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- Review -

The Role of Glutamic Acid-producing Microorganisms in Rumen Microbial Ecosystems

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Microbial protein is one of the sources of protein in the rumen and can also be the source of glutamate production. Glutamic acid is used as fuel in the metabolic reaction in the body and the synthesis of all proteins for muscle and other cell components, and it is essential for proper immune function. Moreover, it is used as a surfactant, buffer, chelating agent, flavor enhancer, and culture medium, as well as in agriculture for such things as growth supplements. Glutamic acid is a substrate in the bioproduction of gamma-aminobutyric acid (GABA). This review provides insights into the role of glutamic acid and glutamic acid-producing microorganisms that contain the glutamate decarboxylase gene. These glutamic acid-producing microorganisms could be used in producing GABA, which has been known to regulate body temperature, increase DM intake and milk production, and improve milk composition. Most of these glutamic acid and GABA-producing microorganisms are lactic acid-producing bacteria (LAB), such as the *Lactococcus*, *Lactobacillus*, *Enterococcus*, and *Streptococcus* species. Through GABA synthesis, succinate can be produced. With the help of succinate dehydrogenase, propionate, and other metabolites can be produced from succinate. Furthermore, clostridia, such as *Clostridium tetanomorphum* and anaerobic micrococci, ferment glutamate and form acetate and butyrate during fermentation. Propionate and other metabolites can provide energy through conversion to blood glucose in the liver that is needed for the mammary system to produce lactose and live weight gain. Hence, health status and growth rates in ruminants can be improved through the use of these glutamic acid and/or GABA-producing microorganisms.

Key words : Gamma-aminobutyric acid, glutamate decarboxylase gene, glutamic acid, lactic acid bacteria, rumen

Introduction

All animals including ruminants require amino acids, which are the monomers of proteins. Amino acids are necessary for optimal growth, reproduction, lactation, and maintenance [20]. Glutamic acid is one of the amino acids (non-essential) that is used to form proteins. It is used by almost all living things and can be found in all foods containing protein. It is also a neuroexcitatory neurotransmitter chemical that helps nerve cells in sending and receiving information from other cells [8]. Glutamic acid is an important metabolic intermediate that can be synthesized from glutamine by the enzyme glutaminase (glutamine amidohydrolase) and glutamine synthetase (glutamate-ammonia ligase). Moreover, it is used as fuel in the metabolic reaction in the body, synthesis of all proteins for muscle and other cell components, and very essential for proper immune function [10]. Furthermore, glutamic acid is a precursor of arginine which may contribute to blood pressure reduction [34]. Aside from the above-mentioned application of glutamic acid, it is also used as surfactants, buffer, chelating agents, food additive, flavor enhancer, culture medium, and in agriculture such as growth supplements [10, 31].

In the body, glutamic acid turns into glutamate, an ionic form of glutamic acid. Glutamates are carboxylate anions and salts of glutamic acid [10] that are the most abundant transmitter in the nervous system that transmits 40% of all synapses in the brain [1]. It is an important metabolite that links the metabolism of carbon and nitrogen [30]. It also function as substrate for the synthesis of various metabolites, nucleic acids, nucleotides, and amino acids [36]. This plays a pivotal role in the life processes has many functions such as a substrate for protein synthesis, a precursor of glutamine, N transport (muscle-glutamine; brain), a neurotransmitter (and γ-aminobutyrate), polyglutamate and cell signaling, δ-

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Carboxylation of glutamate, a substrate for glutathione production, a precursor of N-acetyl glutamate, active sites of enzymes, an inhibitor of glutaminase reaction, citric acid cycle intermediate, and energy source for some tissues (mucosa) [38]. Moreover, glutamate uses several enzymes in its metabolism and these are glutamine synthetase, glutaminase, glutamate dehydrogenase, aspartate transaminase or glutamate oxaloacetate transaminase, and glutamic acid decarboxylase (GAD) [10].

Glutamic acid decarboxylase

Glutamic acid decarboxylase (GAD) is an important enzyme involved in the synthesis of gamma-aminobutyric acid (GABA) (Fig. 1). Gad gene manipulation can also either increase or decrease the activity of enzymes in bacteria [34]. Its activity depends on vitamin B6 and a sufficient level of sulfate ions and PLP cofactor are needed for this process [16]. The GAD has isoforms such as GadA, GadB, and GadC [23]. GadA and GadB catalyze the conversion of L-glutamic acid to GABA [3] while GadC encodes the antiporter implicated in GABA export [23] that transported L-glutamic acid into a cell [7]. The decarboxylation of L-glutamic acid is catalyzed by GAD with cofactor pyridoxal-5′ -phosphate (PLP), and leads to the formation of GABA and release of CO_2 as a byproduct (Fig. 1). Finally, through GadC, the GABA decarboxylated product is exported to the extracellular matrix. Cui et al. [7] stated that the expression of enzymes glutamate decarboxylase (GadB/GadA); glutamate: γ-aminobutyrate antiporter (GadC); L-glutamate dehydrogenase (GDH); glutamate synthase (GltB); isocitrate dehydrogenase (Icd), and phosphoenolpyruvate carboxylase (PEPC) will increase GABA production while the expression of enzymes GABA aminotransferase (GABA-AT), succinate semialdehyde dehydrogenase (SSADH), and malate dehydrogenase (MDH) will decrease GABA production.

Glutamic acid and gamma-aminobutyric acid (GABA)

Glutamic acid and gamma-aminobutyric acid are both from the glutamine/glutamate family of amino acids [27]. Glutamic acid is a substrate in the bioproduction of gamma-aminobutyric acid (GABA). Gamma-aminobutyric acid (GABA) is an amino acid not found in proteins that are widely distributed in plants, animals, and microorganisms [21]. It is considered as a potent bioactive compound that improves brain plasma levels, protein synthesis, and growth hormone [5] that made it effective in the treatment of hypotension, sedation, diuretics as well as diabetes [9, 18]. It has also other known physiological functions, including protective effects against neurotoxicant-induced cell death [5] and improving the growth rates and health status of calves [24].

GABA in the central nervous system of mammals is a major inhibitory neurotransmitter. There are two types of GABA receptors, GABA1 and GABA2, which function as the ionotropic and metabotropic receptors for action [13]. It is ultimately derived from glucose metabolism [4], the most important physiological event that stimulates mRNA translation and insulin gene transcription. GABA synthesis depends on the enzyme glutamic acid decarboxylase (GAD) [25]. It is synthesized through the irreversible α-decarboxylation of L-glutamic acid, which is catalyzed by GAD, and in the process consumes one proton and releases CO_2 (Fig. 1) [5, 11, 16].

The intermediary metabolite, α-ketoglutarate also named 2-oxoglutarate links glutaminolysis in the tricarboxylic acid (TCA) cycle. Then, with the help of the enzyme GABA α-oxoglutarate transaminase (GABA-T) α-ketoglutarate transaminated to the amino acid glutamate [13]. GABA is also used as a transmitter in the cell wherein the glutamate derived from α-ketoglutarate transforms to GABA with the presence of the enzyme GAD. Through the GABA shunt (Fig. 2), the GABA transaminase enzyme catalyzes the con-

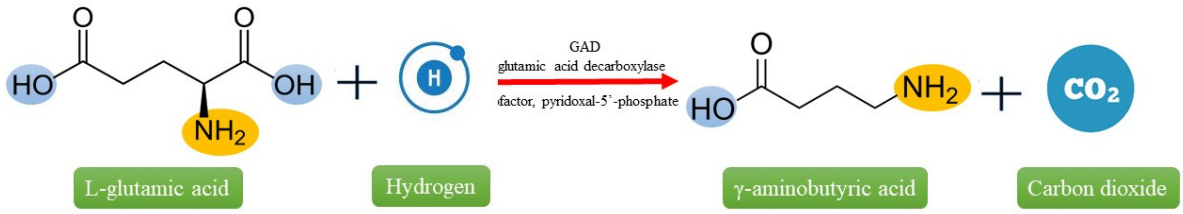

Fig. 1. Decarboxylation catalyzed by glutamic acid decarboxylase (GAD).

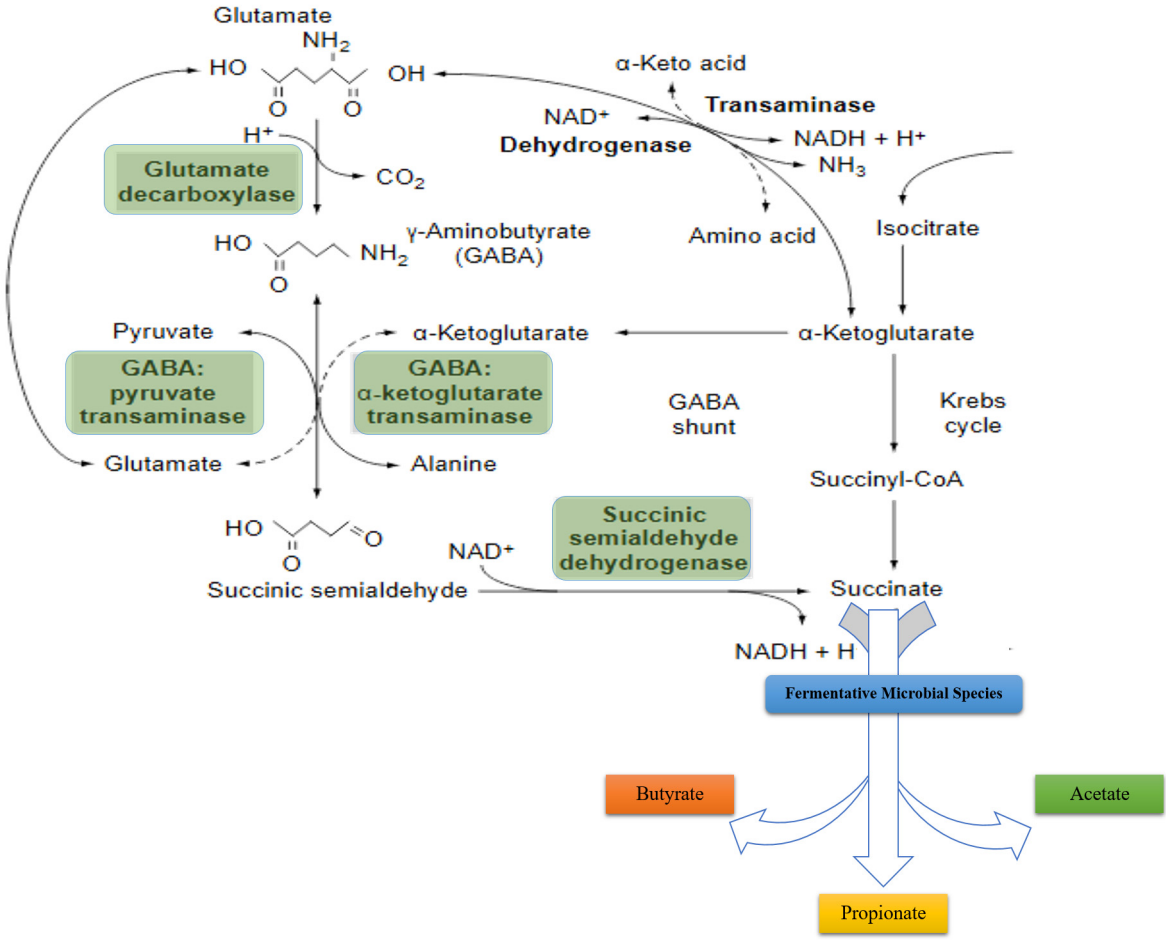

Fig. 2. The GABA shunt.

version of GABA and 2-oxoglutarate into succinic semialdehyde and glutamate, respectively. Gagné, F. [13] stated that the key enzyme in the TCA cycle is the 2-oxoglutarate dehydrogenase complex (ODHC). This enzyme acts as the branching point of metabolic flux between energy supply and L-glutamate synthesis [13]. Moreover, ODHC and GDH compete for the substrate α-ketoglutarate [7]. The succinic semialdehyde dehydrogenase is then oxidized succinic semialdehyde into succinic acid. Then, it enters the citric acid cycle and is used as a source of energy [29]. Cui et al. [7] stated that the expression of enzymes glutamate decarboxylase (GadB/GadA), glutamate: γ-aminobutyrate antiporter (GadC), L-glutamate dehydrogenase (GDH), glutamate synthase (GltB), isocitrate dehydrogenase (Icd), and phosphoenolpyruvate carboxylase (PEPC) will increase GABA production.

Microorganisms' glutamic acid and GABA production in the rumen

In the rumen, there are several sources of protein. One of which is the microbial protein that can also be the source for glutamate production. However, glutamate production is one of the factors affecting the fermentation process and the biosynthesis of GABA in microorganisms. Van Den Hende et al. [15] stated that there is very little information available concerning rumen bacteria's mechanism on the glutamic acid fermentation. They stated on their study on the fermentation of glutamic acid using washed suspension of rumen bacteria that the optimum pH fermentation of glutamate was measured by rate of ammonia production and the optimal pH for deamination of glutamic acid varied from 6.5 and 7, which is optimal pH for ruminants due. On the other hand, Dhakal et al. [9] stated that most of the glutamic acid and GABA-producing microorganisms produced GABA the highest at pH 5.0 or below. However, decreased ruminal and reticular pH resulted in changes in the bacterial composition and lower bacterial diversity due to higher acidity [17]. With this, the supplementation in combination of glutamic

acid and GABA producing bacteria in the rumen will balance the pH in the rumen, and thus, beneficial for ruminants.

Traditional fermented foods are produced by microbial fermentation. During microbial fermentation, metabolites are produced through the action of glutamic acid decarboxylase. Table 1 shows the beneficial microorganisms that have glutamic acid decarboxylase and/or produce glutamic acid and/or GABA. The production of glutamic acid and GABA by microorganisms vary and is species-dependent [9]. Most of these microorganisms are lactic acid-producing bacteria (LAB) such as Lactococcus, Lactobacillus, Enterococcus, and Streptococcus species. In addition, different strains and species of Clostridia had been investigated as having anaerobic metabolism of glutamic acid [15]. Two of these are *Clostridium tetanomorphum* and anaerobic Micrococci that ferments glutamate and formed acetate and butyrate during fermentation [15].

Glutamic acid and GABA in ruminants

Microbial protein synthesis in the rumen and the undegraded dietary amino acid in the rumen sources are the

Table 1. Beneficial microorganisms that produce glutamic acid and/or GABA

	Microorganism	Growth temperature range / Optimum growth temperature	Presence of GAD	Glutamic Acid Production	GABA production	Reference
1	*Brevibacterium* sp.	4-42℃ / 21-28, 37℃		Yes		[12, 26]
2	Corynebacterium glutamicum	25-37℃		Yes		[2, 14]
3	*Enterococcus avium*	37℃	Yes			[7, 39]
4	*Enterococcus faecium*	0.1-53.4 / 30℃	Yes			[7, 22]
5	*Enterococcus faecalis*	30℃	Yes			[7]
6	*Lactobacillus acidophilus*	37℃	Yes			[7]
7	*Lactobacillus antri*	28-37℃	Yes			[7]
8	*Lactobacillus brevis*	30-32℃	Yes		Yes	[9, 34, 35]
9	*Lactobacillus buchneri*	22-28℃			Yes	[9]
10	*Lactobacillus casei*	30℃	Yes			[34]
11	*Lactobacillus coleohominis*		Yes			[7]
12	*Lactobacillus curvatus*	28-38℃	Yes			[7]
13	*Lactobacillus delbrueckii* subsp. *bulgaricus*	42℃			Yes	[9, 37]
14	*Lactobacillus farraginis*		Yes			[7]
15	*Lactobacillus fermentum*					[35]
16	*Lactobacillus futsaii*	37℃	Yes			[7, 37]
17	*Lactobacillus gastricus*		Yes			[7]
18	*Lactobacillus oris*		Yes			[7]
20	*Lactobacillus paracasei*	48℃	Yes		Yes	[9, 34, 37]
21	*Lactobacillus paraplantarum*		Yes			[7]
22	*Lactobacillus plantarum*	37℃	Yes	Yes	Yes	[9, 34, 40, 41]
23	*Lactobacillus reuteri*		Yes			[33]
24	*Lactobacillus rossiae*		Yes			[7]
25	*Lactobacillus sakei*		Yes			[7]
26	*Lactobacillus zymae*		Yes			[7]
27	*Lactococcus garvieae*		Yes			[7]
28	*Lactococcus lactis*	30℃	Yes		Yes	[9, 34, 37]
29	*Monascus purpureus*				Yes	[9]
30	*Pediococcus acidilactici*	30℃	Yes			[7]
31	*Rhizopus microspores* var. *oligosporus*				Yes	[9]
32	*Streptococcus salivarius subsp. thermophilus*				Yes	[9]
33	*Streptococcus thermophilus*	30℃	Yes			[34, 37]
34	*Streptomyces bacillaris*				Yes	[9]

GABA - Gamma-aminobutyric acid
GAD - Glutamic acid decarboxylase

sources of the absorbed amino acid in ruminants [20]. The protein digested in cattle constitutes more than 50% of the microbial crude protein [32]. The average glutamic acid composition was 12.83, 13.11, and 14.36 g of amino acids per 100 g of amino acids in cattle rumen fluid-associated and particle-associated, and protozoa, respectively [32]. Rumen bacteria washed suspensions degraded L-glutamate and L-glutamine and produced acetic acid, propionic acid, and butyric acid of 112 and 110, 30 and 25, 15 and 16 μmoles per 100 μmoles substrate, respectively [15]. These acetate, propionate, butyrate, and other metabolites produced by the microorganisms can be used as the source of energy in ruminants that eventually improves animal performance.

GABA has certain physiological functions such as increase DM intake, milk production, improve milk composition, and regulating body temperature. GABA may be integral to optimal digestion and absorption of nutrients from different segments of the ruminant gastrointestinal tract when nutrient flows from feed do not allow optimal digestion. GABA is synthesized from glutamate by GAD and is metabolized by GABA-AT to produce succinate [6](Fig. 2). Propionate can be produced from succinate through succinate dehydrogenase, which increased the propionate production in the study of Ku et al. [19] when they amended GABA-producing bacteria. In addition, propionic acid can also be produced from pyruvate in the presence of acetyl phosphate [15]. The propionate produced in the rumen is the most important and single main precursor required that makes a significant net contribution (quantitatively) for glucose synthesis. It provides energy via blood glucose conversion in the liver that supplies 32% to 73% glucose demands [28]. These are then needed in producing lactose in the mammary system lactose and increase the live weight that improves ruminants' animal performance.

Future research

Determination of glutamate concentration in the rumen and isolation of glutamic acid-producing (GAP) microorganism containing glutamate decarboxylase (GAD) gene that could enhance the production of GABA that eventually be used as a feed additive for ruminants could help in the health and production of ruminants. A deeper understanding of GAD activity and GABA and endogenous and extracellular GABA content, and volatile fatty acid production of the GAP isolates containing the GAD gene could help resolve the mechanism behind the improvement in cattle production. Furthermore, we will enhance the production of GAP isolates containing the GAD gene through media additives, determination of suitable pH, and arginine addition suitable for ruminants' productivity, health status, and performance.

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The Conflict of Interest Statement

The authors declare that they have no conflicts of interest with the contents of this article.

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초록 : 반추위 미생물생태계에서의 글루탐산을 생성하는 미생물의 역할

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반추가축의 반추위내 미생물단백질은 단백질의 공급원중 일부이며 글루타메이트 생산을 위한 공급원이기도 하다. 글루탐산은 신체의 대사반응, 근육 및 기타 세포구성에 필요한 단백질 합성물질로 이용되며 면역기능항진에도 매우 필수적으로 이용된다. 또한 계면활성제, 완충제, 킬레이트제제, 향미 증강제, 배양배지 및 농업 분야에서 성장촉진제로 이용된다. 글루탐산은 감마-아미노부티르산(GABA)생산을 위한 기질로서 본 연구는 글루탐산의 기능과 글루탐산 탈 탄산효소 유전자를 포함하는 미생물에 대한 정보를 제공하는데 있다. GABA는 체온 조절, 건물섭취량, 유생산량 및 유성분을 개선시키는 것으로 알려져 있다. 대부분의 글루탐산과 GABA 생성 미생물은 대부분 Lactococcus, Lactobacillus, Enterococcus 및 Streptococcus 종과 같은 젖산생성 미생물로 이루어져 있다. 반추위내 대사기전을 보면 GABA 합성을 통해 succinate 생산과정을 거치고, succinate는 탈수소효소반응을 통해 프로피온산과 기타 대사산물을 생산할 수 있다. 또한 *Clostridium tetanomorphum*과 혐기성 Micrococci는 글루타메이트 발효과정에서 아세트산과 낙산을 생성한다. 프로피온산과 기타 대사산물은 간에서의 혈당으로 전변되어 반추가축의 유선세포에서 유당 및 체중증가를 위한 에너지를 제공한다. 이를 통해 반추가축의 건강상태 개선 및 성장촉진을 위한 중요한 미생물로 이용가능하다.