Sister Chromatid Exchange in Polish White Improved Goats (Capra hircus)

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The study was aimed at evaluating the frequency of spontaneous sister chromatid exchange in Polish WhiteImproved goats (*Capra hircus*). The mean number of SCEs/cell was 2.73 ± 1.84 . The effect of sex and age on SCE incidence was also investigated. No statistically significant differences in the number of SCEs/cell were observed between the males and females. On the other hand, age was found to significantly influence SCE frequency. A lower SCE frequency was observed in younger goats. A positive correlation between chromosome length and SCE number was identified. The longer the chromosome, the more exchanges occurred. The highest number of SCEs was observed in the interstitial region, the lowest in the distal area.

Key words: Sister chromatid exchange, chromosome instability, mitotic chromosome, goat.

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Goat breeding in Poland has a long-standing tradition but has never played any significant role. The beginning of significant development in goat breeding dates back to the end of the 20th century. The political and economic transformation in the country and a worldwide vogue for ecological products and healthy food have suddenly made goat breeding much more popular in Poland. Goat foodstuffs, especially dairy products, have been sought after and have reached high prices on the market. Goat milk has exceptional health-promoting properties. Processed goat milk products, such as cheeses or yoghurt, are highly valued by a broad spectrum of consumers. Goat meat is appreciated both for its taste and nutritional value. The White Improved goat is a popular breed in Poland. It is a milk-producing goat breed developed in Poland by improvement crossing of local White Silesian goats with Saanen goats and White German Noble goats. The goat has a white coat with short shiny hair. The females are specific in having so-called bells on their necks. The males often have a beard and fringe above their eyes. Both sexes are either horned or hornless.

The interest devoted to cytogenetic diagnostics of goats is much lower in comparison to other farm animal species. There are few publications that provide information on chromosome instability (DI MEO *et al.* 1993; DI BERARDINO *et al.* 1996). The goat karyotype is characteristic in having a diploid chromosome number of 2n=60. All the autosomes are acrocentric. The X heterochromosome is also acrocentric. Only the Y chromosome is a small metacentric. The standard of G and R banding patterns has been determined (DI BER-ARDINO *et al.* 2001). Knowledge on the karyotypes of particular species makes it possible to conduct further in-depth analyses. It is especially important to detect damage in chromosome structure or identify an increase in sister chromatid exchanges.

Sister chromatid exchange (SCE) consists in a two-way swapping of homologous segments of chromatids belonging to the same chromosome. SCEs take place after replication, during the cell cycle, when sister chromatids are linked by rings of cohesive proteins and exchange occurs between identical DNA sequences located close to each other. SCE incidence is correlated with recombination repair, point mutation induction, gene amplification and cytotoxicity. SCE may be associated with sudden discontinuities in the banding patterns of two chromatids in the same chromosome. The occurrence of an SCE is confirmed in the presence of asymmetrically pigmented chromatids in the chromosome (GERMAN & ALHADEFF 2001; BAYANI & SQUIRE 2005).

The molecular mechanism of SCE occurrence has not been entirely explored. Spontaneous and

induced SCEs differ, suggesting the existence of more than one molecular path leading to SCE. As SCE occurs when the intermediary product of the Holliday connection is distributed in one of two directions, a change in the direction causes inconsistencies and errors (WILSON & THOMPSON 2007). SCE is associated with semi-conservative DNA replication which must be extremely precise. Any error may result in genetic information loss or initiation of SCE. Any resultant DNA damage should be repaired before the cell enters the S phase of the cell cycle, as unrepaired breakage multiplies SCEs (WÓJCIK et al. 2004; BAYANI & SOUIRE 2005; SIMPSON & SALE 2006). Sister chromatid exchange is initiated by breaks in the DNA strand caused by endo- and exogenic factors. Erroneous DNA damage repair mechanisms contribute to SCE incidence. The principal mechanism that repairs single-strand DNA breakages and contributes to SCE occurrence is BIR (break induced replication). On the other hand, the repair mechanism for double strand breaks is NHEJ (nonhomologous end-joining), often imprecise and introducing changes into a DNA sequence observed as SCEs. According to SONODA et al. (1999) and WILSON and THOMPSON (2007), the main repair procedure responsible for SCE incidence in cells of vertebrates is HR (homologous recombination).

The study was aimed at analysing the frequency of spontaneous sister chromatid exchanges in Polish White Improved goats (*Capra hircus*).

Material and Methods

The study was carried out according to the guidelines of the III Ethical Committee in Warszawa (No. 36/2011 and No 37/2011 from the 22 June 2011).

Peripheral blood of Polish White Improved goats (*Capra hircus*) constituted the experimental material. The blood was sampled from 20 animals (10 males and 10 females). The age of the animals ranged from 5 months to 3 years. The first group comprised goats aged up to one year, the second one those above one year of age. 30 metaphases were analysed for each animal. The chromosome preparations were obtained from our in vitro culture of peripheral blood lymphocytes. In the 24th hour of culture duration we added 10 μ g/ml of BrdU. The FPG (Fluorescence plus Giemsa) method of chromosome staining, as defined by KIHLMAN and KRON-BORG (1975) was used. The staining procedure involved the following stages: one-hour 0.01% RNase treatment at 37°C, followed by one-hour room temperature incubation in a 0.5×SSC solution (0.75M sodium chloride + 0.075 sodium citrate;pH=7.0) including Hoechst's solution (the basic

solution consisted of 0.5 mg Hoechst 33258/1ml ethanol). The working solution was 0.1 ml of the basic solution per 100 ml 0.5×SSC. The preparations were treated with UV radiation for 1 hour, and then left at 4°C in darkness for the entire night. Following 24-hour incubation, the preparations were treated with UV rays once more for 0.5 hours, and then incubated at 58°C for 2 hours. The preparations were stained with Giemsa.

The preparations were analysed using a microscope and a PC. The effects of sex and age on SCE frequency were studied using bivariate analysis of variance. Moreover, all the chromosomes in the karyotype were minutely analysed. The number of SCEs in the particular chromosomes, the sister chromatid exchange sites and the number of single and double SCEs were determined. The correlation between chromosome length and the number of SCEs identified in the chromosomes was determined using the Pearson correlation coefficient.

Results

The karyotype of the goats was analysed for exchanges of stained DNA segments between sister chromatids in the chromosomes. Figure 1 shows the metaphase plates with the observed sister chromatid exchanges in goats.

The mean number of SCEs/cell in the examined 600 cells and 36,000 chromosomes was 2.73 ± 1.84 for the goat population. A higher mean value was identified for females -2.76 ± 1.86 than for males -2.70 ± 1.83 , the difference was statistically insignificant. A higher mean number of SCEs/cell was observed in goats over 1 year of age (3.19 ± 1.89) as compared with the first age group (2.27 ± 1.75) .

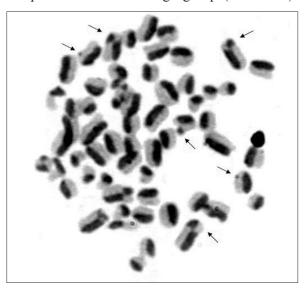


Fig. 1. A metaphase plate of the chromosomes of the Polish White Improved goats stained using the SCE technique (SCEs indicated with arrows).

A bivariate analysis of variance revealed that age significantly influences SCE frequency, whereas sex has no such effect. The age-related F_{emp} was 69.98 at P=0.00, whereas the F_{emp} for sex was 0.47 at P=0.50.

Additionally, SCE frequency in the chromosomes was analysed in detail. The highest number of SCEs was observed in the 1^{st} and the lowest in the 29^{th} chromosome (Fig. 2). The number of SCEs identified was proportional to chromosome length – the longer the chromosome, the more exchanges occurred. A positive correlation between the characteristics was detected. The Pearson correlation coefficient was 0.92 (P<0.01). Sister chromatid exchanges were observed in the proximal, interstitial and distal areas of the chromosomes. SCE distribution in the respective chromosome regions was analysed. The majority of exchanges were identified in the interstitial part of the analysed chromosomes (42%), followed by the proximal (34%) and distal (24%) regions. Arrows in Figure 3 indicate sister chromatid exchange sites in the respective chromosome regions.

Single as well as double (few) exchanges (Fig. 4) between sister chromatids were observed in the

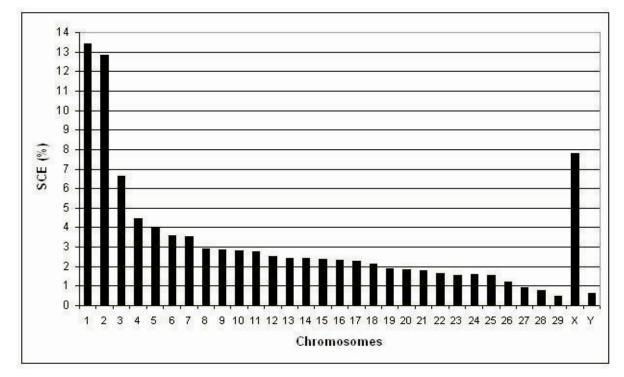


Fig. 2. SCE percentage distribution in the analysed chromosomes.

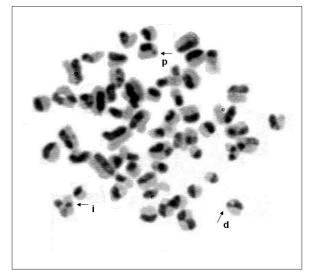


Fig. 3. A metaphase plate of the goat chromosomes (arrows indicate SCEs in the proximal -p, interstitial -i and distal -d region).



Fig. 4. A metaphase plate of goat chromosomes. Arrows indicate single and double SCEs.

chromosomes. The most numerous were single SCEs (79%), followed by double SCEs (21%).

Discussion

The phenomenon of sister chromatid exchange has received much interest for years. TAYLOR (1958) was the first to provide a detailed description of SCE in plant cells stained with tritiated 3H-thymidyne. Sister chromatid exchanges can also be identified with non-radioactive methods using BrdU and fluorescent Hoechst 33258 (LATT 1973), as well as BrdC (ZAKHAROV & BAIRAMJAN 1980). Chromosomes have been stained with Giemsa (ZAKHAROV & EGOLINA 1972; KOREN-BERG & FREEDLENDER 1974; WOLFF & PERRY 1974) or acridine orange (KATO 1974) and DAPI (LIN & ALFI 1976). SCE can also be detected using the FISH technique (BRUCKMANN et al. 1999; WÓJCIK et al. 2004, RUDD et al. 2007; WILSON & THOMPSON 2007). Using this technique, it is possible to visualise SCEs even in the smallest chromosome regions, e.g. in telomeres and subtelomeric regions, where the standard SCE detection technique is not sensitive enough. The present study employed one of the most readily used methods of SCE detection, with the simultaneous use of fluorescent dyes and Giemsa (KIHLMAN & KRONBORG 1975). The mechanism of SCE detection consisted of substituting part of the thymidyne in the DNA chain with BrdU. The incorporated BrdU was dehalogenated into uracil. Dehalogenation consisted of eliminating the bromide ion from the bromodexyuridine molecule by means of uracil-DNA glycosylase. This was followed by incorporation of uracil into the damaged single strand either by means of abasic endonuclease or further dehalogenation (WILSON & THOMPSON 2007). The strand in which thymidine was substituted by BrdU, following the application of Hoechst and Giemsa staining, contained less prominent chromatids. On the other hand, chromatids without BrdU substitution displayed more prominent fluorization and were darker in colour than the Giemsa-stained chromatids. Intermediary fluorization and stainability was detected in chromatids in which only one DNA strand had been substituted. Chromatids that contained BrdU in both strands were the least fluorescent and least stainable.

BrdU is a strong SCE inducer. The higher its concentration, the more difficult it is to determine the spontaneity of SCEs. The appropriate BrdU dose that needs to be applied in order to obtain spontaneous SCE is controversial. According to LEINBENGUTH and THIEL (1986), the optimal BrdU dose is 15-30 μ g/ml. CIOTOLA *et al.* (2005)

and PERETTI *et al.* (2006, 2008) recommend 10 μ g/ml. On the other hand, VIJH *et al.* (1992), DI BERARDINO *et al.* (1995; 1996) and ARIAS (2000) defined the proper BrdU concentration as 5 μ g/ml. WILSON and THOMPSON (2007) consider spontaneous SCEs to be those that occur at a very low or zero level of BrdU. The previous conclusions and our own results were used to determine a BrdU dose of 10 μ g/ml so as to rule out the appearance of additional BrdU-induced SCEs and guarantee spontaneous sister chromatid exchange.

The mean number of SCEs/cell in the Polish White Improved goats was 2.73±1.84. DI MEO et al. (1993) observed the mean number of SCEs in Maltese and Syrian goats to be 6.64±3.03 and 6.60±3.07 (respectively). On the other hand, DI BREARDINO et al. (1996) found the mean SCE frequency to be 3.28±1.71 in Ionica goats. The divergence between the our results and those of the above-mentioned researchers may stem from the use of different goat breeds, since breed has a significant effect on SCE incidence (WÓJCIK et al. 2011). This relationship was also observed by CATALAN et al. (1995), IANNUZZI et al. (1991a) and CIOTOLA et al. (2005) in their studies concerning different cattle breeds, and PERETTI et al. (2006) and RUBES (1987) who experimented on pigs. On the other hand, WULFF and NIEBUHR (1985) – between human races, and DI MEO et al. (2000) – between sheep breeds did not identify any effect of breed on SCE frequency.

According to MARGOLIN and SHELBY (1985), HUSUM et al. (2008) and WULFF and NIEBUHR (1985), an important factor influencing SCE incidence in man is sex. SCE analyses performed on farm animals did not confirm this hypothesis (DI MEO et al. 1993; IANNUZZI et al. 1991b; DI MEO et al. 2000; CIO-TOLA et al. 2005; PERETTI et al. 2006; WÓJCIK et al. 2011). We observed differences between the number of SCEs in males and females. However, as in the examples presented above, the differences were not statistically significant.

The age is a significant factor for the frequency of SCEs. However, there are few scientific publications concerning the effect of this factor on the number of SCEs. PERETTI *et al.* (2006), who analysed two groups of pigs – one comprised of animals under one year of age and another aged over one year, concluded that age does influence SCE frequency. SCE frequency in older animals was much higher. In their study of two groups of horses (up to six years and above six years of age), WÓJCIK *et al.* (2011) observed a rise in SCE frequency in the group of horses aged over six years. A similar relationship was also observed in humans (SINHA *et al.* 1985; LAZUTKA *et al.* 1994;

HUSUM *et al.* 2008). We found that age was a significant factor for the number of SCEs. A higher SCE number was observed in goats above one year of age.

Chromosome length and the SCE site in the chromosome are factors that may significantly affect SCE incidence. The longer the chromosome, the higher the number of exchanges that take place. This correlation was observed in various animal species and in man (LATT 1974; IANNUZZI et al. 1991b; ARIAS 2000; CORRANO & WOLFF 1975; VIJH et al. 1991). We also identified a positive correlation between the number of SCEs and chromosome length. DI MEO et al. (1993) obtained different results than those mentioned above. In a detailed examination of the 1st chromosome and the X chromosome, the authors observed a higher SCE frequency in the first chromosome and a lower frequency in the X chromosome relative to chromosome length. They accounted for this observation by stating that the X chromosome of goats does not have a heterochromatic band in the centromere, whereas the 1st chromosome, as all autosomes, has a heterochromatic band (rich in A-T) in the centromere region. Thus, more BrdU is required for incorporation during late S-phase replication. In this way SCE induction is increased.

The present study revealed the highest number of SCEs in the interstitial parts of the chromosomes. These were areas in which heterochromatin bordered on euchromatin. Slightly fewer SCEs were identified in the proximal region than in the interstitial area. In their analyses of human and cattle chromosomes, LATT (1974) and IANNUZZI et al. (1991b), respectively, showed that most SCEs occur in the G bands of chromosomes. In humans, LATT (1974) observed definitely fewer SCEs in the centromere region. Additionally, ARIAS (2000) (in hens), and WÓJCIK et al. (2011) (in horses) observed the same regularity. On the other hand SCEs were observed mostly in the centromere regions in the Chinese hamster (MARTIN & PRES-COTT 1964), rats (GIBSON & PRESCOTT 1972) and mice (LEE 1975; LIN & ALFI 1976). In Indian Muntjacs, CORRANO and WOLFF (1975) observed more SCEs in the heterochromatin area than in the euchromatin regions or at sites where euchromatin abutted on heterochromatin. According to LINDAHL (1993), the variability in SCE location may be due to species-specific differences in heterochromatin configuration in the centromeres. The present authors also observed sister chromatid exchanges in the distal chromosome regions. According to KAWANISHI and OIKAWA (2004), the terminal region is especially vulnerable to damage caused by oxidative stress. As a result, the number of discontinuities in single-strand telomeric DNA rises, and repair defects are identified as SCEs. Applying the CO-FISH technique (chromosome orientation-fluorescence in situ hybridization), RUDD *et al.* (2007) identified a high (up to 17%) SCE frequency in the terminal chromosome region.

Few studies have examined multiple sister chromatid exchanges in chromosomes. PERETTI *et al.* (2008) observed double and triple SCEs in Mediterranean Italian buffaloes affected by limb malformation (transversal hemimelia). They found that double SCEs were more numerous than triple ones. We observed single and double SCEs in the chromosomes. The phenomenon of elevated exchange frequency with multiple SCEs (more than two) was observed in humans in various syndromes, e.g. Bloom syndrome (YOUSSOUFIAN & PYERITZ 2002; AMOR-GUERET 2006).

The SCE test employed in this study is an exceptionally useful cytogenetic tool that enables the detection of DNA damage caused by the dysfunction of repair mechanisms due to contact with mutagens. Apart from assessing the effect of genotoxic agents on chromosomes, the test can also be used to evaluate human and animal genetic resistance.

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