds produced under high-temperature conditions (Chebrolu et al., 2016; Köhler et al., 2019). In these genotypes, heat not only triggered lipid accumulation by upregulating genes associated with seed lipid biosynthesis (*BCCP2* and *KAS1*) and lipid biosynthesis regulation (*WRI1* and *DREBL*) but also inhibited lipid

degradation by downregulating genes related to lipid degradation, such as *ACX*s. Taken together, these studies demonstrate the variations in gene expression under stress conditions within the **soybean** germplasm that could facilitate enhancements in seed lipid content under water-limited conditions.

Under eCO_2 levels (550 ppm), **soybean** oil content was found to increase (Li et al., 2018). Importantly, the effect of eCO_2 seems to be exacerbated when combined with elevated temperatures, negatively impacting the content of fatty acids such as palmitic, stearic, oleic, and linolenic acids but leading to a general increase in oil concentrations, although the response seems to be highly dependent on the developmental stage of the grain (Palacios et al., 2019; Qiao et al., 2019). Interestingly, the effect of heat on soybean seems to consistently lead to decreased levels of linoleic acid (Palacios et al., 2019; Blanco et al., 2022; Bukowski and Goslee, 2024). In **mung bean**, eCO_2 (670 ppm) also decreased palmitic acid accumulation in seeds but increased the ratio of omega-3 to omega-6 fatty acids (Ziska et al., 2007). Notably, crude fat concentration was not affected by eCO_2 (600 ppm) in **common bean** and **soybean** (Köhler et al., 2019; Soares et al., 2019b). The contrasting observations among these studies on legume lipid profiles can be attributed to various factors, including specific experimental conditions such as temperature, humidity, and soil type, as well as the diversity of genotypes utilized in the experiments, as shown in Table 5. Additionally, differences in the developmental stages of the plants at the time of sampling and analysis also contribute to the variability in results. Nevertheless, preserving the lipid profile of legumes under environmental stress is critical for maintaining their nutritional quality, supporting plant resilience, ensuring seed viability, and securing consistent crop yield and quality (Sharma et al., 2023).

Bioactive Compounds

Legumes are recognized as valuable sources of bioactive compounds crucial for human nutrition, including polyphenolic compounds and vitamins (Geraldo et al., 2022; Duarte et al., 2024). Polyphenols derived from legumes offer a plethora of health benefits, such as antioxidative and anti-inflammatory properties, support for cardiovascular health, regulation of blood sugar levels, promotion of gut health, potential prevention of cancer, and neuroprotective effects (Ferreira et al., 2021). However, some phenolics can also act as antinutrients by interfering with the bioavailability of essential minerals, such as iron, as their effects on nutrient absorption can be both inhibitory and promotive depending on the specific compounds and food matrix (Hart et al., 2015).

Regarding the effect of adverse environmental conditions in polyphenols accumulation, in **common bean** cv. Pinto Durango, both terminal drought (no irrigation during the reproductive phase) and limited irrigation throughout the growing period have been shown to elevate the concentrations of various polyphenolic compounds, encompassing phenolic acids, flavonoids, as well as other bioactive

phytochemicals like steroidal glycosides, and saponins; and organic acids like ferulic acid and derivatives of gallic, protocatechuic, hydroxybenzoic, and caffeic acids (Herrera et al., 2019). Additionally, a comparative metabolomic study on 44 advanced **chickpea** breeding lines (18 kabuli and 26 desi), grown under rainfed conditions to simulate water-limited environments alongside irrigated (well-watered) controls, demonstrated that desi genotypes, typically with dark seed coat colour, have higher leaf phenolic levels under drought. In contrast, kabuli genotypes, with light seed coat colour, exhibited lower leaf phenolic levels. The elevated phenolic compounds, including antioxidants, likely contribute to the resilience of desi chickpeas to water stress (Nisa et al., 2020). Similarly, exposure to heat stress (36/24 ºC day/night) has been observed to increase the levels of antioxidant metabolites, including tocopherols, flavonoids, phenylpropanoids, and ascorbate precursors in **soybean** seeds (Chebrolu et al., 2016). In **lentils**, water and heat stresses have differential effects on seed polyphenolics in an intraspecific manner. Generally, total phenolics levels rise under stress conditions (La et al., 2023; Prakash et al., 2024), and tannins, which are polyphenols with an important role plant defence, also follow this trend, although a great natural variation occurs both among different legume species and within certain varieties (Singh et al., 2017; Rao et al., 2020). Specific accessions showed a significant increase in total flavonoid content in response to high temperatures, when at the first day of the anthesis phase, plants were exposed to temperatures above 32 °C for four hours in a growth chamber for a period of seven days, but tannin content was affected similarly across almost all accessions (El Haddad et al., 2023). Overall, results suggest that tolerant accessions produce higher concentrations of polyphenolic compounds than sensitive accessions subjected to high-temperature or drought-stress conditions, resulting from the upregulation of key genes involved in the phenylpropanoid biosynthesis pathway, such as *PAL1* (Chebrolu et al., 2016, Herrera et al., 2019; Herrera et al., 2021; El Haddad et al., 2023; Farooq et al., 2024).

Similarly, eCO_2 (550 and 700 ppm) was shown to induce the accumulation of polyphenolics in **faba bean** (Garmendia et al., 2022) and to upregulate several genes involved in the phenylpropanoid biosynthesis pathway in **chickpeas** (Palit et al., 2020). Interestingly, no significant effects of eCO_2 (600 or 700 ppm) on phenolic content were observed in **soybean**, **common bean** or **pea** (Soares et al., 2021; Garmendia et al., 2022), despite previous studies in soybean reported the downregulation of several transcripts related phenylpropanoid, flavonoid, stilbenoid, diarylheptanoid, and gingerol biosynthesis, including *PAL1*, *CAD6*, and *CYP78A5* (Bencke-Malato et al., 2019). When assessing the impact of climate change on the accumulation of polyphenolic compounds in legume seeds it is also important to consider that phenolic compounds can interact with both starches and proteins, impacting their structure, digestibility, and nutritional quality (Buitimea-Cantúa et al., 2018). Reduced digestibility of starch due to phenolic interaction may contribute to lower postprandial glucose responses, beneficial for metabolic health (Ngo et al., 2022;

Luo et al., 2024). On the protein side, decreased digestibility can lower amino acid availability but may also have antioxidant benefits due to the phenolics' bioactive properties (Kieserling et al., 2024).

Significantly, phytic acid accumulation appears to occur in the seeds of **common bean** (Hummel al., 2018; Soares et al., 2021), **chickpea** (Boominathan et al., 2004; Joshi-Saha 2015), and **lentil** (Bansal et al., 2023) under drought stress, likely due to its role in mitigating oxidative stress in legumes during challenging conditions (Hummel al., 2018). In **lentil** seeds, increased phytic acid levels have also been observed when plants were exposed to elevated temperatures of 32°C at the flowering stage (Choukri et al., 2022). This observation is particularly pertinent as phytic acid is recognized for its ability to chelate positively charged cations like K, Mg, Ca, Fe, and Zn (Sparvoli and Cominelli, 2015). Consequently, when included in human diets, it may bind to these minerals in the intestinal tract, forming mixed salts that are typically excreted from the body, thereby reducing the bioavailability of these essential nutrients (Gupta et al., 2015). Given that many regions grappling with malnutrition are also susceptible to drought and heat waves (Amondo et al., 2023), this poses a serious threat to food security. Also, as phytate is one of the main forms of P storage in the grains, phytate synthesis depends on the translocation and partitioning of P to this organ (Coelho et al., 2002). Some biofortification efforts have therefore focused on developing low-phytic acid mutants to enhance mineral availability, but without compromising the content of P. However, these modified lines often experience a trade-off, with a decrease in agronomic quality as a consequence (Sparvoli and Cominelli, 2015). Additionally, consumption of low-phytic acid beans has been associated with gastric discomfort and poor cooking quality, which could impact their acceptability and nutritional benefits (Petry et al., 2016).

In contrast to phytic acid, biotin and folate (or vitamins B7 and B9, respectively) play crucial roles in the breakdown and utilization of nutrients from food. They aid in the absorption of essential nutrients such as minerals, fats, carbohydrates, and proteins, supporting overall nutrient utilization and ensuring optimal health. In **peas** subjected to drought the gene of *SBP65* was upregulated, underpinning the potential accumulation of a seed-specific biotinylated protein (Wang et al., 2012), while in **chickpea** eCO_2 (550 and 700 ppm) impaired several enzymes present in the folate biosynthesis pathway (Palit et al., 2020). Nevertheless, the precise alterations in biotin, folate and other vitamin accumulations due to climate change remain elusive in legume seeds, warranting further investigation.

Conclusions

The findings presented underscore the complex challenges of predicting the impacts of climate change on legumes and their nutritional profiles. They emphasize the necessity of implementing multidisciplinary research, integrating plant physiology, agronomy, genetics, soil science, climate science, nutrition, and

data modelling through studies conducted in both field and controlled environments to effectively address these climate-related challenges. As some inconsistencies were found, it is also important to consider species, genotype, stress combinations, and environmental conditions when interpreting these results.

Figure 1 provides a summary of the traits that could be targeted for improvement in different crops, which could be relevant as recommendations for future research efforts. Across all legumes, improving protein content and essential amino acids under drought and heat stress is a critical priority. This includes increasing the stability of proteins and lysine, threonine, and tryptophan. Regarding minerals, Fe, Zn and P are decreased in most crops under the different stress conditions, and breeding for improved mineral uptake and retention would be valuable, particularly in chickpea, lentil, and soybean, that were the species registering the greatest impact in the cited studies. Finally, crops like chickpea, lentil, and mungbean show significant reductions in carbohydrates (e.g., starch, glucose) and enhancing carbohydrate metabolism under stress conditions could ensure consistent energy yield. For crops like chickpea, lentil, and mungbean, starch and fat stability could also be key breeding targets to ensure their overall nutritional and caloric value in a changing climate.

Some additional key points can be inferred from the gathered evidence, namely, the need to shift the cultivation practices, to improve farming system's sustainability; that the interaction between multiple stressors often leads to more severe or, at least, different impacts than individual stressors alone; and that a major part of these findings are based on controlled laboratory or greenhouse, being necessary studies under field conditions, where environmental conditions are not tightly regulated.

In the face of these challenges, farmers are less prone to take risks and adopt new crops, new farming practices, or any other change that could contribute to improving value chains (European Commission, 2017). To add on to this, several technological lock-ins contribute to farmers' economic insecurity, specifically, the lack of investment in breeding of new varieties, in input products (namely, fertilizers and plant protection products) development well adapted to legumes, and the lack of technical knowledge and scientific-based practice at the farm-level.

Author contributions

CSS outlined the topic of the manuscript and together with MWV acquired the funding. JM, CSS and MNS performed the bibliographic research and drafted the paper under the guidance of MWV. All authors read and approved the final manuscript.

Conflict of interest

No conflict of interest was declared.

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Tables

Table 1: Impact of different environmental conditions on protein content of grain legumes

Stress	**Crop**	**Number of cultivars / genotypes**	**Stress Level**	**Environment**	**Decrease (↓), increase (↑) or not affected (NA) over control**	**Reference**
DROUGHT	Chickpea	2	Severe and moderate drought	Field	↓ 33% (under moderate drought) and ↓ 41% (under severe drought)	Ashrafi et al., 2015
		2	75, 50 and 25% FC	Climate chamber (controlled environment)	NA	Medeiros et al., 2024
		140	no irrigation provided	Field	↑ 6-35%	Samineni et al., 2022
		2	Withholding water for 14 day (at 7-9 pods per plant stage)	Not specified	↓ 40 (Desi) and ↓ 46% (Kabuli)	Nayyar et al., 2006
	Common bean	8	irrigation after 100-110 mm evaporation	Field	↓ 7%	Ghanbari et al., 2013

		2	Terminal drought (TD - withheld at the beginning of flowering) and restricted irrigation (RI - soil moisture kept at 40% FC during the whole cycle after seedling emergence)	Field (with a rainout shelter)	↓ up to 5% (TD) and ↓ up to 9% (RI)	Herrera et al., 2021
	Faba bean	1	early season severe water stress	Field	↑ 14%	Al-Suhaibani, 2009
	Lentil	2	50% FC	Field	↓ 45% [s]	Sehgal et al., 2019
	Lupin	1	55 and 35% FC	Climate chamber (controlled environment)	↑ 33% (under 55% FC) and ↑ 54% (under 35% FC)	Khalil et al., 2010
	Mungbean	9	Severe drought	Field	↑ 10%	Yagoob & Yagoob, 2014

	Soybean	1	severe drought at seed filling	Greenhouse	↑ 5%	Dornbos et al., 1992
		4	kept between −90 and −100 kPa	Greenhouse	↑ up to 7%	Bellaloui et al., 2013
HEAT	Chickpea	43	32°C	Field	↑ 10%	Benali et al. 2023
		140	>35 °C at reproductive stage	Field	NA	Samineni et al., 2022
		4	32/20 °C day/night	Climate chamber (controlled environment)	↓ 43–57% [s]	Devi et al., 2023
	Lentil	2	33/28°C mean day/night	Climate chamber (controlled environment)	↓ 42% [s]	Sita et al., 2018
		2	33/28 °C day/night	Climate chamber (controlled environment)	↓ 26% [s]	Sehgal et al., 2019
		100	>35 °C	Field	↓ 14%	Choukri et al., 2020

		20	>32 °C at reproductive stage	Field	↓ 16%	El Haddad et al., 2021
	Mungbean	13	38 - 40°C	Field	↓ 4% to 9%	Batra et al., 2023
		2	42°C/30°C day/night	Climate chamber (controlled environment)	↓ 48% [s]	Priya et al., 2023
DROUGHT + HEAT	Lentil	2	33/28°C day/night + 50% FC	Climate chamber (controlled environment)	↓ 55% [s]	Sehgal et al., 2019
		100	>35 °C + no irrigation during the reproductive phase	Field	↓ 57%	Choukri et al., 2020
		20	>32 °C + no irrigation during the reproductive phase	Field	↓ 54%	El Haddad et al., 2021
CO_2	Chickpea	1	600 ppm	Open top chamber	↓ 7%	Lamichaney et al., 2021

	Common bean	1	800 ppm	Climate chamber (controlled environment)	↑ 6%	Soares et al, 2019
		1	710 ppm	Greenhouse	NA	Garmendia et al., 2022
		1	800 ppm	Climate chamber (controlled environment)	↑ 30%	Deuchande et al., 2023
	Faba bean	1	700 ppm	Greenhouse	NA	Garmendia et al., 2022
	Mungbean	1	600 ppm	Open top chamber	↓ 8%	Lamichaney et al., 2022
	Pea	1	700 ppm	Greenhouse	↑ 120%	Garmendia et al., 2022
	Soybean	13	600 ppm	FACE facility	↓ 6%	Soares et al., 2021

[S] refers to the percentages of increase or decrease observed for the sensitive genotypes vs. tolerant genotypes.

Table 2: Impact of different environmental conditions on several amino acids of grain legumes

Stress	Crop	Number of cultivars / genotypes	Stress Level	Environment	Amino Acid Affected	Decrease (↓), increase (↑) or not affected (NA) over control	Reference
DROUGHT	Chickpea	2	Withholding water for 14 day (at 7-9pods per plant stage)	Not Specified	Alanine	NA (Desi) and ↓35% (Kabuli)	Nayyar et al., 2006
					Arginine	↑ 27% (Desi) and ↑ 21% (Kabuli)	
					Aspartic acid	NA (Desi) and NA (Kabuli)	
					Glutamic Acid	↑ 38% (Desi) and ↑ 25% (Kabuli)	
					Glycine	↑ 48% (Desi) and ↑ 31% (Kabuli)	
					Histidine	NA (Desi) and ↓50% (Kabuli)	

					Isoleucine	↑ 17% (Desi) and ↑ 21% (Kabuli)	
					Leucine	NA (Desi) and ↑ 16% (Kabuli)	
					Lysine	NA (Desi) and ↓ 46% (Kabuli)	
					Methionine+cystine	↓ 40% (Desi) and ↓39% (Kabuli)	
					Phenylalanine+tyrosine	↓ 13% (Desi) and ↓30% (Kabuli)	
					Proline	↑ 38% (Desi) and ↑ 65% (Kabuli)	
					Serine	NA (Desi) and NA (Kabuli)	
					Threonine	↓ 32% (Desi) and ↓29% (Kabuli)	

					Tryptophan	↓ 50% (Desi) and ↓60% (Kabuli)	
					Valine	↓ 25% (Desi) and ↓28% (Kabuli)	
	Common Bean	12	terminal drought - no irrigation provided after 25 days from sowing	Field	Aspartic acid	↑ 38%	Smith et al., 2019
					Glutamine	↑ 75%	
					Glycine	↑ 22%	
					Leucine	↑ 24%	
	Lentil	2	50% FC	Climate chamber (controlled environment)	Alanine	↑ 20% [s]	Sehgal et al., 2019
					Arginine	↓ 26% [s]	
					Aspartic acid	↓ 33% [s]	
					Glutamic acid	↓ 41% [s]	
					Glycine	↑ 46% [s]	
					Histidine	↓ 57% [s]	
					Isoleucine	↑ 24% [s]	
					Leucine	↑ 14% [s]	
					Lysine	↑ 26% [s]	
					Methionine+cystine	↓ 48% [s]	

					Phenylalanine+tyrosine	↓ 39% [S]	
					Proline	↓ 22% [S]	
					Serine	↓ 45% [S]	
					Threonine	↓ 62% [S]	
					Tryptophan	↓ 35% [S]	
HEAT	Lentil	2	33/28°C mean day/night	Climate chamber (controlled environment)	Alanine	↓ 16% [S]	Sita et al., 2018
					Arginine	↓ 27% [S]	
					Aspartic Acid	↓ 10% [S]	
					Glutamic Acid	↓ 30% [S]	
					Glycine	↓ 25% [S]	
					Histidine	↓ 32% [S]	
					Isoleucine	↓ 16% [S]	
					Leucine	↓ 10% [S]	
					Lysine	↓ 12% [S]	
					Methionine+cystine	↓ 29% [S]	
					Phenylalanine+tyrosine	↓ 29% [S]	
					Proline	↓ 24% [S]	

					Serine	↓ 31% [S]	
					Threonine	↓ 31% [S]	
					Tryptophan	↓ 23% [S]	
		2	33/28 °C day/night	Climate chamber (controlled environment)	Alanine	↑ 32% [S]	Sehgal et al., 2019
					Arginine	↓ 16% [S]	
					aspartic acid	↓ 21% [S]	
					glutamic acid	↓ 28% [S]	
					Glycine	↑ 54% [S]	
					Histidine	↓ 32% [S]	
					Isoleucine	↑ 29% [S]	
					Leucine	↑ 14% [S]	
					Lysine	↑ 30% [S]	
					methionine+cystine	↓ 14% [S]	
					phenylalanine+tyrosine	↓ 37% [S]	
					Proline	↑ 35% [S]	
					Serine	↓ 28% [S]	
					Threonine	↓ 43% [S]	
					Tryptophan	↓ 26% [S]	

DROUGHT + HEAT	Lentil	2	33/28 °C day/night + 50% FC	Climate chamber (controlled environment)	Alanine	↓ 24% [S]	Sehgal et al., 2019
					Arginine	↓ 38% [S]	
					Aspartic acid	↓ 54% [S]	
					Glutamic acid	↓ 68% [S]	
					Glycine	↓ 33% [S]	
					Histidine	↓ 69% [S]	
					Isoleucine	↓ 31% [S]	
					Leucine	↓ 30% [S]	
					Lysine	↓ 35% [S]	
					Methionine+cystine	↓ 73% [S]	
					Phenylalanine+tyrosine	↓ 54% [S]	
					Proline	↓ 43% [S]	
					Serine	↓ 70% [S]	
					Threonine	↓ 75% [S]	
					Tryptophan	↓ 51% [S]	
CO_2	Soybean	4	550 ppm	Open top chamber	Arginine	↓ 29%	Li et al., 2018
					Asparagine	↓ 12%	
					Serine	↓ 30%	

					Total free aminoacids	↓ 15%	

[S] refers to the percentages of increase or decrease observed for the sensitive genotypes vs. tolerant genotypes.

Table 3: Impact of different environmental conditions on mineral content of grain legumes

Stress	Crop	Number of cultivars / genotypes	Stress Level	Environment	Mineral Affected	Decrease (↓), increase (↑) or not affected (NA) over control	Reference
DROUGHT	Chickpea	140	No irrigation provided	Field	Fe	↑ 3.3-3.9%	Samineni et al., 2022
					Zn	↓ 5 - ↑ 15%	
		2	75, 50 and 25% FC	Climate chamber (controlled environment)	B	NA	Medeiros et al., 2024
					Ca	NA	
					K	NA	
					Mg	NA	
					Mn	NA	
					P	NA (75% FC), ↓ 29% (50% FC) and ↓ 24% (25% FC)	
					Zn	NA	

		2	Withholding water for 14 days (at 7-9 pods per plant stage)	Not Specified	Ca	↓ 19% (Desi) and ↓23% (Kabuli)	Nayyar et al., 2006
					Fe	↓ 39% (Desi) and ↓58% (Kabuli)	
					P	↓ 44% (Desi) and ↓50% (Kabuli)	
	Common bean	2	terminal drought (TD - withheld at the beginning of flowering) and restricted irrigation (RI - soil moisture kept at 40% FC during the whole cycle after seedling emergence)	Field (with a rainout shelter)	Fe	↑ up to 55% (TD) and ↑ up to 26% (RI)	Herrera et al., 2021
					Zn	↑ up to 10% (TD) and ↑ up to 19% (RI)	
	Lentil	2	50% FC	Climate chamber (controlled environment)	Ca	↓ 25% [s]	Sehgal et al., 2019
					Fe	↓ 36% [s]	
					Mg	↓ 30% [s]	

					K	↓ 28% [s]	
					P	↓ 18% [s]	
					Zn	↓ 48% [s]	
	Soybean	4	Kept between −90 and −100 kPa	Greenhouse	Ca	↓ up to16%	Bellaloui et al., 2013
					B	↓ up to 33%	
					Fe	↓ up to 44%	
					K	↓ up to 28%	
					N	↓ up to 25%	
					P	↓ up to 52%	
HEAT	Chickpea	140	>35 °C at reproductive stage	Field	Fe	↓ 7-13%	Samineni et al., 2022
					Zn	NA	
		43	32°C	Field	Fe	↓ 10%	Benali et al. 2023
					Mg	↑ 19%	
					Mn	↑ 16%	
					Zn	NA	
		4	32/20 °C day/night		Ca	↓ 47-54% [s]	Devi et al., 2023
					Fe	↓ 59% [s]	

				Climate chamber (controlled environment)	P	↓ 33–37% [s]	
	Lentil	2	33/28°C mean day/night	Climate chamber (controlled environment)	Ca	↓ 28% [s]	Sita et al., 2018
					Fe	↓ 52% [s]	
					K	↓ 28% [s]	
					Mg	↓ 35% [s]	
					Zn	↓ 59% [s]	
					P	↓ 54% [s]	
		2	33/28 °C day/night	Climate chamber (controlled environment)	Ca	↓ 17% [s]	Sehgal et al., 2019
					Fe	↓ 26% [s]	
					P	↓ 12% [s]	
					K	↓ 17% [s]	
					Mg	↓ 19% [s]	
					Zn	↓ 33% [s]	
		100	>35 °C	Field	Fe	↓ 18%	Choukri et al., 2020
					Zn	↓ 22%	
		20		Field	Fe	↓ 15%	El Haddad et al., 2021

			>32 °C at reproductive stage		Zn	↓ 14%	
	Mungbean	2	42°C/30°C day/night	Climate chamber (controlled environment)	Ca	↓ 41% [s]	Priya et al., 2023
					Fe	↓ 26% [s]	
					Mg	↓ 21% [s]	
					K	↓ 28% [s]	
					P	↓ 19% [s]	
					Zn	↓ 38% [s]	
DROUGHT + HEAT	Lentil	2	33/28°C day/night + 50% FC	Climate chamber (controlled environment)	Ca	↓ 39% [s]	Sehgal et al., 2019
					Fe	↓ 58% [s]	
					P	↓ 54% [s]	
					K	↓ 38% [s]	
					Mg	↓ 38% [s]	
					Zn	↓ 65% [s]	
		100	>35 °C + no irrigation during the reproductive phase	Field	Fe	↓ 30%	Choukri et al., 2020
					Zn	↓ 36%	

		20	>32 °C + no irrigation during the reproductive phase	Field	Fe	↓ 20%	El Haddad et al., 2021
					Zn	↓ 18%	
CO_2	Chickpea	1	550 ppm	Field (FAOCE rings)	Ca	↓ 5%	Bhatia et al., 2021
					K	↓ 10%	
	Common bean	1	800 ppm	Climate chamber (controlled environment)	Fe	↓ 10%	13 et al., 2019
					Mn	↓ 25%	
					Mg	↑ 20%	
					K	↓ 6%	
	Faba bean	1	710 ppm	Greenhouse	Fe	↓ 57%	Garmendia et al., 2022
					P	↓ 13%	
	Soybean	1	600 ppm	SoyFACE field	Ca	↓ 6%	Köhler et al., 2019
					Fe	↓ 9%	
					Zn	↓ 9%	
		4	550 ppm	Open top chamber	Mg	↑ 13%	Li et al., 2018
					Ca	↑ 3%	
					Zn	↑ 3%	

					Fe	↓ 2%	
					Mn and Cu	↓ or ↑ depending on genotype	
		13	800 ppm	FACE facility	B	↓ 19%	Soares et al., 2021
					Ca	↓ 23%	
					Fe	↓ 28%	
					Mg	↓ 10%	
					Mn	↓ 21%	
					K	↓ 5%	
					P	↓ 9%	
					Zn	↓ 26%	
		1	710 ppm	Greenhouse	Ca	↑ 47%	Garmendia et al., 2022
		1	800 ppm	Climate chamber (controlled environment)	Ca	↑ 50%	Deuchande et al., 2023
					Fe	↓ 50%	

[S] refers to the percentages of increase or decrease observed for the sensitive genotypes vs. tolerant genotypes.

Table 4: Impact of different environmental conditions on carbohydrates of grain legumes

Stress	Crop	Number of cultivars / genotypes	Stress Level	Environment	Carbohydrate Affected	Decrease (↓), increase (↑) or not affected (NA) over control	Reference
DROUGHT	Chickpea	2	Withholding water for 14 day (at 7-9pods per plant stage)	Not Specified	Glucose	↑ 28% (Desi) and ↑ 20% (Kabuli)	Nayyar et al., 2006
					Fiber	↓ 35% (Desi) and ↓67% (Kabul)	
					Fructose	↑ 38% (Desi) and ↑ 15% (Kabuli)	
					Soluble Sugars	↓ 23% (Desi) and ↓ 47% (Kabuli)	
					Starch	↓ 25 (Desi) and ↓ 48% (Kabuli)	

					Sucrose	↑ 34% (Desi) and ↑ 46% (Kabuli)	
	Common bean	2	Terminal drought (TD - withheld at the beginning of flowering) and restricted irrigation (RI - soil moisture kept at 40% FC during the whole cycle after seedling emergence)	Field (with a rainout shelter)	Resistant starch	↓ up to 36% (TD) and ↑ up to 50% (RI)	Herrera et al., 2021
					Raffinose	↓ 15% or ↑ 18% (TD) and ↑ up to 51% (RI)	
					Stachyose	↓ up to 80% (TD) and ↑ up to 300% (RI)	
					Verbascose	↓ 32% or ↑37 (TD) and ↑ up to 105% (RI)	
					Total carbohydrates	↓ NA (TD) and up to 3% (RI)	
					Ash	↓ up to 10% (TD) and ↓ up to 12% (RI)	

					Total dietary fiber	↓ up to 3% (TD) and ↓ up to 10% (RI)	
					Soluble dietary fiber	↑ up to 33% (TD) and ↓ up to 3% (RI)	
					Insoluble dietary fiber	↓ up to 17% (TD) and ↑ up to 21% (RI)	
	Lentil	8	50% FC	Field	Starch	↓ 37–60%	Sehgal et al., 2017
					Sucrose	↑ 39–67%	
		2	50% FC	Climate chamber (controlled environment)	Fructose	↑ 49% [S]	Sehgal et al., 2019
					Glucose	↑ 32% [S]	
					Soluble Sugars	↑ 48% [S]	
					Starch	↓ 35% [S]	
					Sucrose	↓ 37% [S]	
	Soybean	4	Kept between −90 and −100 kPa	Greenhouse	Fructose	↓ up to 45%	Bellaloui et al., 2013
					Glucose	↓ up to 41%	
					Raffinose	↑ up to 35%	

					Stachyose	↑ up to 84%	
					Sucrose	↓ up to 38%	
HEAT	Chickpea	4	32/20 °C day/night	Climate chamber (controlled environment)	Fructose	↑ 50–60% [S]	Devi et al., 2023
					Glucose	↑ 33–35% [S]	
					Starch	↓ 47–54% [S]	
					Sucrose	↓ 53–55%[S]	
	Lentil	8	30/20°C day/night	Field	Starch	NA	Sehgal et al., 2017
					Sucrose	↑ 23–53%	
		2	33/28°C mean day/night	Climate chamber (controlled environment)	Fructose	↓ 23% [S]	Sita et al., 2018
					Glucose	↓ 29% [S]	
					Starch	↓ 43% [S]	
					Sucrose	↓ 45% [S]	
		2	33/28 °C day/night	Climate chamber (controlled environment)	Fructose	↑ 26% [S]	Sehgal et al., 2019
					Glucose	↑ 17% [S]	
					Soluble Sugars	↑ 43% [S]	
					Starch	↓ 18% [S]	
					Sucrose	↓ 22% [S]	

	Mungbean	2	42°C/30°C day/night	Climate chamber (controlled environment)	Carbohydrate accumulation	↓ 45% [S]	Priya et al., 2023
DROUGHT + HEAT	Lentil	8	30/20°C day/night + 50% FC	Field	Starch	↓ 50–70%	Sehgal et al., 2017
					Sucrose	↑ 55–76%	
		2	33/28 °C day/night + 50% FC	Climate chamber (controlled environment)	Fructose	↓ 48% [S]	Sehgal et al., 2019
					Glucose	↓ 47% [S]	
					Sucrose	↓ 49% [S]	
CO_2	Chickpea	1	580 ppm	Open top chamber	Starch	↓ 8-12%	Saha et al., 2015
		1	600 ppm	Open top chamber	Starch	↑ 18%	Lamichaney et al., 2021
	Common bean	1	710 ppm	Greenhouse	Carbohydrates	↓ 31%	Garmendia et al., 2022
	Soybean	13	600 ppm	FACE facility	Soluble Sugars	↑ 9%	Soares et al., 2021
					Starch	↑ 16%	

[S] refers to the percentages of increase or decrease observed for the sensitive genotypes vs. tolerant genotypes.

Table 5: Impact of different environmental conditions on the lipid content of grain legumes

Stress	Crop	Number of cultivars / genotypes	Stress Level	Envirnoment	Affected Trait	Decrease (↓), increase (↑) or not affected (NA) over control	Reference
DROUGHT	Chickpea	2	Withholding water for 14 day (at 7-9 pods per plant stage)	Not Specified	Fat	↓ 39% (Desi) and ↓46% (Kabuli)	Nayyar et al., 2006
	Common bean	2	Terminal drought (TD - withheld at the beginning of flowering) and restricted irrigation (RI - soil moisture kept at 40% FC during the whole cycle after seedling emergence)	Field (with a rainout shelter)	Lipids	↑ up to 22 (TD) and ↑ 177% (RI)	Herrera et al., 2021

	Soybean	4	kept between −90 and −100 kPa	Greenhouse	Fat	↓ up to 4%	Bellaloui et al., 2013
HEAT	Chickpea	4	32/20 °C day/night	Climate chamber (controlled environment)	Fat	↓ 70% [S]	Devi et al., 2023
	Mungbean	2	42°C/30°C day/night	Climate chamber (controlled environment)	Fat	↓ 55% [S]	Priya et al., 2023
CO_2	Soybean	1	800 ppm	Open-top chambers	Seed oil concentration	↓ 9 to 12%	Palacios et al., 2019
		3	550 ppm	Climate chamber (controlled environment)	Linoleic acid	↑ 24%	Blanco et al., 2022
					Oleic acid	↓ 24%	
					Palmitic acid	↓ 37%	
					Stearic acid	↓ 36%	

[S] refers to the percentages of increase or decrease observed for the sensitive genotypes vs. tolerant genotypes.

Figure legends

Fig. 1 Main common and individual target traits for improvement in soybean, common bean, lentil, mung bean and chickpea seeds for nutritional quality under climate change. The diagram summarizes key nutritional components — protein, amino acids, minerals, carbohydrates, lipids, and phenolics — that registered consistent changes across individual or combined stress conditions. Different symbols indicate the dominant stress type affecting each nutrient: for elevated CO_2 (eCO_2), for drought, and for heat stress. Macronutrients are colour-coded in black and minerals in dark blue.

Figure 1