

Climate change and the antinutrient–antioxidant puzzle in common bean seeds

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Abstract

Non-proteinaceous and proteinaceous antinutrients in common bean (*Phaseolus vulgaris* L.) seeds can negatively affect human nutrition by reducing mineral bioavailability and impairing protein digestibility during digestion, respectively. However, many of these compounds also possess strong antioxidant properties that can help protect the plant from oxidative stress. While strategies to reduce antinutrient levels have been proposed to enhance the nutritional value of beans, less attention has been given to their potential protective functions, particularly under abiotic stress conditions. In the context of ongoing global climate change – marked by more frequent and prolonged drought and heat stress – there is a significant research gap concerning the influence of these environmental stresses on the accumulation and function of seed antinutrients in common beans. This perspective paper reviews current knowledge on the production of antioxidative antinutrients in response to abiotic stress and highlights the dual role of these compounds. It also outlines key research directions needed to better understand how climate-induced stress may alter antinutrient levels, and the implications this may have for both human nutrition and plant resilience.

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INTRODUCTION

Non-proteinaceous antinutrients can limit the bioavailability and bio-accessibility of minerals, while proteinaceous antinutrients may inhibit the digestibility of proteins in the digestive system.¹ Pulses – the edible seeds of plants in the legume family – represent a particularly underutilized nutritional resource in many developed countries and contain high levels of both non-proteinaceous and proteinaceous antinutrients.² Among the predominant non-proteinaceous antinutrients in pulses are phytic acid and polyphenols, whereas the main proteinaceous antinutrients include lectins, saponins, and serine protease (trypsin) inhibitors. Due to their ability to reduce nutrient absorption in humans, efforts have been made to lower antinutrient concentrations in bean seeds to enhance their overall nutritional value.³

Ongoing global climate change is contributing to prolonged drought periods, frequently accompanied by extreme heat. These conditions result in a significant depletion of soil water content, which adversely impacts plant growth and productivity.⁴ Among crops affected by climate change, common bean (*Phaseolus vulgaris* L.) – a focus of our current research – is particularly vulnerable.^{5–7} As the most widely cultivated and consumed food grain legume globally, approximately 60% of common bean production relies on rain-fed agriculture, making it susceptible to drought and heat stress.⁵ The common bean's relatively shallow root system further contributes to its sensitivity to soil water deficits. However, no substantial negative effect on seed nutrient or amino acid

concentrations have, to our knowledge, so far been observed following stress exposure.

In addition to their role as antinutrients, some of these compounds also exhibit potent antioxidant properties, thereby protecting the plant against phytotoxic oxidative stress triggered by both biotic and abiotic factors, including drought and heat stress associated with current climate change.^{8,9} Stress-induced production of reactive oxygen species (ROS) can damage cellular components and accelerate seed aging.^{10,11} Antinutrients with antioxidative capacity can reduce ROS levels, however, and thereby protect cellular integrity. To date, this antioxidative role has been primarily investigated in the vegetative parts of plants, with limited attention paid to common bean seeds themselves.

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Phytic acid (PA) and polyphenols (e.g., tannins) are the main antinutrients in common bean seeds with antioxidative activity. PA accumulates during seed maturation and can chelate metal ions such as free iron (Fe).¹² The Fe-chelating activity prevents Fenton-type reactions, in which free Fe ions react with oxygen to produce phytotoxic ROS. During seed maturation, levels of the antioxidant ascorbic acid declines, and mature dry seeds (such as pulses) typically lack this compound. This raises an important question: can PA partially, or fully, replace the antioxidative function of declining levels of, for example, ascorbic acid during seed maturation to maintain a protective effect against ROS during unfavorable environmental conditions?¹³

From our perspective, there is a critical knowledge gap regarding whether the concentrations of proteinaceous and non-proteinaceous antinutrients with antioxidant functions increase in common bean seeds in response to environmental stress related to climate change, particularly drought and heat stress. The aim of this perspective paper is first to synthesize current knowledge on the abiotic stress-induced accumulation of antioxidative antinutrients in common bean seeds (Fig. 1). We then propose future research directions to investigate more thoroughly how such stresses may influence seed antinutrient content, with potential implications for both human nutrition and plant resilience.

NON-PROTEINACEOUS SEED ANTINUTRIENTS

Phytic acid accumulation, nutritional implications and its role in stress response

During common bean seed development, minerals accumulate in storage tissues, and phosphorus is converted into PA within the cytoplasm of storage tissue cells and accumulate in the post-ripening phase.¹⁴ PA concentration in the seed increases following the cell division phase and continues to accumulate during the stationary phase at the end of cell expansion.¹⁵ In common bean seeds, PA is transported to cellular protein storage vacuoles (PSVs) by a specific multidrug resistance-associated protein (MRP)-ATP-binding cassette (ABC) transporter, contributing to

the formation of solid globoid structures.¹⁶ Globoids also serve as the principal Fe storage pool, with Fe accumulating in a bound form.^{17,18} Ultimately, up to 85% of the plant's total phosphorus is stored within these globoids – an amount nearly 1000 times higher than in vegetative tissues such as roots, stems, and tubers. The primary form of stored PA is phytate or phytin, a calcium/magnesium salt of PA.²

Apart from its storage function, PA and its precursor molecules – including lower inositol phosphates and *myo*-inositol and its derivative molecules inositol pyrophosphates (IP₇ and IP₈) – play critical roles in plant development and signaling processes. These include, for example, responses to abiotic and biotic stress, auxin storage and transport, phosphatidylinositol signaling, and phosphorus homeostasis.^{15,19} During seed germination and early seedling growth, phytase-mediated hydrolysis of stored phytate releases inorganic phosphorus, bound micronutrients, and *myo*-inositol, essential for seedling development.^{20,21}

Due to its strong negative charge, PA chelates essential minerals, such as Zn²⁺, Fe^{2+/3+}, Ca²⁺, Mg²⁺, Mn²⁺, and Cu²⁺, reducing their bioavailability and impairing micronutrient absorption in monogastric organisms, including humans.² Since humans lack endogenous phytase to break down phytate, PA-rich diets can contribute to mineral deficiencies.^{21,22} Consequently, efforts have been made over the past decades to develop low phytic acid (*lpa*) mutants in various crops, including common bean, to enhance mineral bioavailability as a strategy to combat human nutrient deficiencies.¹⁵ Although such mutants offer potential nutritional benefits, they have received limited attention due to concerns that reduction of PA, not present in human biofluids,²³ may not be entirely beneficial. Some *in vitro* studies and animal trials in which purified PA has been administered suggest, however, that PA exhibits antioxidant and anticancer properties.²⁴

Phytic acid as a natural antioxidant in plants

In plant tissues, PA also functions as a natural antioxidant by chelating free Fe ions, thereby preventing oxidative damage. The Fenton reaction, in which free Fe ions react with oxygen to produce reactive oxygen species (ROS), can severely damage cellular components.²⁵ Studies on maize *lpa1-241* mutants have

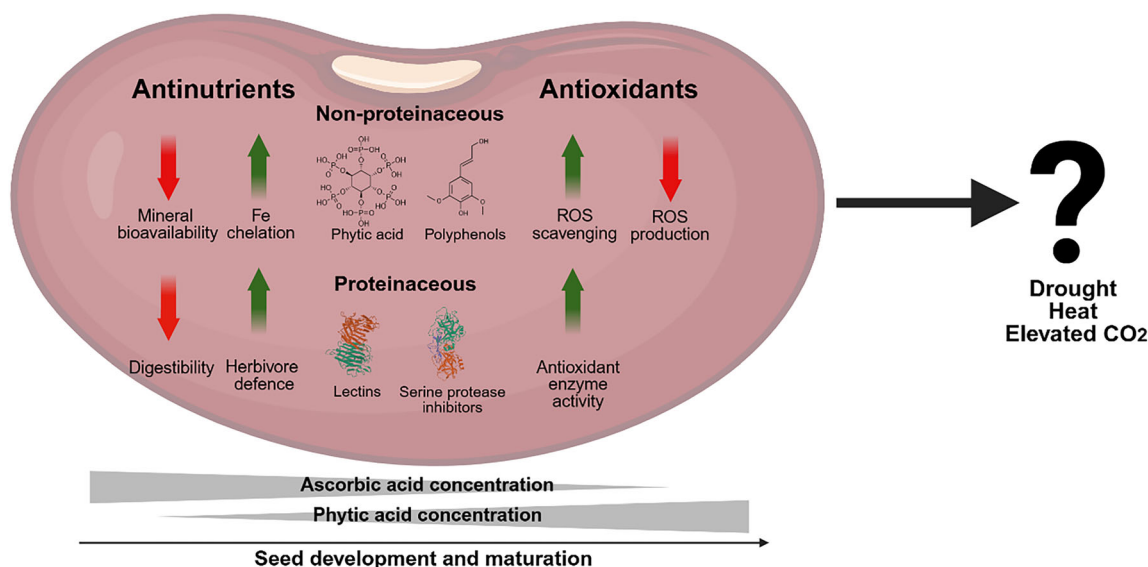


Figure 1. Schematic summary of the dual role of plant compounds, both as antinutrients and antioxidants.

demonstrated that seeds with 50% less PA exhibit a corresponding increase in free Fe, as well as higher levels of free radicals and increased carbonylation of seed proteins after accelerated aging.¹⁹ Furthermore, PA biosynthesis genes in rice and wheat are upregulated by abscisic acid (ABA), a key plant stress hormone involved in drought adaptation.^{26,27} Cultured rice cells exposed to ABA shows an increase in PA production, suggesting a link between PA metabolism and abiotic stress responses.^{28,29} Additionally, knockout studies indicate that reduction in IP₆ levels can alter stress tolerance in plants.³⁰

The impact of abiotic stress on phytic acid in legume seeds

Despite what is known about the role of PA in stress response, it remains unclear whether PA concentrations in legume seeds are significantly influenced by abiotic stress conditions associated with climate change. Existing research has shown that PA accumulates in chickpea seeds under soil water deficit conditions.³¹ Similarly, an increase in PA content was observed in common bean seeds harvested during Malawi's dry winter/off-season compared to those grown under rainfed summer conditions.³² However, our research group has not detected a significant increase in PA levels in common bean seeds subjected to drought stress during pod development, either in greenhouse or field experiments (unpublished results). Further studies are needed to determine the extent to which PA accumulation in legume seeds is influenced by drought, heat, and other climate-related stressors. A deeper understanding of these mechanisms could provide valuable insights into seed nutrient dynamics and their implications for both plant resilience and human nutrition.

Polyphenols, tannins, and saponins: dual roles as antinutrients and antioxidants

Polyphenols, due to their strong protein-binding properties, function both as antinutrients and antioxidants. In the gastrointestinal tract, they inhibit the digestion of starch, lipids, and proteins by interacting with digestive enzymes.³³ Synthesized via the phenylalanine and shikimate pathways, polyphenols include a broad range of compounds, from simple phenolic acids to highly polymerized metabolites.³⁴ As antinutrients, polyphenols form insoluble and non-digestible complexes with proteins – particularly tannin–protein complexes. Additionally, polyphenols rich in catechol or galloyl groups, such as tannic acid, can chelate Fe, reducing its bioavailability through the formation of insoluble mineral complexes.^{35,36}

Apart from their antinutritional effects, polyphenols – characterized by aromatic rings with hydroxyl substitutions – exhibit significant antioxidant properties through their ability to scavenge ROS. The antioxidant capacity of these compounds is influenced by both the number and degree of polymerization of their hydroxyl groups.³⁷ Among polyphenols, tannins are particularly potent antioxidants.³⁸ Initially synthesized as colorless epicatechin compounds, tannins are transported into specialized vacuoles during seed maturation. Within these vacuoles, they undergo polymerization and oxidation, forming glycosylated conjugates as the seed dries.³⁹ Genes involved in tannin biosynthesis, transport, and regulation have been well characterized. Importantly, the expression of tannin biosynthetic genes can be triggered by abiotic stress conditions.³⁸ Although relatively few studies have explored this in depth, tannins have been implicated in phytohormone-mediated responses to environmental stresses such as light and cold.³⁹

Saponins – another class of plant secondary metabolite – likewise display both antinutritional and antioxidant properties. Structurally, saponins consist of a carbohydrate moiety attached to either a triterpenoid or steroid aglycone.⁴⁰ In aqueous environments, they form stable, soap-like foams. As antinutrients, saponins can bind minerals – thereby reducing mineral bioavailability – and interfere with their absorption in the intestine. As antioxidants, saponins can scavenge free radicals. Their biosynthesis is upregulated in response to various environmental stimuli, including light, temperature fluctuations, and drought stress.⁴¹ This stress-induced regulation suggests a potential protective role for saponins in mitigating the effects of abiotic stress in legume plants. In common bean seed saponins are, however, only present in trace amounts and their importance both as antinutrient and antioxidant might be negligible.⁴²

PROTEINACEOUS SEED ANTINUTRIENTS

Lectins

Lectins are carbohydrate-binding proteins distributed across various plant tissues, including storage organs such as seeds and tubers.⁴³ Raw legume seeds often contain high levels of lectins. These proteins act as antinutrients by reversibly binding to glycoconjugates. They are stable in the acidic environment of the gastrointestinal tract and resist degradation.⁴⁴ In humans, lectins interfere with the intestinal absorption of key minerals, including calcium, iron, phosphorus and zinc.⁴⁵ A well-studied example from common bean is phytohemagglutinin (PHA), a tetrameric lectin (~120 kDa) composed of E and L polypeptide subunits. The subunit combinations (L₄, L₃E, L₂E₂, LE₃, E₄) define its erythroagglutinating (PHA-E) and leucoagglutinating (PHA-L) properties, responsible for its binding to erythrocytes and leukocytes, respectively.⁴⁶

In plants, lectins contribute to defense mechanisms against herbivores and pathogens. In common beans, lectins are synthesized and stored within the cotyledons along with other seed storage proteins during seed development.⁴⁷ These proteins are later mobilized during germination to support seedling growth. Beyond nutrient storage, nucleocytoplasmic lectins have roles in plant development, reproduction, and abiotic stress signaling.⁴⁸ Their synthesis can be modulated in response to environmental stressors and is involved in managing the accumulation and degradation of misfolded or stress-induced proteins.^{49–51} However, the precise functional mechanisms of lectins in these pathways still needs to be studied in detail. Using sodium dodecyl sulfate–polyacrylamide gel electrophoresis analysis, our group detected no significant changes in the accumulation of major common bean seed storage proteins, including those in the lectin migration region, in plants subjected to water deficit stress during pod development in greenhouse experiments (unpublished results).

Serine protease (trypsin) inhibitors

Serine protease inhibitors – particularly trypsin inhibitors – are another class of proteinaceous antinutrients abundant in common bean seeds. These inhibitors modulate protease activity *in vivo* by binding and inactivating serine proteases, thereby regulating protein catabolism during seed development, storage, and germination.^{52–55} In legumes, serine protease inhibitors can form up to 10% of total seed protein content.

There are two major families of serine protease inhibitors in legumes: namely, the Bowman–Birk inhibitors and the

Kunitz-type inhibitors, both of which form stable complexes with their target enzymes.⁵⁶ The Bowman–Birk inhibitors represent the predominant family in legume seeds.⁵² In soybeans, for example, at least 11 Bowman–Birk inhibitor genes have been identified, with only three expressed in developing seeds to regulate serine proteases during key developmental phases.^{55,57} These inhibitors also serve a defensive function by inhibiting the digestive processes of seed predators such as insects.⁵⁸

Serine protease inhibitors, particularly trypsin inhibitors, are known to interfere with digestive processes in humans and monogastric animals. High intake of raw or improperly cooked beans, rich in these inhibitors, can result in severe indigestion.⁵⁹ Nonetheless, these compounds have also demonstrated potential colorectal chemo-preventive properties.^{60,61} In breeding programs, the introduction of a KTI (Kunitz trypsin inhibitor) null allele has been used to reduce trypsin inhibitor activity.⁶² Mutations in highly expressed, seed-specific Bowman–Birk inhibitor genes have also led to significantly reduced trypsin and chymotrypsin inhibition activity.⁵⁷

Serine protease inhibitors are also implicated in the plant response to abiotic stress.⁶³ Although they do not function as direct antioxidants, they contribute to cellular defense by inhibiting uncontrolled cell proliferation and enhancing the activity of ROS-scavenging enzymes.⁶⁴ In plants, these inhibitors are generally expressed in response to various environmental stresses, such as drought and elevated CO₂ levels – conditions increasingly associated with ongoing climate change.^{65–69} However, the extent to which such stress-responsive expression occurs specifically in common bean seeds remains largely poorly studied.

FUTURE DIRECTIONS

Will the antinutrient content of pulse seeds change under abiotic stress conditions driven by climate change? To date, research in this area has largely focused on vegetative plant tissues, especially with respect to antioxidants that may also act as antinutrients. In contrast, relatively few studies have addressed how abiotic stresses affect the accumulation of antinutrients in seeds. Although emerging evidence suggests that certain antinutrients – such as PA and phenolics – can accumulate in pulse seeds (e.g., common bean, chickpea, cowpea) in response to drought and heat stress, strong and consistent evidence of a general increase in seed antinutrient production under such conditions remains lacking.^{31,32} Consequently, a key research priority should be the systematic assessment of seed antinutrient profiles in pulses following exposure to climate-relevant abiotic stresses. Elevated atmospheric CO₂ levels – a characteristic of climate change – may reduce PA content in some pulses, as demonstrated in field peas.⁷⁰ Whether this trend extends to other legumes, including common beans, and could enhance seed nutritional quality is an intriguing question deserving further study.

In addition to phenotypic studies, more detailed gene expression studies are required. For instance, it remains unclear how abiotic stress influences PA biosynthesis and its transport into seed globoids. PA is synthesized in the cytosol and transported to globoids via ATP-binding cassette (ABC) transporters. A mutation in one such transporter gene in common bean (*PvMRP1*) significantly reduced seed PA levels.^{71,72} This raises important questions about whether, under stress conditions, transport of PA and other antinutrients with antioxidative traits is enhanced to protect against oxidative damage or stored for seed germination. How

much of the synthesized PA is transported and stored in bean seeds under stress conditions needs to be investigated in more detail.

Another important question concerns whether low PA seed content, while nutritionally favorable, may increase susceptibility to oxidative damage from ROS. Low PA seeds have been associated with reduced germination and seed weight, and stunted growth in other crops.^{12,14} Moreover, reduced PA levels may lead to greater bioavailability of iron and zinc. However, free, unchelated Fe can participate in Fenton-type reactions, generating ROS that damage cellular components and accelerate seed ageing.⁷³ An interesting developmental dynamic is the inverse relationship between ascorbic acid and PA during seed maturation. Ascorbic acid content decreases while PA levels rise, suggesting a potential compensatory antioxidant role for PA.^{12,13} Understanding the interplay between these two antioxidants could reveal strategies to maintain seed vigor while improving nutritional value.

While reducing antinutrients in seeds is an appealing idea to enhance human dietary intake, potential trade-offs must be carefully considered. Antioxidants with antinutrient activity protect seeds against ROS-induced ageing. Because ROS also act as signaling molecules regulating germination, dormancy, and seed development, lowering seed antinutrients may inadvertently alter these key physiological processes.⁷² Similarly, genetic suppression of protease inhibitors such as trypsin inhibitors – either through genetic engineering or selection for low-activity variants – may weaken the seed's defense against insect predation and internal protease damage during development.^{58,67} It is currently unclear whether the expression of such inhibitors is altered in seeds of pulse crops subjected to climate-related stresses. This gap also applies to proteinaceous antinutrients like lectins, whose stress-induced expression and physiological roles remain poorly understood.

Finally, it is important to consider that pulses are not typically consumed raw. Processing methods such as soaking, cooking, or roasting significantly alter the antinutrient profile. Soaking has been shown to reduce PA levels, while heat treatments effectively denature lectins and inactivate protease inhibitors.^{74,75} However, the degree of inactivation is dependent on both temperature and the duration of heating, and in well-processed pulses residual protease inhibitor activity may be negligible. Whether any remaining activity has meaningful implications for human health is still uncertain.

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CONFLICT OF INTEREST

The authors have stated explicitly that there are no conflicts of interest in connection with this article.

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