Narrative Review Article

Bound Niacin Formation and Biofortification of Free Niacin in Maize

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ABSTRACT

Maize (*Zea mays*) is one of the major staple crops worldwide and plays a crucial role in the human diet as a source of vitamin B3, also known as niacin. However, a large proportion of niacin exists in a bound form that is poorly bioavailable to humans. When a population depends on bound niacin, insufficient niacin availability will lead to pellagra, a disease caused by niacin deficiency. Due to the significant negative impact of pellagra, researchers have examined the biochemical mechanism of bound niacin information. The review summarizes key genes and environmental factors that affect the total niacin and bound niacin concentrations in the maize kernel. Understanding the formation mechanism of bound niacin can inspire scientists to develop possible methods to enhance the bioavailability of niacin and nutritional biofortification, thereby reducing the global issue of niacin-deficiency-induced hidden hunger.

Keywords: Maize; Biofortification; Niacin; Bound niacin; Pellagra; Bioavailability

INTRODUCTION

Maize (*Zea mays*) is one of the most productive and dominant staple crops worldwide, serving as one of three great grain crops in the world (1). More than 1.2 billion people in sub-Saharan Africa and Latin America depend on maize as a dietary staple (2). Maize contains niacin, also known as vitamin B3, which plays an essential role in the human metabolism process of cellular respiration. Niacin is a precursor of NAD+, an essential coenzyme during cellular respiration (3-4). However, a substantial proportion of niacin in maize kernel is in a bound form and is mainly located in the aleurone layer and endosperm cell wall (Figure 1). Bound niacin, as opposed to free niacin, is not easily absorbed in the human digestive system (6). In bound niacin, free niacin is attached to glycopeptides, polysaccharides, and phenolic compounds through ester linkage; therefore, it cannot be broken down by enzymes and acids in the stomach (6-7). Ester linkage is a covalent bond formed between a hydroxyl group and a carboxylic acid group, which is generally

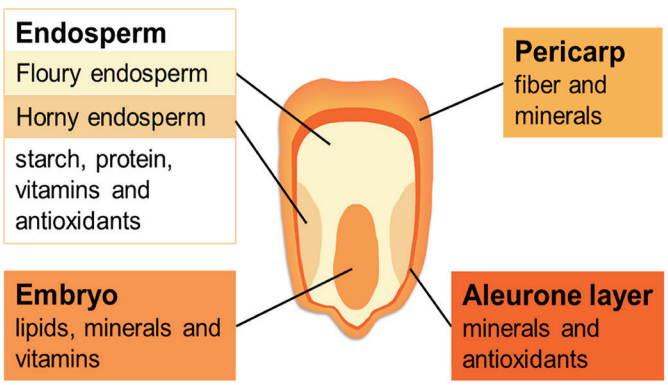

Figure 1. *The structure of the maize kernel and the location of the aleurone layer. Reproduced from reference (27).*

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susceptible to hydrolysis (8). In bound form, the ester linkage is alkali-labile, indicating that bound niacin can be released under basic conditions (6). This property explains why bound niacin has low bioavailability in the human digestive system.

The low bioavailability of bound niacin in maize results in a serious malnutrition-related disease called pellagra. Many areas that depend on a maize-based diet are affected by pellagra, especially in low-income southern African countries (9). Studies indicate that pellagra is caused by niacin deficiency and has a clear correlation with corn consumption, which can be found in many historical events and can be seen as a type of hidden hunger (10). In today's world, even though pellagra has been largely controlled in most developed countries such as the United States, it remains a health concern in several low-income regions, including Malawi, Zambia, Zimbabwe and Lesotho (9). This public health issue highlights the importance of improving the nutritional quality of maize and increasing the free niacin proportion in the maize kernel.

Adequate niacin intake is necessary to prevent pellagra. Besides consuming niacin directly, humans can obtain niacin through the tryptophan metabolic pathway (11-12). As an essential amino acid in the human body, tryptophan can be metabolized into multiple bioactive metabolites, including serotonin, melatonin, kynurenine, and niacin (13). The conversion of tryptophan to niacin is approximately 60:1, meaning that about 60 mg of tryptophan is required to synthesize 1 mg of niacin (14). Therefore, tryptophan metabolism should be considered when evaluating strategies to enhance niacin availability.

Previous studies have suggested that improvement of free niacin content may involve modification of the tryptophan oxidation pathway (15). However, modern science has not yet identified an appropriate model for enhancing niacin levels in maize. Therefore, this review summarizes the molecular and biochemical mechanisms of bound niacin formation and evaluates the potential strategies to increase the free niacin content in maize via key genetic or enzymes involved in the niacin synthesis process.

BIOCHEMICAL BASIS OF BOUND NIACIN FORMATION IN MAIZE KERNEL

Isolation and Characteristics of Niacin

Nixtamalization, a traditional processing method involving alkaline treatment of maize, can release bound niacin and improve its bioavailability (16). This technique highlights the importance of chemical structure in determining niacin availability in maize-based diets.

Understanding pellagra requires investigation of niacin metabolism and bioavailability. Niacin was first isolated, and its nutritional role was characterized by Conrad Arnold Elvehjem and colleagues in 1937 (17). This discovery demonstrated pellagra can be treated with niacin and established the relationship between niacin consumption and pellagra. Following this discovery, researchers further investigated how niacin is synthesized in both humans and plants, including maize kernels. The result demonstrates that niacin can be synthesized through the tryptophan oxidation pathway in both humans and maize (15). In this pathway (Figure 2), the essential amino acid tryptophan is converted into niacin through multiple stages, involving intermediate metabolites such as N'-formylkynurenine, kynurenine, 3-hydroxykynurenine, and 3-hydroxyanthranilic acid (18). This process represents a major route for niacin biosynthesis in both maize and humans. However, in the human body, this conversion is inefficient, requiring approximately 60 mg of tryptophan to produce 1 mg of niacin (14). This low conversion rate highlights the importance of adequate dietary niacin intake. It also emphasizes the importance of increasing bioavailable niacin in maize, particularly in regions that rely on maize as a staple crop.

Structure and Formation of Bound Niacin in Maize Kernel

Bound niacin refers to free niacin molecules that are covalently linked to glycopeptides, polysaccharide

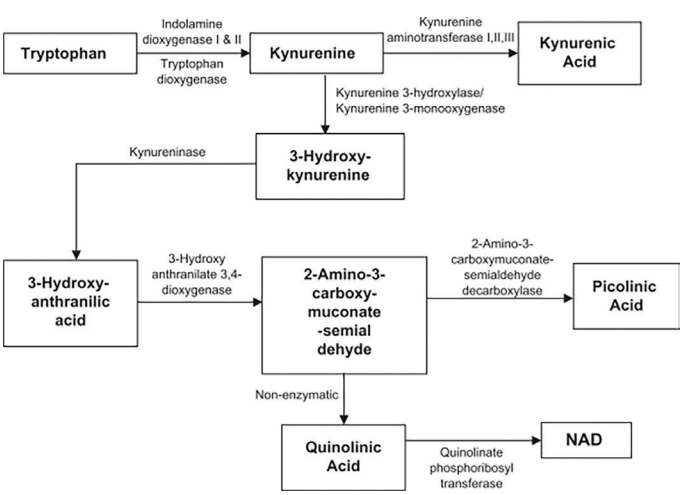

Figure 2. *The tryptophan oxidation pathway (kynurenine pathway). Reproduced from reference (19).*

and phenolic compounds through ester linkage (15). Specifically, niacin is esterified to hydroxyls group of arabinoxylan polysaccharides and peptide-phenolic complexes within the aleurone cell wall matrix. This structure forms when the carboxyl group of niacin reacts with hydroxyl groups on arabinose side chains, peptides, and phenolic acids such as ferulic acid. This complex matrix yields a three-dimensional network that is highly stable under normal digestive conditions. It resists degradation in acidic environments and by digestive enzymes such as amylase, protease, and esterase. Due to the steric hindrance, the structure prevents digestive enzymes from accessing the ester bond. The ester linkage can be broken down under basic conditions, such as during nixtamalization, thereby releasing niacin and improving its digestibility (20).

Anatomical evidence indicates that approximately 60% to 70% of total niacin is localized in the aleurone layer of the kernel. Previous studies have shown that sugary (su) kernels have an aleurone layer that is approximately 1.4 times thicker and 1.8 times heavier than starchy kernels, resulting in a higher total niacin content. Therefore, increasing the proportion of the aleurone layer may enhance niacin concentration in maize kernel (21-22).

Both free niacin and bound niacin accumulate during the maturation stage of maize kernel development (6). However, a large proportion of free niacin becomes bound niacin within the aleurone cell wall matrix (6). This conversion occurs in the late maturation stage of kernel development. It is associated with the formation of the aleurone cell wall, which increases the accumulation of arabinoxylan and phenolic acid, particularly ferulic acid. As a result, the amount of bound niacin increases significantly (6). This discovery also explains why young maize kernels contain more free niacin than mature corn kernels.

Niacin (vitamin B3) correlates with other B vitamins, including vitamin B1 (thiamine), vitamin B2 (riboflavin), and vitamin B6 (pyridoxine). In a study of 156 maize inbred lines, moderate positive correlations were observed between B group vitamins. These findings suggest that high-niacin maize is also associated with high levels of vitamin B1, B2, and B6 (23). Correlated analysis showed that the strongest significant correlation coefficient was extracted between niacin and vitamin B1 (r=0.35), B2 (r=0.50), and B6 (r=0.56). This finding suggests the B group vitamins have a shared metabolic and biosynthetic pathway in maize kernels (23). This discovery is particularly important because it indicates that improving niacin content involves a process of improving multivitamin levels in the maize kernels and gives humans more nutritious foods with maximum benefits.

KEY GENES AND ENZYMES THAT PLAY A ROLE IN NIACIN LEVELS

Genes That Influence Niacin Content via Tryptophan Metabolism

The niacin content is controlled by multiple genes rather than by a single Mendelian gene. These genes can be classified into two categories: those that increase tryptophan and those that directly increase the niacin (24). One such gene is opaque-2 (o2), which increases the tryptophan content. Studies indicate that the o2 gene, located on chromosome 7, reduces the zein fraction, a class of prolamin protein, and has a low concentration of tryptophan (25). The o2 also increases the non-zein fraction, which is enriched in essential amino acids such as tryptophan and lysine (25-26). In the study of o2 introgression, the recurrent parent UMI1200 is a maize inbred line that is well adapted to tropical and semi-arid regions and has excellent agronomic performance. However, it contains a low level of several essential amino acids, including tryptophan and lysine. The donor parent, VQL1, is a maize inbred line carrying an o2 mutation; however, it has poor yield and produces kernels with a soft, opaque texture, traits that are undesirable to consumers. The results of hybridization of UMI1200 and VQL1, together with the corresponding tryptophan concentrations are shown in Table 1.

Table 1. *Tryptophan Concentrations in Kernels of the Offspring Derived from VQL1 × UMI1200, demonstrating the improvement in tryptophan content compared to the recurrent parent. The offspring have relatively high tryptophan content. Data adapted from (25).*

Offspring line (VQL1 donor parent × UMI1200 recurrent parent)	Tryptophan concentrations
DBT-IC-β2σ5-9-51-51	0.081%
DBT-IC-β2σ5-9-52-52	0.083%
DBT-IC-β2σ5-9-53-53	0.078%
DBT-IC-β1σ4-4-8-8	0.082%
DBT-IC-β1σ4-9-21-21	0.079%
DBT-IC-β1σ4-10-1-1	0.081%

As shown in Table 1, the offspring line has a relatively higher concentration of tryptophan than the recurrent parent UMI1200, which contains 0.013% of tryptophan (26). This result is consistent with the recessive inheritance of o2, in which the high-tryptophan phenotype is expressed only in homozygous recessive individuals. However, the disadvantage of o2 is associated with a chalky texture. To address this problem, marker-assisted selection (MAS) can be used to identify the individual that contains the target gene and favorable markers associated with improved kernel texture (26-27).

Several enzymes are involved in tryptophan synthesis. As an aromatic amino acid, tryptophan synthesized through the shikimate pathway (13). In this pathway, one of the most important enzymes is anthranilate synthase (ASA), which is the rate-limiting enzyme in tryptophan synthesis and converts chorismate to anthranilate (28). However, when the tryptophan concentration becomes sufficiently high, tryptophan acts as a feedback inhibitor. It binds to the allosteric site of anthranilate synthase, causing a conformational change that decreases catalytic activity and suppresses the pathway (13). These findings highlight the importance of regulating genes associated with anthranilate synthase in order to enhance tryptophan content and indirectly influence the total niacin content.

Genes Directly Influence the Niacin Level

Moreover, some genes directly influence the niacin concentration in the maize kernel. Currently, one of the most well-studied loci is the Su/su system, where Su is the dominant gene with the phenotype of starchy kernel and su is the recessive gene with phenotype of sugary kernel (24, 29).

Five major endosperms of maize kernel, pop, flint, dent, flour and sweet have been identified in maize varieties originating from Maize of American Indigenous Societies (MAÍS) Southwest, and controlled grow-outs at the New Mexico State University Agricultural Science Center fields. All the maize kernel samples were analyzed at the Food Product and Safety Lab for biochemical compositional trait analysis (29). The result shows that sweet corn has the highest total niacin level with 3.63mg/100g. The four remaining endosperm types have a total niacin concentration ranging from 1.13mg/100g to 1.92mg/100g. The sweet endosperm type demonstrates substantially higher total niacin content compared to the other varieties (29)

Most of the niacin is located in the aleurone layer of the maize kernel (21). Because starch occupies a large proportion of the endosperm, the relative proportion of the aleurone layer is reduced, leading to a decrease in niacin content (21). Conversely, carrying the su gene has a reduced proportion of starchy endosperm and induced aleurone layer proportion, which is associated with higher niacin concentration. Therefore, sweet maize kernels (su) retain significantly higher concentrations of niacin than starchy maize kernels (Su).

Moreover, the effects of the su allele on niacin content are not uniform across sweet maize inbred lines. This suggests that its allelic effects vary among genetic backgrounds and may be influenced by other regulatory genes and environmental factors.

Quantitative Trait Loci Associated with Niacin Content in Maize

In addition to gene o2 and su, studies determined that the inheritance of niacin content in maize is also influenced by quantitative trait loci (QTLs). These QTLs have been detected on chromosomes 4, 8 and 10 (30). QTL is a genomic region associated with variation in quantitative trait (31).

These loci influence two major traits: total niacin concentration (including bound niacin and free niacin) and free niacin concentration. For example, on chromosome 4, qFNA4a regulates free niacin concentrations, whereas qTNA4a regulates the total niacin concentration. These QTLs share a common molecular marker, umc1294 (bin 4.02). The naming of these QTLs reflects the trait and chromosomal location: "q" denotes QTL, "FNA" and "TNA" refer to free and total niacin, respectively, and "4a" indicates their position on chromosome 4 (30). Similarly, qFNA8b and qTNA8c are associated with free niacin and total niacin content and share a common interval between marker umc1959-umc1562 (Bin 8.05), indicating that genes controlling niacin content are likely located within this region. "umc" refers to a microsatellite marker system developed by the University of Missouri, Columbia, used to identify specific genomic positions.

A cluster of minor-effect QTLs was also identified on chromosome 10 (bin10.01~bin10.03). Moreover, the heritability of both total niacin and free niacin concentration has been estimated at approximately 70%, indicating strong genetic control and potential for breeding programs targeting increased niacin levels (30).

ENVIRONMENTAL FACTORS THAT PLAY A ROLE IN NIACIN LEVELS

Temperature Effects on Niacin Content in Maize

Since niacin synthesis and its conversion to the bound form are closely linked to kernel development, cell wall formation, and shared metabolic pathways with other B vitamins—any external factors that influence the maturation of maize kernel may also affect total niacin levels. Therefore, environmental factors are also important and need to be considered.

The same study of 156 maize inbred lines reported the maize with the same genotype, when grown in Ledong, Hainan, China (longitude: 108.884767; latitude: 18.708674), and Langfang, Hebei, China (longitude: 116.61489; latitude: 39.608688), have significant variation in their B vitamins levels (23). The study reported that niacin content in the inbred lines was approximately twofold higher in Hebei than in Hainan (112.80 ± 1.86 μg/100 g vs. 44.66 ± 0.76 μg/100 g). Meanwhile, the maize inbred lines grown in Hebei also showed significantly higher levels of B1, B2, B5 and B6 than those grown in Hainan (23).

The results indicate that the environmental effects on B vitamins accumulation are significant. The possible explanation for this occurrence is variation in climate conditions, such as temperature. As a tropical region, Hainan has an annual mean temperature of approximately 26.7°C. In comparison, Hebei has a temperate monsoon climate with an annual mean temperature of approximately 12.5°C. An experiment conducted in Palmerston, New Zealand, showed that higher temperature increased maize growth rates (32). Therefore, temperatures may also affect the accumulation of niacin during maize kernel maturation.

Influence Of Soil Nitrogen Availability on Niacin Content in Maize

Given that tryptophan is the precursor of niacin, environmental factors that affect tryptophan synthesis are likely to alter total niacin concentration. As an essential element in organisms, nitrogen plays a crucial role in building important organic molecules, including amino acids. After nitrate (NO_3^-) or ammonium (NH_4^+) is absorbed by the roots, it is assimilated into glutamate and glutamine, which serve as the primary donors for amino acid biosynthesis (33-34). Therefore, low soil nitrogen availability may reduce the efficiency of amino acid biosynthesis. Consequently, reduce tryptophan content and indirectly lower niacin content.

CONCLUSION

The review examined the formation mechanisms of bound niacin and methods to enhance free niacin and total niacin in maize kernels. Niacin in maize is synthesized via the tryptophan oxidation pathway and during maturation (15). Free niacin binds to the arabinoxylan polysaccharides, peptides and phenolic acids found on the cell wall of the aleurone layer in the maize kernels. This review also summarized several target genes and loci that directly or indirectly regulate total and bound niacin content, including o2, su, anthranilate synthase and the QTLs that regulate the niacin concentration. Moreover, environmental factors also play a vital role in niacin content.

As a serious public health issue, hidden hunger has also gradually come to the forefront (35). Hidden hunger occurs when people consume an energy-dense, but nutrient-poor diet, which results in the deficiencies of multiple micronutrients such as niacin, vitamin A, zinc, iodine and iron (35). Statistically, over 2 billion people worldwide are affected by hidden hunger, particularly in low- and middle-income countries where people usually do not have the ability to process food or reach high-nutrient food (35). Meanwhile, maize has become the second most abundant cereal crop, and hundreds of millions of people depend on it as a major food source (36). For this reason, the task of enhancing the nutritional value of maize and releasing bound niacin becomes particularly important. In addition, the success of breeding the high-free niacin maize may provide a beneficial model for scientists to apply to other crops that require improvement in the levels of B vitamins or other members of the B vitamins. By studying high-free-niacin maize, researchers can better understand plant metabolic systems, particularly B-vitamin and niacin metabolism.

However, current researchers still have a poor understanding about the deeper formation mechanism of bound niacin in maize kernels, such as the genes and enzymes that directly cause the ester linkage between free niacin, polysaccharides, peptides, and phenolic acids. Therefore, one problem is limited literature and research that directly examines the release of niacin from its bound form during the maturation of maize kernels, highlighting a significant gap in present nutritional biofortification studies. Likewise, current studies are lacking the effective model for the relationship between the environmental conditions and the niacin bioavailability. These gaps suggest that future studies should focus on the genes and enzymes that take part

in the regulation of bound niacin, and different natural environmental conditions.

Given the importance of improving niacin levels and bioavailability in maize, it is essential to explore practical strategies to achieve this vision. By understanding the mechanisms of bound niacin formation, future research should focus on the tryptophan enhancement and the maturation regulation. One of the most efficient approaches is the use of gene-edition technologies to target key genes that affect the genotype and enzyme, such as marker assisted selection (MAS), which is a widely used and efficient method to achieve the target genes for the crops (27). Besides, future breeding programs could also focus on incorporating favorable alleles such as o2 and su into maize through genetic engineering or conventional hybridization to enhance both protein quality and niacin bioavailability. Furthermore, these studies suggest that environmental factors, such as temperature and soil fertility, play a significant role in nutritional value and global public health.

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CONFLICT OF INTEREST

The author declares that there are no conflicts of interest related to this work.

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