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Review article

Review: The promise and limits for enhancing sulfur-containing amino acid content of soybean seed

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ABSTRACT

Soybeans are an excellent source of protein in monogastric diets and rations with ∼75% of soybeans produced worldwide used primarily for animal feed. Even though soybeans are protein-rich and have a well-balanced amino acid profile, the nutritive quality of this important crop could be further improved by elevating the concentrations of certain amino acids. The levels of the sulfur-containing amino acids cysteine and methionine in soybean seed proteins are inadequate for optimal growth and development of monogastric animals, which necessitates dietary supplementation. Subsequently, concerted efforts have been made to increase the concentrations of cysteine and methionine in soybean seeds by both classical breeding and genetic engineering; however, these efforts have met with only limited success. In this review, we discuss the strengths and weakness of different approaches in elevating the sulfur amino acid content of soybeans. Manipulation of enzymes involved in the sulfur assimilatory pathway appears to be a viable avenue for improving sulfur amino acid content. This approach requires a through biochemical characterization of sulfur assimilatory enzymes in soybean seeds. We highlight recent studies targeting key sulfur assimilatory enzymes and the manipulation of sulfur metabolism in transgenic soybeans to improve the nutritive value of soybean proteins.

1. Introduction

Soybean is a remarkable crop that in recent times has drastically changed the landscape of agriculture in the United States of America. Although soybeans have been cultivated in Asian countries for centuries, they were introduced into the US as a forage crop in the early 20th century, but have steadily gained in importance and now ranks as the second most important crop in US. The history of soybean introduction to US has been well documented [1]. Currently, the US is the leading global producer of soybean and accounts for ∼34% of worldwide soybean production. In 2016, US farmers planted 83.7 million acres of soybeans worth $38 billion post-harvest (https://www.ers.usda.gov/topics/crops/soybeans-oil-crops/related-data-statistics/).

The two most important reserve components of soybean are the protein and oil. Current commercial soybean varieties accumulate up to 36% protein and 18% oil in their seeds [2], which are processed to yield both meal and oil (http://ncsoy.org/media-resources/uses-of-soybeans/). Soybean is the most dominant oil seed crop and accounts for ∼90% of US oilseed production [3]. Soybean oil is mainly used as edible vegetable oil throughout the world and a portion of it is processed for numerous industrial applications. In recent times, the use of soybean for biodiesel production has been promoted by federal and state subsidies. The other processed byproduct, soybean meal, serves as the world's largest source of animal protein feed. Soybean meal is considered as "gold standard" to which other protein sources are compared [4].

Today, soybean meal is in most animal feed because of its high protein content, balanced amino acid profile, ready availability and relatively low cost; however, the nutritional value of this crop could be improved by enhancing the content of certain amino acids. In particular, the sulfur-containing amino acids cysteine and methionine are not found at adequate levels in soybean seed for optimal growth and development of monogastric animals. The United Soybean Board's Better Bean Initiative (BBI) and poultry industry has identified the improvement of sulfur amino acid content (Methionine + Cysteine) of soybean from the current level of 1.4% to 2.1% as one of the primary meal targets (http://soybeaninnovationlab.illinois.edu/files/PoultrySoybeanUse.pdf). In this review, we highlight recent studies targeting key sulfur assimilatory enzymes and the manipulation of sulfur metabolism in transgenic soybeans to improve the nutritive value of soybean proteins.

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2. Importance of sulfur-containing amino acids in human diet and animal feed

Sulfur-containing amino acids, cysteine and methionine, play a vital role in human health and nutrition [5]. Methionine is an essential amino acid and cysteine is considered to be a 'conditionally' essential amino acid because animals can convert methionine to cysteine. Mammals cannot synthesize either amino acid de novo and are dependent on dietary sources to fulfill their sulfur amino acid requirements. Methionine plays key role in multitude of cellular functions and has a central role in the initiation of mRNA translation. It serves as the precursor of S-adenosylmethionine (SAM), which in turn regulates the levels of other important metabolites like ethylene, biotin, and polyamines. Additionally, SAM is the main methyl group donor that regulates plant growth and development. Cysteine is an important structural and functional component of proteins and enzymes, but also required for cellular components containing reduced sulfur, including methionine, glutathione, homoglutathione, iron-sulfur clusters, vitamin cofactors like biotin and thiamin, and multiple secondary metabolites [6]. Recent studies suggest a role for these amino acids in promoting human health, including cancer prevention, proper function of the immune system, and development of cardiovascular disease [7]. As such, these two sulfur-containing amino acids are indispensable for human and animal nutrition.

It now known that not only the quantity but also the quality of protein is critical for optimum growth of animals. This observation is especially relevant with regard to sulfur-containing amino acids. Deficiency of the sulfur amino acids limits animal growth, results in lowered resistance to disease, and can retard mental and physical development in children [7]. Diets devoid of animal products are deficient in sulfur amino acids. Nutritional sulfur amino acid deficiency is widespread in countries where the intake of animal products is very limited and where diets are primarily based on pulses and cereals. The dietary requirement of sulfur amino acids for humans ranges between 6 and 13 mg per kg body weight or 910–1120 mg per day [7,8]; levels that a Western diet, which contains about 3.6 g per day sulfur amino acids, fulfills [5].

For animals, soybean meal is a preferred protein source in poultry and livestock feed rations. An ideal animal diet should include all nutrients required for maintenance, growth, reproduction, and production of products such as meat, eggs, and milk (https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1046729.pdf). The high protein content of soybean is ideally suited for formulation of animal rations; however, one limiting aspect of soybean protein is the apparent deficiency in cysteine and methionine. The sulfur amino acid content of soybean is about 1.3 g per 100 g per g of protein, which does not adequately meet the recommended 3.5 g of sulfur-containing amino acids per 100 g protein [9]. Consequently, synthetic sulfur amino acids are added during the formulation of diets to maintain the optimal growth and development of poultry and livestock.

3. Supplementing with synthetic amino acids in mixed corn- and soybean-based animal rations

Livestock rations are typically corn and soybean meal based. Poultry and swine are the major consumers of soymeal and account for 22–55% of total soymeal used in livestock rations [10]. Corn is deficient in lysine, but rich in methionine, while soybeans contain relatively high amounts of lysine but low amounts of sulfur-containing amino acids. By balancing soybean and corn in livestock rations, adequate amounts of cysteine and methionine can be provided; however, the amount of methionine available in the soybean-corn based feeds is not optimal to fully meet methionine requirements of poultry and swine [10]. This is especially true with regard to poultry, where methionine deficiency results in retarded growth and poor feed conversion, as well as poor feather growth and increased feather pecking, which could lead to cannibalistic behavior [10]. In the case of pig rations, the most limiting amino acid is lysine followed by methionine, threonine, and tryptophan [11]. A review of the literature indicates that nursery and growing pigs require 10.4–11.2 mg of digestible sulfur amino acids per g of body weight gain [11]. Methionine deficiency can be overcome by inclusion of excessive protein; however, this approach leads to excretion of excess nitrogen, which contributes to environmental degradation and a substantial increase in feed cost.

Alternatively, adding synthetic amino acids to feeds provides a cost-effective solution for meeting the essential amino acid requirements of livestock. Inclusion of synthetic amino acids ensures high levels of feed efficiency and protects the environment by lowering nitrogen excretion. Additional benefits offered by amino acid supplementation include reduction in crude protein content, improved energy utilization, higher availability of amino acids compared with protein bound amino acids, and prevention of digestive disorders [10]. Although the inclusion of synthetic amino acids has advantages, it is also more expensive and organic producers oppose this practice. One potential way to avoid the addition of synthetic molecules to feeds is to develop soybean cultivars with elevated amounts of sulfur-containing amino acids. Population growth mostly in developing countries has elevated the demand for livestock products and prompted the feed industry to look for alternative and cost-effective sources of protein for animal feeds. Soybeans with improved sulfur amino acid content will enhance the nutritive value of soybean not only in animal feed but also as a protein source for humans. In countries where the use of animal protein is limited, the use of nutritionally improved soybean and their derived products such as soy milk should aid in alleviating malnutrition.

4. Can traditional plant breeding improve sulfur-containing amino acid content in soybean?

Better understanding of animal nutrition has highlighted the importance of amino acid profile to animal performance. It is believed that the value of soybean meal is less a function of its protein content and more a function of its amino acid profile [12]. Increasing the concentration of essential amino acids, especially methionine and cysteine, remains a goal in soybean breeding because this crop is the predominant protein source in monastic rations [13]. An estimated 10% increase in methionine content in soybean seed will result in economic benefit of $5 per ton [14].

There is an inverse relationship between soybean seed yield and seed protein content. Early studies have examined the relationship between protein and methionine content of soybean seeds [15,16]. No correlation was found indicating methionine is not likely to decrease as a result of selection for higher protein soybean lines. Variation in the concentration of sulfur amino acid levels in soybean seeds has been reported and could be influenced by environmental factors, nitrogen source, and the availability of reduced forms of sulfur [17–20]. Quantitative trait loci (QTL) associated with methionine and cysteine concentrations in soybean seed have been identified and are found on chromosomes 1, 3, 4, 5, 6, 7, 9, 10, 13, 15, 17, 18 and 20 (https://soybase.org) [19,20]. Several recombinant inbred lines (RILs) were found to contain cysteine and methionine levels above the United Nations Food and Agriculture Organization (FAO) standards [19]. Using a linkage map derived from soybean RIL mapping populations, new QTLs for cysteine and methionine concentration were reported on chromosomes 2 and 20 [21]. Population-based mapping approaches such as genome-wide association (GWA) scans revealed the presence of strong candidate alleles for sulfur amino acid content on chromosomes 1 and 8 [22]. Even though several QTLs and candidate alleles associated with amino acid content have been reported, they have not resulted in the commercial development of soybean cultivars with improved sulfur amino acid content.

Further investigations of the genetic basis for soybean seed protein quality both by family-based and population-based mapping