



**Review Article**

**DGAT1 Gene in Dairy Cattle**

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**ABSTRACT**

The interest in the bovine *DGAT1* gene has increased during the last few years. *DGAT1* gene, encodes a microsomal enzyme that by using diacylglycerol and fatty acyl CoA as substrates catalyzes the terminal and committed step of triacylglycerol biosynthesis. This step is the most important storage form of energy for eukaryotic cells. *DGAT1* is also important for the physiological processes involving triacylglycerol metabolism such as intestinal fat absorption, lipoprotein assembly, adipose tissue formation and lactation. Lactation was impaired in female mice lacking both copies of *DGAT*. This observation leads to a suggestion that *DGAT1* gene was the functional candidate gene for milk production traits. The frequency of polymorphism in *DGAT1* gene has been found to be very high in dairy cattle. Some associated studies such as, milk yield, fat content, protein yield and content have been carried out in dairy cattle. These associations will provide insight in to the underlying mechanism of *DGAT1* gene and polymorphisms that can be used for selection purposes in dairy cows.

**Keywords:** Bovine, Fat content, Lactation, Milk yield, Triacylglycerol Metabolism.

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**INTRODUCTION**

During the last decade, the progress in molecular genetics has lead to the discovery of individual genes or candidate genes which exerts substantial effects on traits of economic importance.

Candidate gene strategy has been proposed by direct search for quantitative trait loci (QTL). In other words, the genetic variation in a gene, affects the physiological pathways and phenotype. Moreover, the proportion of genetic and phenotypic variation would be likely to affect the breeding strategy for improvement of important traits in the future. Genetic markers

associated with traits of interest, can be searched directly by applying molecular biology techniques. These techniques can identify genetic variation at specific loci and analyze the relationship between genetic variation at QTL and production traits. Application of molecular genetics for genetic improvement, relies on the ability to genotype individuals for specific genetic loci. The information utility from candidate genes in breeding programs potentially enhance the accuracy of selection.

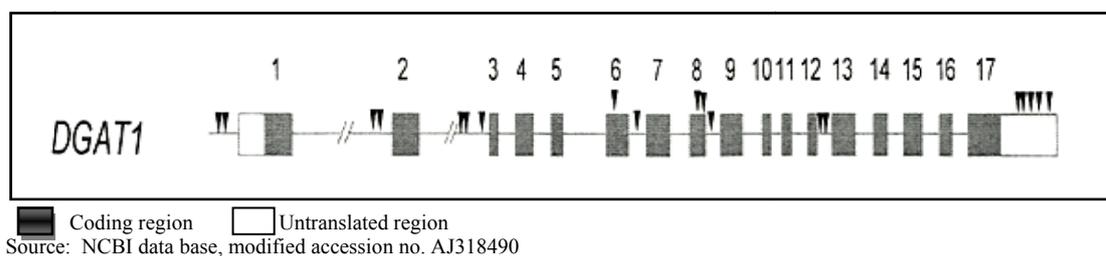
The QTL are chromosomal positions delimited by genetic markers, with the marker alleles being associated with a measurable effect on a quantitative characteristic. Mapping of QTLs is a first step towards identifying genes that contribute to variation in quantitative traits. A second approach is to identify the functional candidate genes based on metabolic pathways.

Mackay (2001) reported that the major goal of dairy cattle genomics is to identify the gene representing the QTL and subsequently to identify the polymorphic site within the gene that causes the differences in the trait phenotype (the quantitative trait nucleotides, QTNs). Many candidate genes with different functions in metabolism have been proposed as affecting milk yield and composition in dairy cattle, such as, Diacylglycerol acyltransferase1 (*DGAT1*).

Many studies reported that *DGAT1* gene is the candidate gene that influences milk fat content and yield. Therefore, the aim of this article is to review the published papers that studied *DGAT1* gene which have an influence on economic traits and could be applied for a direct search of QTL in order to plan breeding programs in the future.

### Discovery of *DGAT1* Gene

The *DGAT* activity was first described by Weiss and Kennedy in the 1950's (Kennedy *et al.*, 1957; Weiss *et al.*, 1956). *DGAT1* gene was localized on centrometric end of the bovine chromosome 14<sup>th</sup>. A span 14,117 bp consists of 17 exons.



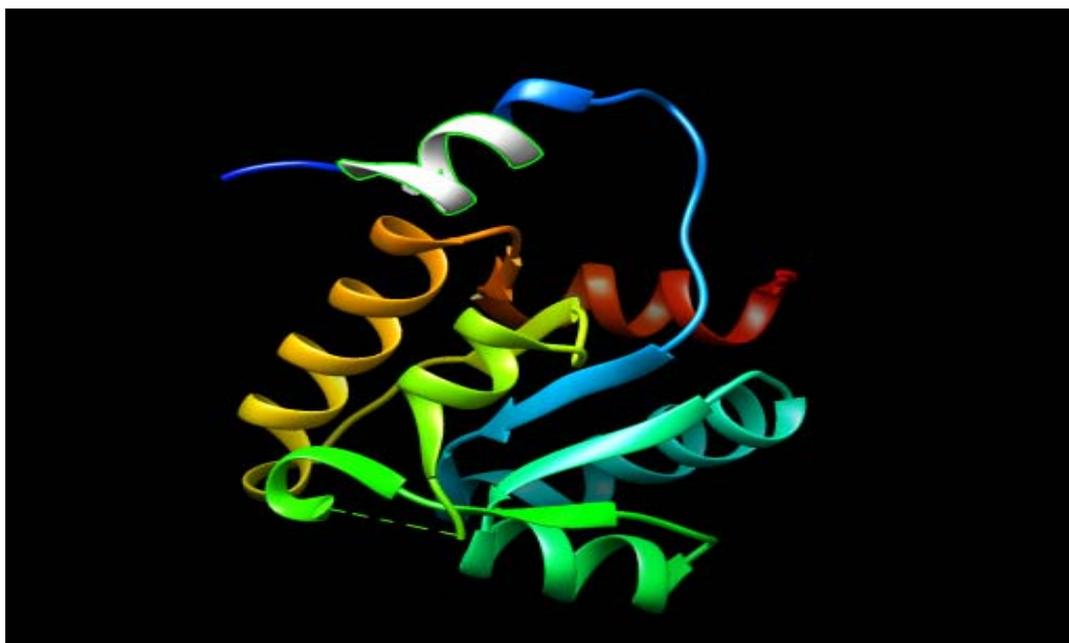
**Fig. 1.** Gene structure of the *DGAT1* gene

### Roles of *DGAT1* in Triacylglycerol Metabolism

The role of *DGAT1* in Triacylglycerol (TG) metabolism should be considered in the following tissues:

**Small intestine:** In the small intestine, *DGAT* is required for the absorption of dietary triglycerides. Dietary TGs are non-polar molecules and are unable to cross the intestinal lumen to enterocytes in its intact form. Instead, TGs in the small intestine are emulsified and digested by lipases producing 2-monoacylglycerol and unesterified fatty acids, which can readily cross the lumen of the gut into enterocytes. In the enterocyte, TGs are re-synthesized, mainly by monoacylglycerol acyltransferase and *DGAT*. TGs are incorporated in chylomicrons so as to deliver dietary lipids through the lymphatic system into the circulation where the fatty acids are taken up by muscle, liver, adipose tissue, etc. (Stone, 2011).

**Liver:** In the liver, *DGAT* has a role in synthesizing TGs from either fatty acids synthesized from the beginning or from fatty acids taken up from the circulation. These TGs are incorporated in lipoproteins of a very low density for delivery to extra-hepatic tissues where they are stored (adipose tissue) or oxidized (skeletal and cardiac muscle).



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**Fig. 2: Three dimensional of *DGATI* molecule**

Mammary gland: TGs, a major component of milk. They are stored in adipocytes in the lactating mammary gland and provide an essential source of energy to new-borns. Fatty acids released by the hydrolysis of TGs are stored in the adipose tissue are re-esterified to TGs by *DGAT* in the mammary gland.

**Adipose tissue:** Adipose tissue has the highest content of TGs in mammals and is the main tissue for storage of TG. TGs are delivered to adipose tissue through the circulation by chylomicrons and very low density lipoproteins (VLDL). Lipoprotein lipase present in the blood capillaries in adipose tissue hydrolyze TGs contained within these lipoproteins. The unesterified fatty acids are taken up by adipocytes, re-esterified to TGs mainly by the Kennedy pathway involving *DGAT* and stored in cytosolic lipid droplets. When required, TGs in the adipose tissue are hydrolyzed to fatty acids and glycerol. These compounds are released into the circulation. Fatty acids are then transported in an albumin-bound form to tissues such as muscle and liver where they are oxidized to promote the synthesis of ATP.

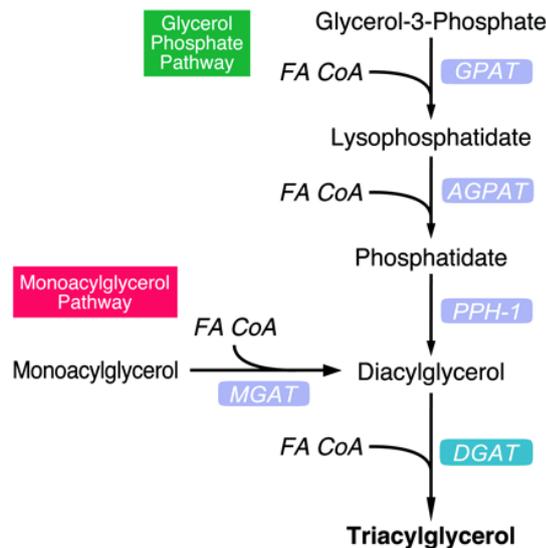
### ***DGATI* Enzymes and Triglyceride Synthesis**

*DGATI* catalyses the final step in the triglyceride synthesis (Mayorek *et al.* 1989). Diacylglycerol acyltransferase1 (*DGATI*) gene encodes an enzyme which plays a major role in the synthesis of triglycerides. Triglycerides which are the major components of fat are formed by binding of diacylglycerol to long chain fatty acyl CoAs. This reaction is catalyzed by at least two enzymes. One of these enzymes is encoded by *DGATI* (Cases *et al.* 2001 and Winter *et al.*, 2002). Lactation impairment was observed in female mice lacking both copies of *DGAT*, probably due to stop of triglyceride synthesis in mammary gland. After this observation *DGATI* gene was suggested as a functional candidate gene for milk production traits (Smith *et al.*, 2000 and Winter *et al.*, 2002).

### ***DGATI* and Milk Fat Association**

Milk fat composition has a major influence on dairy products, where a more unsaturated milk fat is preferred from human nutritional and health perspectives. This may, however, render the milk fat more susceptible to oxidation, giving a 'carbon', 'metal', 'talcum' or 'fishy' flavour to the milk (Shipe *et al.*, 1978). The off-flavour is one of the most common in milk and results

from volatile compounds that accumulate in the milk through the oxidation of the double bonds between the carbon atoms in unsaturated fatty acids (FA). Oxidation is often initiated by prooxidants such as copper and iron but these can be balanced by antioxidative substances like  $\beta$ -carotene and  $\alpha$ -tocopherol found in the milk. Barrefors *et al.*, (1995) found that the higher the proportions of the unsaturated FAs Linoleic (C18:2) and Linolenic (C18:3) in the milk, the higher is the risk of 'oxidized' flavour. The fatty acids composition varies due to factors like feed, stage of lactation, parity, season, and genotype of cow (Palmqvist *et al.*, 1993; Syrstad *et al.*, 1982). In studies by Renner & Kosmack (1974a) and Syrstad *et al.*, (1982), the heritability ( $h^2$ ) estimates for individual FAs or groups of FAs were shown to vary between low and moderately high, but were generally lowest for the long chained FA.



**Figure 3:** Triglycerides synthesis and *DGAT* enzymes

The FA synthesis is mediated by a variety of enzymes, ending up in the triacylglyceroles being formed in the udder. In cow's milk there are the short chained FAs C4 and C6, which are unique to ruminant milk and that give its special characteristics. C4 and C6 are predominantly bound to the glycerol molecule at the *sn*-3 position according to the stereospecific numbering (Palmqvist *et al.*, 1993). The final step in the synthesis, in which diacylglycerol is transformed to triacylglycerol, is catalysed by the enzyme Acyl-CoA:diacylglycerol acyltransferase1 (*DGATI*). A dinucleotide substitution in the gene coding for *DGAT1* has been shown to be the causative mutation behind an observed QTL for milk fat content. The substitution results in a replacement of the amino acid lysine (K) with Alanine (A) (K232A) which in turn results in increased yields of protein and milk, and a decrease in yield of fat, and concentrations of fat and protein (Grisart *et al.*, 2002). Grisart *et al.*, (2004) have shown that the enzyme encoded by the K allele is characterized by a higher velocity rate ( $V_{max}$ ) in producing triacylglycerols than the A allele. Due to the *DGATI* enzyme's specific role to attach FAs to position 3, the only place on the triacylglycerol molecule where the C4 and C6 fatty acids are found, the A allele may be associated with a lower proportion of these short chained FAs.

## The Effect of *DGAT1* gene Polymorphisms on Milk Production

### 1. *DGAT1* K232A polymorphisms

Mapping studies in cattle resulted in the identification of an Adenine/Adenine to Guanine/Cytocine dinucleotide substitution in exon 8, which cause a Lysine K to Alanine

amino acid substitution at position 232 K232A (Farnir *et al.*, 2002; Grisart *et al.*, 2002; Winter *et al.*, 2002). This substitution of a positively charged Lysine residue with a neutral hydrophobic Alanine residue in the *DGATI* gene has a major effect on fat content and other milk characteristics (Farnir *et al.*, 2002; Rahmatalla *et al.*, 2008; Sanders *et al.*, 2006; Thaller *et al.*, 2003; Winter *et al.*, 2002). The lysine variant at *DGATI* increases fat and protein contents, as well as fat yield, whereas the *DGATI* Alanine variant increases milk and protein yields (Farnir *et al.*, 2002; Thaller *et al.*, 2003; Winter *et al.*, 2002).

The effect of the *DGATI* K232A polymorphism on fat composition has different causes: a higher activity of *DGATI* and alteration of specificity of *DGATI*. Expression study using a baculovirus system, shown that 232K variants has greater enzyme activity level (Vmax) than 232A in producing triglycerides, which is consistent with the *in vivo* effect of the K232A polymorphism (Grisart *et al.*, 2004). Furthermore, the mathematical model of Shorten *et al.* (2004) predicted that an increase in fat yield because of 232K corresponds with a 120% increase in the *DGATI* acylation rate and, consequently, is associated with a more saturated fatty acid composition. For the second, the specificity of the *DGATI* enzyme could be altered by the K232A polymorphism.

**Table 1: Frequency of the allele and genotypes of *DGATI* K232A in some dairy cattle**

breed	Frequency	KK	AK	AA	Source
Montbéliarde	0.040	0	14	370	Mgautier, 2007
Normande	0.130	11	122	402	Mgautier, 2007
French Holstein	0.369	177	944	965	Mgautier, 2007
German Holstein Friesian	44.20	19.13	50.15	30.72	Rahmatalla, 2010
Kenana	0.97	0.97	0.03	0	Lutfi <i>et al.</i> , 2007
Butana	0.75	0.75	0.19	0.06	Lutfi <i>et al.</i> , 2007
Swedish Red breed	0.91	0.01	0.16	0.83	Naslund and.Fikse, 2008
Swedish Holstein breed	0.86	0.03	0.20	0.76	Naslund and.Fikse, 2008

The lysine variant (K allele) at the K232A polymorphism frequency ranged from 0.04 in the Montbéliarde to 0.75 in Butana breed (Table 1). The table also shows the distributions of genotypes for the 5 breeds. Only 14 out of the 384 Montbéliarde bulls were heterozygous for K232A and none was homozygous for the lysine variant (KK). Indeed, most animals were homozygous for the Alanine variant (AA) in both the Montbéliarde and Normande breeds. In the French Holstein breed, where the K allele is much more frequent, approximately 10% of the bulls were homozygous (KK) and 43% were heterozygous (Mgautier, 2007), while in German Holstein there were more heterozygous than homozygous AA genotypes, (Rahmatalla, 2010). In Kenana breed 28 out of 29 were homozygous for the lysine variant (KK), and only one was heterozygous, and none was homozygous for the lysine variant (AA) (Lutfi *et al.*, 2007), In the Butana breed 12 out of 16 were homozygous for the lysine variant (KK), only one was homozygous AA, and 3 were heterozygous KA (Lutfi *et al.*, 2007). In Swedish Red breed, only 0.01 out of 146 were KK homozygous, 0.16 were heterozygous in KA, and 0.83 were homozygous AA. while in Swedish Holstein breed 0.03 were KK homozygous 0.20 were heterozygous in KA, and 0.76 were homozygous AA (Naslund and.Fikse, 2008).

## 2. Variable number of tandem repeats (VNTR)

In subsequent studies, at least one additional source of variation besides the diallelic *DGATI* K232A mutation was postulated to be responsible for the QTL in the centromeric region at BTA14 (Winter *et al.*, 2002; Bennewitz *et al.*, 2004). In the German Holstein population, (Kühn *et al.*, 2004) described 5 alleles at a variable number of tandem repeat (VNTR) polymorphism in the *DGATI* promoter, which showed an effect on fat content additional to the *DGATI* K232A mutation.

It was observed that the VNTR allele E showed significant effects for some milk production characteristics compared with all other alleles at the *DGATI* promoter VNTR. The

same results were reported by Kühn *et al.*, (2004) for the *DGATI* VNTR allele 5. However, in contrast to Kühn *et al.* (2004), the VNTR allele E was mainly linked to the K variant at *DGATI* K232A ( Table 2), whereas the *DGATI* VNTR allele 5 showed up with the A variant in the German Holstein Friesian population (Kühn *et al.*, 2004). It is likely that the VNTR allele E corresponds to the *DGATI* VNTR allele 5 of Kühn *et al.*, (2004).

**Table 2: Allele substitution effects of the K variant at *DGATI* K232A and of the *DGATI* promoter VNTR allele E on milk production traits, with standard error SE and P- values, in German Angeln Dairy Cattle.**

Trait	K variant		VNTR allele E		SE	P- value
	A	SE	P- value	a		
Milk yield ( kg)	-77.26	20.17	<0.001	-20.74	20.29	0.31
Protein yield( kg)	-0.98	0.69	0.155	-0.68	0.70	0.33
Protein content %	0.03	0.005	<0.001	0.002	0.005	0.75
Fat yield( kg)	3.59	1.07	<0.001	-0.71	1.08	0.52
Fat content %	0.12	0.01	<0.001	0.007	0.01	0.54
Lactose yield (kg)	-6.46	2.66	0.015	-5.53	2.67	0.04
Lactose content %	0.009	0.003	0.007	-0.008	0.004	0.03
Milk energy yield ( ME)	0.30	0.17	0.088	-0.29	0.17	0.10
Milk energy content( ME/kg)	0.08	0.007	<0.001	0.01	0.007	0.07
SCS	-0.03	0.01	0.038	0.03	0.01	0.04

### 3. Cytochrome P450, family 11, subfamily B (*CYP11B1*)

Kuhn *et al.*, (2004) reported strong evidence for segregation of at least three alleles in the promoter region of the *DGATI* (gene up-stream of the *DGATI*) that affects milk fat percentage. In the centromeric region of BTA14, was suggested to be the causative gene for the QTL related to fat metabolism (de Roos *et al.*, 2007). The *CYP11B1* gene was negatively associated with milk yield and protein yield, but positively associated with fat content (Kaupe *et al* 2007).

In some species, the *CYP11B1* gene has developed into distinct isoforms (Kawamoto *et al.*, 1992; Mellon *et al.*, 1995; Bülow *et al.*, 1996; Muller, 1998), whereas in pig, sheep, and cattle functional unity is conserved (Bülow *et al.*, 1996; Muller, 1998). In all mammals *CYP11B1* Pseudogenes exist (Kirita *et al.*, 1990; Mellon *et al.*, 1995). Because the *CYP11B1* coding gene has been mapped to BTA14q12 (Kaupe *et al.*, 2004a) and HSA8q21-23 (Wagner *et al.*, 1991; Taymans *et al.*, 1998), this gene can be considered as a positional candidate gene. Because *CYP11B1* is involved in energy metabolism, this gene can also be considered as a functional candidate gene for milk production.

*DGATI* gene encodes a microsomal enzyme that by using diacylglycerol and fatty Acyl CoA as substrates catalyzes the terminal and committed step of triacylglycerol biosynthesis, which is the most important storage form of energy for eukaryotic cells. *DGATI* is also important for physiological process involving triacylglycerol metabolism such as intestinal fat absorption, lipoprotein assembly, adipose tissue formation and lactation (Cases *et al.*, 1998), and it was presumed to be rate limiting with respect to lipid metabolism (Nina *et al.*, 1989).

## CONCLUSIONS

Nowadays, the sophisticated use of molecular and quantitative information on an industry-wide scale will require robust systems that can cope with imperfect data as well as the development of selection indices to take full advantage of the information.

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