Milk Transcriptome

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Abstract

Milk transcriptome sequencing is a promising technology, which closes the gap between high density genotyping and phenotyping data. In addition to the power to discover a large number of genetic polymorphisms, the sequencing of the transcriptome can offer important information on transcriptional activity of mammary gland cells which cannot be collected at DNA level. The most important findings in this context are related to posttranscriptional modifications in the mammary gland and detection of transcripts representing non-protein coding regions of the genome. Among them are most prominent regions coding different types of RNA (lncRNA, miRNA, siRNA, piRNA, snoRNA) which are involved in complex regulatory networks. Transcriptome sequencing has also potential to identify novel causative SNPs associated with complex phenotypic traits. These novel informative SNPs are good candidates for marker assisted selection in dairy herds.

Keywords: Lactation; Mammary gland; Milk; RNA-seq; Transcriptome

Abbreviations: FAANG: Functional Annotation of Animal Genomes; EGF: Epidermal Growth Factor; QTL: Quantitative Trait Loci; STAT5A: Signal Transducer and Activator of Transcription 5A; RNASEH2B: Ribonuclease H2 Subunit B; PROP1: Prophet of Pit 1; QC: Quality Control; SNP: Single Nucleotide Polymorphisms; GEO: Gene Expression Omnibus; SRA: Sequence Read Archive; MECs: Mammary Epithelial Cells; PMN: Polymorphonuclear; PPAR: Peroxisome Proliferator-Activated Receptor;

Introduction

Understanding the relationship between genetic variability and phenotypic variation in domestic animals is one of the central problems in animal breeding. In the past, selection in farm animals was based on reliability of pedigree data and more or less precise recording of phenotypic data describing economically important traits. With the development of molecular genetics, different types of molecular data, characterizing animal genome were used to study association between genotype and phenotypic traits.

The early studies were based on relatively small sets of data, including mainly polymorphisms located within selected DNA regions, coding for proteins involved in shaping of phenotypic traits [1]. Later, some other genetic markers (microsatellites, single nucleotide polymorphisms - SNP) were used, allowing more precise mapping of candidate regions affecting complex quantitative traits. In spite of the fact that the number of markers was growing fast, the intervals between markers were still relatively long and there was always the risk, that the identified SNP was not a causal one, but only linked to the causal mutation, which remained hidden in the region not covered by genetic markers [2].

This problem could be solved using whole genome sequences for genotyping instead of several hundreds of thousands of SNP markers. However, due to the high number of sequence differences between individuals and technical problems related with genome annotation, sequencing errors and genomic structural variation, it is often difficult to identify causal mutations, which have significant effect on complex phenotypic traits, from whole genome sequencing data [2]. Due to the fact that in each tissue/cell type only a portion of coding regions of the genome is transcriptionally active, the number of potential causal mutations for a certain phenotypic trait is considerably reduced. Therefore, sequencing of RNA from tissues which are involved in expression of a certain phenotypic trait is a good possibility to focus genomic analysis only on regions which are transcriptionally active in the tissue/cells associated with phenotypic trait of interest [3]. Analysis of tissue specific transcriptome enables detection of genetic variation at posttranscriptional level, which cannot be detected at the DNA level (e.g. alternative splicing, differential allelic expression).

Compared with whole genome sequencing, sequencing of transcriptome offers a cheaper alternative for identification of genetic variants associated with phenotypic variation. RNA sequencing also offers an insight into identification of new regulatory pathways affecting expression of complex traits [4]. In addition to detection of genetic variants within coding regions for proteins involved in shaping quantitative traits, provides RNA sequencing valuable information about genetic variants in non protein coding genomic regions (lncRNA, miRNA, siRNA, piRNA, snoRNA). It has been estimated, that functional non-coding elements represent up to 98 % of human transcriptome

[5]. Identification of these functional elements in animal genomes is an important task of international consortium for Functional Annotation of Animal Genomes (FAANG) [6].

Milk Transcriptome

Transcriptomic studies in the mammary gland have been performed using mainly two technologies: expression microarrays and RNA-Seq. Both technologies have been widely used in lactation research, however due to the rapid development of the next generation sequencing technology, RNA-Seq is becoming the most frequently used approach for transcriptomic analyses in mammary gland [3]. Different platforms using next generation sequencing methodology enabled collection of large amount of transcriptomic data from different species, stages of lactation and different production levels [7].

Biological material used for RNA isolation plays an important role in transcriptome analysis. For analysis of mammary gland transcriptome, material as biopsies of mammary gland tissue, milk somatic cells, laser dissections of frozen mammary gland tissue, milk fat globules and antibody captured milk mammary epithelial cells have been used. Especially the last method allows precise separation of different cell sub-types and development of for certain cell types specific transcriptomic profiles [8]. Canovas et al. (2010) compared the transcriptomic profiles from different sources and concluded that milk somatic cells and milk fat globules represent a reliable source for RNA isolation for milk transcriptomic studies.

Transcriptomic studies have revealed more than 33000 SNPs associated with lactation, which can be used as genetic markers for marker assisted selection in dairy cows [9]. Differentially expressed genes between high and low producing animals deserve special attention. These genes reflect the role of a number of specific biologic processes involved in lactation [10]. The other group of promising candidate genes are genes that are expressed in the mammary gland and are located within the quantitative trait loci (QTL) related to lactation traits. This strategy can help to identify novel candidate genes associated with lactation traits.

Transcriptomic analysis in different stages of lactation identified some important biological pathways associated with paired-end read format.

the development of mammary gland and lactation. During the pregnancy, genes involved in development of morphogenesis of mammary ducts and differentiation of the mammary alveoli play an important role [11]. For the initiation of lactation is characteristic up-regulation of genes involved in milk synthesis together with the inhibition of genes related to cell proliferation. During the very early lactation, some immune- and development-related miRNAs are highly expressed [12]. Genes involved in synthesis of milk constituents and milk synthesis-related pathways are constantly expressed during lactation [13]. Finally, during the involution the most prominent groups of expressed genes are immune and antioxidant-related genes, whereas genes related to milk synthesis are down regulated [14]. Genomic and transcriptomic studies revealed several loci associated with milk production traits. So were gene polymorphisms in epidermal growth factor (EGF) and signal transducer and activator of transcription 5A (STAT5A), as well as missense mutation of prophet of Pit 1 (PROP1) and deletion of Ribonuclease H2 Subunit B (RNASEH2B) associated with milk production [15].

Bioinformatics Approach

The transcriptome profiling is typically performed using expression microarrays or RNA-Seq methodology. Both methods produce extensive data and require complex bioinformatics analysis. Microarrays are effective in expression profiling of known genes and transcripts, and were the method of choice until the late 2000s [16]. RNA-Seq is not dependent on existing genomic data, and offers more comprehensive investigation of the transcriptome. With its advantages, it has slowly replaced microarray-based transcriptome analyses.

Transcriptome of human milk has been analysed using expression microarrays [17]. However, RNA-Seq is now predominant method used in milk transcriptome profiling. Milk transcriptome sequencing data sets generated from different studies on humans, mouse, livestock and other mammals, such as rhesus macaque, and Tasmanian devil were deposited in NCBI's Gene Expression Omnibus (GEO) database, Sequence Read Archive (SRA) or BioProject (Table 1). Sequencing of milk transcriptomes in some studies was performed on Illumina Genome Analyzer IIx, but in most of the studies on Illumina HiSeq2000 in a single or

Table 1: Milk transcriptome sequencing data.

Study	Species	Sequencing Technology	Accession Number	Reference
Expression profiling of genes expressed in milk somatic cells of transition (day 15), peak (day 90) and late (day 250) lactation in Holstein cows.	Cow (*Bos taurus*) Holstein	Illumina Genome Analyzer (GAII), 36-40 bp short sequence reads	/	Wickramasinghe Saumya, et al. [24]
MicroRNA expression profiles of bovine milk exosomes in response to *Staphylococcus aureus* infection.	Cow (*Bos taurus*) Holstein	Illumina Genome Analyzer II, 40 bp single-end sequencing	GSE55144 (GEO)	Sun, et al. [39]
Differential expression of genes in milk fat globules at day 10 and day 70 after calving between two groups of cows with extremely high and low 305-day milk yield, milk fat yield and milk protein yield.	Cow (*Bos taurus*) Chinese Holstein	Illumina HiSeq 2000, paired-end	SRP064718 (SRA)	Yang, et al. [41]

Differential expression of genes in goat colostrum and mature milk.	Goat (Capra *hircus*)	Genome Analyzer IIx, 79 bp paired-end sequence reads	SRP057582 (SRA)	Crisa, et al. [34]
Transcriptome profile during three stages of lactation: colostral, transitional, and mature milk production.	Human *(Homo sapiens)*	Illumina HiSeq 2000, 20 million 100 bp paired-end reads per sample	GSE45669 (GEO)	Lemay and Ballard, et al. [38]
Cellular miRNA profile of human milk collected before and after feeding.	Human *(Homo sapiens)*	Illumina HiSeq 2000, 293,932,547 reads	GSE71098 (GEO)	Alsaweed, et al. [31]
Insight into porcine milk exosomal mRNA and proteins.	Pig (*Sus scrofa*) Landrace	Illumina HiSeq 2000, single-end sequence reads	SSR3436404 (SRA)	Chen Ting, et al. [32]
Assessment of suitability of lactating rhesus macaques as a model for lactating humans.	Rhesus macaque *(Macaca mulatta)*	Illumina HiSeq 2000, 100 bp single-end sequence reads	GSE49765 (GEO)	Lemay, et al. [37]
Effect of high-fat diet on secreted milk composition.	Mouse (Mus musculus)	Illumina HiSeq 2000	SRP109609 (SRA)	Chen, et al. [33]
Transcriptome profiling of the sheep lactating mammary gland.	Sheep (Ovis aries)	Illumina HiSeq 2000 sequencer, between 35–45 million 75 bp paired-end reads	GSE74825 (GEO)	Suárez Vega Aroa, et al. [40]
Diet induced differences in milk composition. Transcriptome of milk from dairy ewes at 90 day of lactation and after 3 weeks of diet supplementation with extruded linseed.	Sheep (Ovis aries) Comisana breed	Illumina HiSeq 2000	GSE89163 (GEO)	Giordani Tommaso, et al. [35]
The identification of immune genes in the milk transcriptome of the Tasmanian devil.	Tasmanian devil *(Sarcophilus harrisii)*	Illumina HiSeq 2000, 22.5 million 100 bp paired-end reads	PRJNA274196 (BioProject)	Hewavisenti Rehana V, et al. [36]

Major steps in an RNA-Seq study are experimental design, quality control, alignment of reads, genes and transcripts level quantification, visualization, differential gene expression, alternative splicing, functional analysis, gene fusion detection and eQTL mapping [18]. Millions of short reads are the starting point of RNA-Seq bioinformatics analysis. Quality control (QC) of raw sequencing data is essential step in RNA-Seq data analysis. Parameters of raw sequencing data examined by QC tools are total number of reads sequenced, GC content and the overall base quality score. Data that pass raw read data QC is then aligned to the reference genome or transcriptome. Accurate transcript identification depends on the availability of a high quality assembly of the reference genome.

Milk Transcriptome Profile depends on Different Cell Types

Milk contains somatic cells, which are one of the important defence mechanisms against intramammary infections [19] and their count serves as an indicator of milk quality and intramammary infections. The somatic cell fraction in milk is composed of mammary epithelial cells (MECs) and immune cells – leukocytes [20]. Immune cells represent the major part of milk somatic cells, whereas exfoliated MECs usually represent only several percent of the bulk somatic cell fraction [21]. The most abundant immune cells in normal bovine milk are macrophages, followed by polymorphonuclear (PMN) cells (neutrophils), and lymphocytes [22]. In mastitic milk the proportion of PMNs has been shown to increase (up to 90%) [23].

Therefore, not only the total count of somatic cells is important, but also the differential cell count, which could be used for assessment of mammary health status [21]. Somatic cells

are a heterogeneous mixture of cells and it has been shown that approximately 70% of the annotated bovine genes are expressed in bovine milk somatic cells [24]. Sequencing of the single cell transcriptomes of cells circulating in milk, would eventually enable transcriptome-based discrimination between different somatic cell types. Changes in milk transcriptome profiles can be correlated with mammary infections, lactation stage, and different mammary traits. For example, expression profiling in milk somatic cells has been used to study mammary gland response to infection [25]. Additionally, biology of lactation was studied by following changes in bovine lactome extracted from milk samples from animals in different lactation stages [24].

Transcriptome Association with Lactation Parameters

In addition to molecular markers used in marker assisted selection schemes, the transcriptomic studies offer new opportunity for identification of novel candidate genes related to lactation traits in dairy species. Transcriptomic approach revealed more than 33,000 SNPs associated with lactation traits in dairy cows. The analysis of gene expression levels during lactation identified 31 differentially expressed genes between extremely high and low milk protein and fat producing Holstein cows. Among them were parathyroid hormone-like hormone, ribosomal protein L23a, serum amyloid A, tribbles homolog 3 and vascular endothelial growth factor A as potential candidates for regulation of protein and fat percentage in milk.

Transcriptomic studies in Holstein dairy cows detected expression of genes, which are required for the synthesis and secretion of milk [26]. Based on mammary expression profiles the researchers concluded that at the beginning of lactation the most important functions of the mammary gland are milk synthesis and

inhibition of cell proliferation [27]. During the course of lactation insulin induced gene 1, peroxisome proliferator-activated receptor (PPAR) and PPAR coactivator 1 are involved in regulation of lipid synthesis, whereas insulin is involved in regulation of protein synthesis [28]. An important result of transcriptomic studies is detection of expression of a wide range of miRNAs during lactation in dairy cows [29]. In the bovine mammary gland, 884 unique miRNA sequences were found and 56 of them were differentially expressed between lactating and non-lactating mammary glands. Upregulated genes in lactating mammary gland are associated with various macromolecular metabolic processes and increased metabolic activity of mammary gland cells during lactation [30-38].

Conclusion

Transcriptomic analysis allows complex, tissue specific analysis of gene expression during different stages of lactation. Differences in the transcriptome in different cell types, different stages of lactation and at different production levels allow identification of genes, which are up- or downregulated in different physiological situations. Selection of biological material for transcriptomic analysis of lactation offers a good opportunity to decipher transcriptome of different cell types in lactating mammary gland [39-41]. In addition to detection of transcribed genomic regions and quantification of allele specific transcripts, transcriptomic analysis also allows identification of post-transcriptional changes and detection of non-protein coding transcripts (miRNA, siRNA, lncRNA,…) which can play an important role in regulation of gene expression in the mammary gland. In combination with SNP analysis and exploitation of QTL data represents RNA-Seq a promising approach for identification of novel informative SNP markers for marker assisted selection.

Acknowledgement

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