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Bovine chromosomal regions affecting rheological traits in rennet-induced skim milk gels

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ABSTRACT

Optimizing cheese yield and quality is of central importance to cheese manufacturing. The yield is associated with the time it takes before the gel has an optimal consistency for further processing, and it is well known that gel formation differs between individual milk samples. By identifying genomic regions affecting traits related to rennet-induced gelation, the aim of this study was to identify potential candidate genes affecting these traits. Hence, rennet-induced gelation, including rennet coagulation time, gel strength, and yield stress, was measured in skim milk samples collected from 379 animals of the Swedish Red breed using low-amplitude oscillation measurements. All animals had genotypes for almost 621,000 segregating single nucleotide polymorphisms (SNP), identified using the Bovine HD SNPChip (Illumina Inc., San Diego, CA). The genome was scanned for associations, haplotypes based on SNP sets comprising highly associated SNP were inferred, and the effects of the 2 most common haplotypes within each region were analyzed using mixed models. Even though the number of animals was relatively small, a total of 21 regions were identified, with 4 regions showing association with more than one trait. A major quantitative trait locus for all traits was identified around the casein cluster explaining between 9.3 to 15.2% of the phenotypic variation of the different traits. In addition, 3 other possible candidate genes were identified; that is, UDP-*N*-acetyl-α-D-galactosamine:polypeptide *N*-acetylgalactosaminyl-transferase 1 (*GALNT1*), playing a role in O-glycosylation of κ-casein, and 2 cathepsins, *CTSZ* and *CTSC*, possibly involved in proteolysis of milk proteins. We have shown that other genes than the casein genes themselves may be involved in the regulation of gelation traits. However, additional analysis is needed to confirm these results. To our knowledge, this is the first study identifying quantitative trait loci affecting rennet-induced gelation of skim milk through a high-density genome-wide association study.
Key words: genome-wide association study, dairy cattle, milk gelation, casein

INTRODUCTION

In 2011 more than 18 million tonnes of cheese were produced in the world (International Dairy Federation, 2013). Both milk composition and other milk properties (e.g., SCC and pH) have considerable effects on cheese yield and composition (Walstra et al., 2006), thus making it important to optimize the yield in cheese manufacturing. In rennet-induced gelation of milk, the CN (α_{S1}-, α_{S2}-, β-, and κ-CN) in the form of micelles are of great importance. When rennet (chymosin) is added to milk, κ-CN is hydrolyzed, which leads to a destabilization of the micelles, and aggregates start to form (Walstra et al., 2006). Within cheese making, the aggregation time and the time it takes before the gel can be cut are important parameters. Rennet-induced gelation differs between milk samples from individual cows because of differences in, among others, the contents of total protein, CN, calcium, and pH of milk (Frederiksen et al., 2011b; Gustavsson et al., 2014b). In addition, it has been observed that milk from some cows coagulates poorly (Ikonen et al., 1999; Gustavsson et al., 2014a); however, the reason for this is not fully understood. Frederiksen et al. (2011a) showed that gelation properties of well-coagulating milk were considerably impaired when adding noncoagulating as well as poorly coagulating milk when using milk from individual cows, showing the importance of optimizing cheese milk quality.

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As reviewed by Bittante et al. (2012), several studies have been conducted regarding the heritability of milk gelation properties. Heritability estimates of 0.21 to 0.38 have been reported for rennet coagulation time (**RCT**) and for gel strength (**G′**) 0.12 to 0.41 (Bittante et al., 2012). These results indicate that it could be possible to breed cows to obtain milk with better milk gelation properties. It is well known that different milk protein genetic variants affect both milk composition and milk gelation properties, as reviewed by Caroli et al. (2009) and Bittante et al. (2012). Documented effect on milk gelation properties has been found on genetic variants of κ- and β-CN and of β-LG (Ikonen et al., 1999; Poulsen et al., 2013). However, conflicting results are found between studies. Some studies also reported effects of genetic variants of α_{S1}-CN on milk gelation properties (e.g., Lodes et al., 1996; Poulsen et al., 2013). The different CN do not only differ from each other regarding genetic variants, but also through different degree of phosphorylation and, in case of κ-CN, also glycosylation (Farrell et al., 2004). Both phosphorylation (Frederiksen et al., 2011a; Jensen et al., 2012) and glycosylation of CN (Robitaille et al., 1993; Jensen et al., 2012; Bonfatti et al., 2014) have been shown to affect rennet-induced gelation properties.

Most studies conducted to investigate the effects of the bovine genome on milk composition and milk gelation properties rely on variations in the genetic variants of major milk proteins (Caroli et al., 2009; Bittante et al., 2012). However, it is difficult to assign effects to a certain variant, because the casein genes are tightly linked. In recent years, the genetic effect on milk composition has been analyzed using full genome studies and genome-wide association studies (**GWAS**; e.g., Kolbehdari et al., 2009; Schopen et al., 2011). Such studies provide substantial information on the chromosomal regions affecting specific milk traits and can be used to generate new hypotheses of genes underlying these traits. Schopen et al. (2011) performed a GWAS to identify chromosomal regions affecting milk protein composition. In their study, a total of 31 genomic regions on 20 bovine autosomes were found showing significant association with milk protein composition, total protein content, or both. Only 3 chromosomal regions harbor the genes coding for the most abundant milk proteins, i.e., BTA 5 (α-LA), BTA 11 (β-LG), and BTA 6 (*CSN* cluster); however, other genes are also involved in the formation of milk proteins. In addition, Schopen et al. (2011) showed that not all genetic variation regarding milk protein composition and total protein content could be explained by the earlier known genetic variants. Furthermore, noncoagulating milk has been analyzed to identify causal genes performing a genome scan using microsatellite markers (Tyrisevä et al., 2008). The aim of this study was to identify regions within the bovine genome affecting rennet-induced gelation. A GWAS was performed in 379 Swedish Red (**SR**) cows using markers from Illumina's Bovine HD SNPchip containing 777,000 SNP. Based on SNP highly associated with the traits, haplotypes across the SNP set regions were inferred and used for further analyses of the associated loci. The aim of the study was to identify genetic markers affecting rennet-induced gelation in general, which could be used within animal genomic breeding schemes to optimize cheese production.

MATERIALS AND METHODS

Animals and Samples

Morning milk samples and blood samples were collected from 395 SR cows in 20 different farms (April to May 2010 and September 2010 to April 2011) located in the same geographical region in the southern part of Sweden. Between 19 and 24 individual milk samples were collected from each herd, and each herd was sampled the same day. The 395 cows descended from 168 sires and 72 paternal grandsires. A total of 100 sires had only 1 daughter, 29 sires had 2 daughters, and the 2 largest families comprised 13 and 17 half-sibs, respectively. In total, 158 maternal grandsires fathered the mothers, among which 26 also fathered some of the cows. The majority of the cows were in lactation number 1 to 3 (1% in lactation number 4) and in lactation wk 7 to 40 (2% before lactation wk 7 and 10% after lactation wk 40). All cows were milked 2 times (in total 287 of the sampled cows from 15 of the herds) or 3 times (in total 108 of the sampled cows from 5 of the herds) per day. Separate milkings were performed on all cows, and the individual milk samples were thoroughly mixed before an aliquot was sampled, cooled, and transported to Lund University, Sweden, arriving at the day of sampling, whereas another aliquot of each sample was cooled and transported to Aarhus University, Foulum, Denmark, arriving the day after sampling. Fresh milk samples were analyzed for contents of total protein, CN, fat, and lactose by an infrared technique (MilkoScan FT2, Foss Electric, Hillerød, Denmark). This method has previously been validated for CN measurements (Sørensen et al., 2003). Somatic cell count was measured by using flow cytometry (CombiFoss 5000, Foss, Hillerød, Denmark) at a certified dairy analysis laboratory (Eurofins Steins Laboratory, Jönköping, Sweden). When collecting the milk samples, milk yield on the day of sampling was recorded. The pH of the milk samples was measured at 10°C the day after sample collection. Of the 395 milk samples, 379 milk samples, corresponding to 96%, had SCC below 300,000

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