Genome-wide scanning for QTL: Mapping methodology and detected QTL in cattle

Aduli Enoch Othniel MALAU-ADULI, Tomomi NIIBAYASHI, Takatoshi KOJIMA, Kazunaga OSHIMA and Masanori KOMATSU[1]

Laboratory of Animal Breeding and Reproduction, Department of Livest ock and Grassland Science, National Agricultural Research Centre for Western Region (WeNARC), 60 Yoshinaga, Kawai, Oda, Shimane 694-0013 JAPAN.

[1] Corresponding Author
E-mail: mkomatsu@naro.affrc.go.jp
Tel: +81-854-82-1285
Fax: +81-854-82-2280

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ABSTRACT

The availability of highly polymorphic microsatellite DNA markers on genetic maps in different livestock species and their association with phenotypes now gives geneticists and breeders an effective tool for the detection of quantitative trait loci (QTL) affecting traits of interest. This paper reviews QTL detection methodology with emphasis on multi-point interval mapping in half-sib populations. It also summarises published reports on QTLs detected by researchers in the bovine genome and suggests the way forward for QTL mapping in Japanese Black cattle.

Key words: QTL mapping, bovine genome, microsatellite markers, Japanese Black cattle

INTRODUCTION

Most economically important traits in livestock are affected by many genes as well as the environment and their interactions. Individual chromosomal locations where these genes responsible for phenotypic variation in a particular trait are called quantitative trait loci (QTL). Identifying QTL has potential to significantly increase the rate of genetic improvement through implementation of marker-assisted selection (MacNeil and Grosz, 2002). For traits that are difficult or expensive to measure, are lowly heritable, occur late in life or are determined post-mortem, marker-assisted selection may substantially increase the rate of response relative to selection based on estimated breeding value alone (Davis and DeNise, 1998). In many livestock species, linkage maps across whole genomes are now possible to access as a result of the availability of highly polymorphic microsatellite DNA markers. These maps provide the basis for finding QTL in whole genome scans. Microsatellite DNA markers on genetic maps are used to identify inheritance patterns of linked segments of the genome in structured pedigree populations. Significant associations of marker allele with the phenotype of interest suggest linkage of the markers to QTL. It is desirable for cattle researchers to have an up-to-date compilation of published detected QTL in

the bovine genome. To our knowledge, no such compilation currently exists, hence the need for this review. Therefore, the aims of this paper were to review the different types of QTL mapping approaches, their advantages and disadvantages, an in-depth description of the multi-point interval mapping methodology in half-sib populations and a compilation of mapped QTLs in the bovine genome. The paper also suggested the way forward in QTL mapping efforts in Japanese Black cattle.

TYPES OF QTL MAPPING APPROACHES

The idea of marker-based QTL mapping is to utilize marker-QTL association created from linkage disequilibrium among loci by matings. These approaches are often used in QTL studies:

The single-marker analysis examines the distribution of trait values separately for each marker locus. The disadvantage of this method is that there is some confounding between additive and dominance effects with the amount of recombination.

The interval mapping approach examines an association between each pair of adjacent markers and a QTL (Lee, 2002). The main advantage is that it offers both the effects of the QTL as well as the position. The disadvantage is that estimates from interval mapping are biased when multiple QTL are involved.

The multi-point mapping strategy involves the use of all the linked markers on a chromosome simultaneously. The main disadvantage is that of over-estimation when the number of explanatory variables is large.

The composite interval mapping method is a modified interval mapping procedure in which a few additional single markers for each analysis are incorporated (Zeng, 1993). The advantage is that resolution of the QTL locations is considerably improved by the introduction of a few additional well-chosen marker loci.

Multiple interval mapping uses multiple marker intervals simultaneously to fit multiple putative QTL directly in the model (Kao et al., 1999). The advantage of this method is that epistasis for QTL can also be estimated. All these methods mentioned above are based on conditional probability of QTL genotype given the observed marker genotype, and are used with various experimental designs for inbred lines (Lee, 2002).

The identity-by-descent (IBD) mapping is often used in outbred populations. This method specifies the expected genetic covariance between arbitrary relatives as a function of the IBD relationships at a QTL and determines proximity based on the number of cases where marker alleles and QTL alleles have not recombined.

Some of the above-mentioned procedures are considered in more details below:

Single marker mapping: With the advent of linkage maps, QTL mapping using single marker analysis has been reported in the literature in which potential candidate gene markers may be mapped a priori in the linkage group in outbred populations (Gelderman 1975, Weller 1986, Beckman and Soller, 1988, Weller et al., 1990, Le Roy and Elsen, 1995). The major drawbacks summarised by Knott et al. (1996) are as follows: Heterogeneity of information content among markers biases the estimation of QTL location toward the more informative rather than the closest marker when multiple markers in the vicinity of the QTL are available. Secondly, there is a confounding between estimates of the QTL position and effects.

Multi-point interval mapping: Lander and Botstein (1989) first proposed the multi-point approach called interval mapping. This approach has less sensitivity to violations of assumptions such as non-normality of distribution and provides more precise estimates of QTL position and effects than the single marker mapping in cross populations of inbred lines (Darvasi and Soller, 1993). The approach involves the analysis using a pair of multiple markers in a linkage group (Kim and Park,

2001). Haley and Knott (1992) developed the least squares regression method that did not require normality of residual terms and was found to be more efficient than the maximum likelihood approach to interval mapping. Knott and Haley (1992b) and Haley et al. (1994) stated that the major disadvantage of the interval mapping method in outbred populations is that missing genotypes and different information contents among marker intervals due to variability in marker heterozygosity cause a bias in the estimated QTL location toward the more informative marker interval. However, this heterogeneity between the marker intervals can be overcome by the simultaneous use of all markers in a linkage group (Knott and Haley 1992a, Knott et al. 1996, Knott and Haley 2000). Another disadvantage is the bias of significance tests and estimates of QTL location and effect due to multiple and linked QTL on the chromosome (Martinez and Curnow 1992). It must be stated that despite efficient applications in line-cross, half- or full-sib populations, these fixed QTL allele models cannot account for the complex data structures in commercial livestock populations in which the number of QTL alleles is unknown and the sires and dams are related across families (Kim and Park 2001). Furthermore, these models cannot provide breeding value estimates of each sire that are due to unlinked polygenic effects.

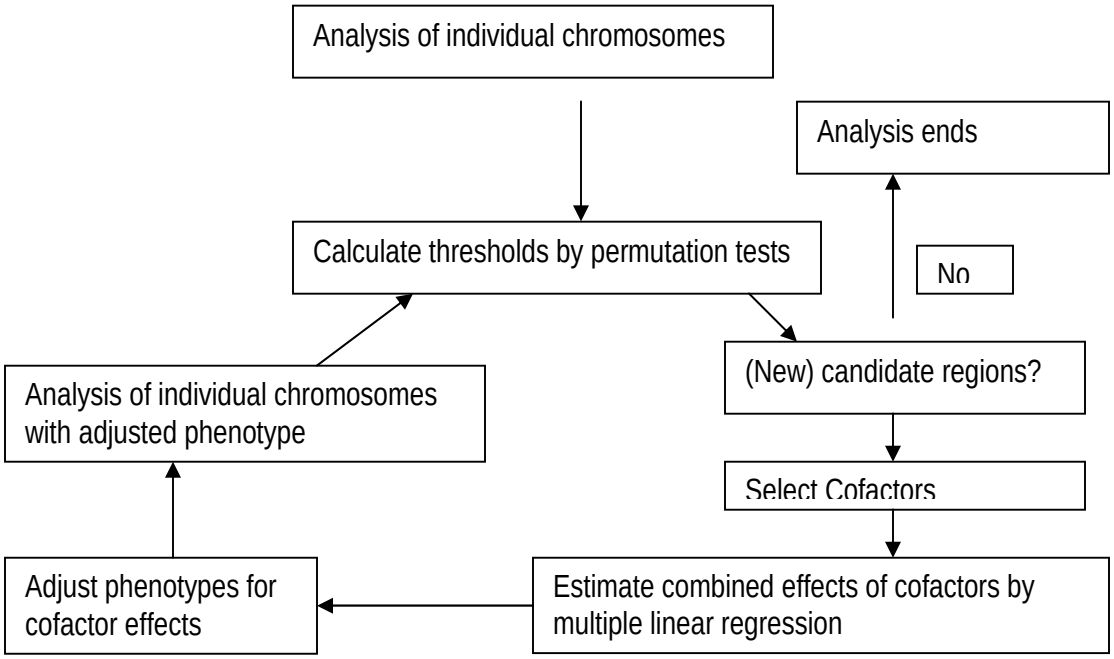
DETECTION AND MAPPING METHODOLOGY OF MULTIPLE QTL IN HALF-SIB POPULATIONS

The first reported detection and mapping of QTLs from genome-wide scans in half-sib livestock populations were those of Andersson et al. (1994) and Georges et al. (1995) in pigs and dairy cattle respectively. The half-sib model of Georges (1998) was based on allele substitution effects at the putative heterozygous QTL of sires and the analysis was performed separately for each family using maximum likelihood. Knott et al. (1996) also provided a fast, efficient and simple least squares multiple regression method for detecting and mapping QTLs in large half-sib population. In their half-sib model, QTL effects were estimated within paternal half-sib families by contrasting the

trait scores of the progeny that inherited the alternate paternal haplotypes. Their approach has been applied to other QTL mapping studies in dairy cattle by Spelman et al. (1996), Uimari et al. (1996), Zhang et al. (1998), de Koning et al. (2001a) and Freyer et al. (2002). It has also been extended to a full-sib model with large full-sib families in poultry (van Kaam et al. 1998). A major advantage of the half-sib model is that the QTL detected in a commercial population can be directly selected within that population by marker assisted selection. Georges (1998) however pointed out that larger experiments are required to compensate for the reduced heterozygosity or information content of markers compared to breed or line cross populations.

Kadarmideen and Dekkers (2001) and de Koning et al. (2001a) described in detail the detection and mapping of multiple QTLs in half-sib population using simple regression. The procedure consists of three stages:

1. To identify candidate gene regions, the chromosomes are analysed individually.
2. The second stage is to choose the best candidate positions as cofactors and their effects are re-estimated jointly with multiple linear regression.
3. The phenotypic data are adjusted for the effects of cofactors and the linkage groups are re-analysed by interval mapping. If this reveals new or better candidate regions, the set of cofactors can be modified and the effects be re-estimated. A flow diagram of the analyses (de Koning et al. 2001a) is presented below:



A detailed description of the above methods now follows. The first step is the analysis of the individual linkage groups using the multimarker approach for interval mapping described by Knott et al. (1996). Briefly, the probability of inheriting the parent's haplotype of a linkage group is calculated for each offspring at fixed intervals (for instance at 1cM). This is conditional on its marker genotype. Subsequently, by regressing the phenotype on the probability of inheriting the first haplotype of the parent, a QTL is fitted at fixed intervals along the linkage group. Thereafter, the analysis is nested within families and the residuals pooled across families to calculate a test statistic. This test statistic is calculated as an F-ratio for every map position within and across families. de Koning et al. (1998, 2001b) gave details of calculating the test statistic. It is important to fit the QTL within families for three reasons:

a) the random assignment of the first haplotype,

b) different QTL genotypes between parents and

c) different phases between markers and QTL between parents.

For every chromosome, the regression model is as follows:

$Y_{ij} = a_i + b_i X_{ij} + e_{ij}$

where Y_{ij} is the trait score of individual j, half-sib offspring from parent i

a_i is the polygenic effect for half-sib family i

b_i is the regression coefficient within family i (i.e. allele substitution effect for a putative QTL)

X_{ij} is the conditional probability for individual j of inheriting the first haplotype from parent i

e_{ij} is the residual effect

The second step involves the identification of candidate regions based on significance levels from permutation tests on the individual chromosomes as described by Churchill and Doerge (1994) and applied to several half-sib studies (Spelman et al. 1996, Vilkki et al. 1997). Spelman et al. (1996) suggested that QTL which exceed a given threshold are the cofactors in the further analyses. For every half-sib offspring, the transmission probabilities of the parent's first haplotype at the positions of the cofactors are taken as "virtual markers" (de Koning et al. 1998). Subsequently, the effects of all cofactors are re-estimated by multiple linear regression as follows:

$$Y_{ij} = a_i + \sum_{k=1}^{n} b_{ik} X_{ijk} + e_{ij}$$

Variables are the same as specified previously except that b_{ik} is the substitution effect within half-sib family i for cofactor k, X_{ijk} is the conditional probability for individual j of inheriting parent i's first haplotype at the position of cofactor k, and n is the number of cofactors in the analysis. The use of transmission probabilities as virtual markers is a convenient alternative to fitting marker scores as cofactors because it allows any position on a linkage group to be included as a cofactor. Also, transmission probabilities use all marker information whereas individual markers are usually not informative in all families.

The third step involves the adjustment of the original phenotypic data for the estimated effects of the cofactors. The phenotypic data are adjusted separately for every linkage group, thus only adjusting for the effects of those cofactors that reside on other linkage groups. Zeng (1994) and Doerge and Churchill (1996) stated that one of the reasons for doing this is that fitting an effect on a linkage group under study reduces the power to find additional QTL on that linkage group. Furthermore, conditioning on only unlinked QTL allows a re-evaluation of the cofactors (i.e. identified QTL) themselves rather than considering them fixed after they are identified. The formula for obtaining the adjusted phenotypes is as follows:

$$Z_{hij} = Y_{ij} - \sum_{k=1}^{n} b_{ik} X_{ijk}$$

Variables are the same as previously described with the extension that Z_{hij} is the adjusted phenotype for animal j of parent i with regard to chromosome h. A cofactor is excluded by putting its estimated substitution effect (b_{ik}) to zero if it is found to have no significant effect. Subsequently, all linkage groups are analysed by interval mapping using the adjusted phenotype Z_{hij} instead of Y_{ij}. If this reveals additional QTL, a new set of cofactors is selected. If the significance drops below the pre-specified threshold, cofactors can either be dropped from the analysis or their position can change. This step is repeated until no new QTL are identified and estimated locations of identified QTL are stable.

Churchill and Doerge (1994) and Doerge and Churchill (1996) have given details of empirically determining significance thresholds by permutation which is the next step. This involves the within half-sib families shuffling of the adjusted phenotypes for each linkage group, but the marker genotypes are retained. By this process, any association between markers on that linkage group and trait values are distorted but those for the unlinked cofactors are kept intact. The permutated

data are analysed and the best test statistic is stored. In order to obtain an empirical distribution of the test statistic under the null hypothesis of no QTL associated with the linkage group under study, the permutation procedure is repeated about 10,000 times (de Koning et al. 1998). This provides a specific test for the chromosome under study rather than a test for the complete multiple QTL model. The desired threshold α can be obtained by taking the (1 - α) percentile of the sorted test statistics. These chromosome-wide thresholds based on 10,000 permutations could be adjusted for genome-wide risk levels by Bonferroni correction (Lander and Kruglyak 1995, de Koning et al. 1998, de Koning et al. 2001b).

A situation where all relationship information between sires or families is included to model covariances at individually marked QTL and to assign random effects to the QTL alleles within the parents of a family is suitable for interval mapping using a variance component approach. Zhang et al. (1998) and Kim (1999) applied this approach in commercial or experimental populations using mixed linear modelling and restricted maximum likelihood to estimate variance due to the QTL alleles, polygene effects and residuals. Grignola et al. (1996, 1997) stated that when the family size is large, this model provides accurate estimates of QTL location and effects and can be fitted to any complex pedigree since it is robust to normality assumptions. A detailed review of other advanced interval mapping procedures such as multiple-QTL, multiple-trait, joint mapping, candidate gene mapping, QTL-fine mapping, identity-by-descent and linkage disequilibrium mapping has been reported by Kim and Park (2001).

A REVIEW OF DETECTED QTL IN CATTLE

Quite a number of detected QTL from the bovine genome has been reported in the literature. An alphabetical compilation of some of them and the cattle breeds concerned is shown in Table 1. QTL detected in beef and dairy cattle are reviewed separately as follows:

Beef cattle: MacNeil and Grosz (2002) conducted genome-wide scans for QTL affecting carcass traits in Hereford x Composite Double backcross populations using 229 microsatellite markers. They detected QTL for liveweight on chromosome 17 located at 52cM and the 95% confidence interval for the location of this effect spanned the interval from 35 to 69 cM covered by the microsatellite markers ILSTS023, IDGVA-40 and ILSTS058. The QTL for marbling was detected on chromosome 2 located at 122cM in which the 95% confidence interval was from 112 to 132cM and included the microsatellite markers IDVGA-2 and FCB11. Other traits and their suggestive QTL locations by them included: Dressing percentage (chromosome 16, 22-26cM), rib eye area (chromosome 12, 34-36cM) and fat depth (chromosome 16, 66-72cM).

Grosz and MacNeil (2001) conducted a genome scan for chromosomal regions influencing birth weight using 151 progeny of a single Hereford x Composite bull and detected a QTL at the telomeric end of chromosome 2 located at 114cM in the interval between BM2113 and OarFCB11 microsatellite markers. In another study that focussed on the use of genetic markers to detect regions of the bovine genome that accounted for variation in birth weight, Davis et al.. (1998) used progeny from three F_1 Charolais x Brahman sires crossed with a composite dam utilising 167 markers. Significant QTL effects on birth weight were detected on five chromosomes – 5, 6, 14, 18 and 21 located at 90, 48, 42, 116 and 4cM respectively.

Napolitano et al. (2001) genotyped 110 Piemontese x Chianina F_1 crossbred and 75 F_2 intercross cattle using IDVGA-46 DNA marker that showed polymorphisms for 3 alleles (205, 207 and 229 base pairs). They investigated the association of marker polymorphism with beef conformation traits and identified a QTL on chromosome 19 for carriers of the 205 allele when inherited from the Chianina. Casas et al. (2000) investigated QTL affecting growth and carcass composition of cattle segregating alternate forms of myostatin. They identified QTL on chromosome 5 located from 50 to 80cM affecting rib bone, dressing percentage, fat depth, retail product yield and yield grade. Stone et al. (1999) performed a primary genomic screening for QTL affecting carcass and growth traits using 238 microsatellite markers on 185 progeny from a Bos indicus x Bos taurus sire mated to Bos taurus cows. They detected a QTL allele of Brahman origin affecting an increase in rib bone and a decrease in dressing percentage on chromosome 5 located from 50 -80cM. Other suggestive QTL peaks for other traits reported by them included rib fat, fat trim yield and retail product yield (chromosome 18, 84cM), birth weight (chromosome 7, 2cM), longissimus muscle area (chromosome 14, 19cM) and rib muscle (chromosome 26, 8cM). Keele et al. (1999) conducted a genome scan using 196 microsatellite DNA markers spanning 29 autosomal bovine chromosomes on the longissimus muscle of 294 progeny from one Brahman x Hereford bull mated to Bos taurus cows to identify QTL for beef tenderness. They detected a QTL located 28cM (95% confidence interval of 17 to 40cM) from the most centromeric marker on chromosome 15. Casas et al. (1998) reported that a locus near the centromere of bovine chromosome 2 was responsible for muscle hypertrophy in two half sib families of Belgian Blue x MARC III and Piedmontese x Angus when they utilized 6 microsatellite markers to determine the presence or absence of the mh allele and confirmed the location to be 4cM from the linkage group with the 95% confidence interval between 2 and 6 cM. A summary of detected QTL for beef traits and their estimated chromosomal locations is presented in Table 2.

Dairy cattle: Freyer et al. (2002) utilized a granddaughter design containing five half-sib families of German Holstein-Friesian for QTL analysis on chromosome 6 using 16 microsatellite markers. They detected significant and putative QTL at 49cM for milk yield, at 70cM for fat and protein yield and at 46cM for protein content. Further QTL positions were suggested mostly for yield traits and protein content in the area of the casein gene cluster at 90-95cM. The presence of two QTL on chromosome 6 was also indicated for milk yield (at about 47 and 91cM). This finding corresponded to earlier studies by Lien et al. (1995) who reported an association of QTL for milk and protein yield to the casein gene cluster (CSN) locus in chromosome 6 at about 95cM. Velmala et al. (1999) also obtained similar results in which significant QTL for fat yield and protein yield at about 70cM which is close to the marker FBN13, were reported. Zhang et al. (1998) reported a QTL for milk yield at 40cM while Georges et al. (1995) found a QTL for milk yield at about 60cM. Similar reports on significant QTL for several traits at 95cM have also been published by Velmala et al. (1999) and Ashwell and Van Tassel (1999). Freyer et al. (2002) stated that the casein cluster (CSN) located on chromosome 6 in particular, has been focussed upon by researchers and significant positive effects of the $CSN2^{A2}$ allele on milk yield have been reported (Bovenhuis et al. 1992, Bovenhuis and Weller 1994, Ng-Kwai-Hang et al. 1986, Ojala et al. 1997, Freyer et al. 1999, Ikonen et al. 2001).

Ashwell et al. (1997) studied associations of seven health and milk production traits with six microsatellite markers on bovine chromosome 23 using an elite Holstein population. They found QTL for protein yield and protein percentage in a single family. A QTL for protein yield had a LOD score of 1.821 and was located between BM1818 and BM1443, while the QTL for protein percentage had a LOD score of 1.554 and was located near marker BM1443. Elo et al. (1999) genotyped 469 bulls for six microsatellite loci in 12 families of Finnish Ayrshire cattle and reported

that a quantitative trait locus for liveweight mapped to bovine chromosome 23 located between markers BM1258 and BoLA DRBP1. These two reports seem to confirm earlier indications that the bovine lymphocyte antigen (BoLA) is associated with milk production traits (Simpson et al. 1990), growth traits (Batra et al. 1989; Stear et al. 1989b) and diseases such as mastitis, ketosis and infertility (Lunden et al. 1990; Mejdell et al. 1994; Dietz et al.. 1997). Bovine chromosome 14 has also been the subject of intense QTL study for dairy traits (Coppieters et al. 1998a, 1998b, Heyen et al. 1999, Looft et al. 2001, Farnir et al. 2002, Kim and Georges 2002). A summary of some detected QTL for dairy traits and their estimated chromosomal locations is presented in Table 3.

QTL MAPPING IN JAPANESE BLACK CATTLE

In Japan, Hirano et al. (1996) reported the isolation of 42 highly polymorphic microsatellite markers from Japanese Black Cattle (Wagyu) in which 41 of the markers were assigned to bovine autosomes with LOD scores >6 and exhibited an average heterozygosity value of 0.67. Collaborative studies on QTL mapping for carcass weight, rib-eye area, marbling and other carcass traits in Japanese Black cattle between the Livestock Improvement Association of Japan, Shirakawa Institute of Animal Genetics and twenty-one Prefectures are on-going (Mizoguchi 1998). From these collaborative studies, some results (Harada et al. 2001, Mizoguchi et al. 2001a, 2001b, Inoue et al. 2001, Hirano et al. 2002, Kobayashi et al. 2002) have been reported either in the form of posters or oral presentations at conferences, but QTL positions have not yet been officially announced except for the QTL affecting oleic acid content in intramuscular fat (Ogura et al. 2001). In addition, two reports of a primary screening of the bovine genome for quantitative trait loci affecting some growth traits of Japanese Black cattle (Komatsu et al. 2002) and Japanese Black x Limousin F2 crossbreds (Abe et al. 2002) have been orally presented at a scientific conference. A number of simulated and theoretical work on marker-assisted selection (Saito and Iwaisaki 1996,

1997a, 1997b, Saito et al. 1998) as well as mathematical modelling of QTL cluster effects in granddaughter design, multi-group and outbred populations (Matsuda and Iwaisaki 2000, 2001a, 2001b, 2001c) have been published.

In view of the fact that huge costs are associated with the development and procurement of microsatellite markers and genotyping large number of sires and offspring, it is suggested that more of such collaborative research between Prefectures should be encouraged. Furthermore, the best way forward in reducing duplication of efforts is to assign specific traits of economic interests as well as different chromosomes to be genotyped to different research centers. Such centers can conduct genome-wide scanning and detailed QTL analysis in Japanese Black cattle from any prefecture in Japan. That way, the coverage is wider, sample size is bigger and the results must be more reliable. A regular forum to discuss progress made, results, exchange of ideas and streamlining of findings would be very useful and beneficial.

In conclusion, this paper has reviewed the different types of QTL mapping approaches with emphasis on multi-point interval mapping in half-sib populations. It has also compiled a reference point of published QTL detected in beef and dairy cattle for researchers in bovine genome scanning. It has also made a suggestion for collaborative efforts in QTL mapping efforts in the Japanese Black cattle.

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Table 1. An alphabetical list of some published QTL research in beef and dairy cattle breeds

Author(s)	Trait(s)	Breed of cattle
Abe et al. (2002)	Growth	Japanese Black x Limous in
Arranz et al. (1998)	Milk yield and composition	Holstein -Friesian
Ashwell et al. (1996)	Somatic cell score	US Holstein
Ashwell et al. (1997)	Milk production and health	US Holstein
Ashwell et al. (1998a)	Conformation type	US Holstein
Ashwell et al. (1998b)	Milk production, health, type	US Holstein
Ashwell & Van Tassel (1999)	Milk production	US Holstein
Beever et al. (1990)	Growth and carcass	Angus
Blattman et al. (1996)	Ovulation rate	Friesian
Casas et al. (1998)	Muscle hypertrophy and carcass	Belgian Blue x MARC III
Casas et al. (2000)	Growth and carcass composition	Piedmontese x Angus
Coppieters et al. (1998a)	Milk yield and composition	Holstein-Friesian
Coppieters et al. (1998b)	Milk production	Holstein -Friesian
Davis et al. (1998)	Birth weight	Charolais x Brahman
Elo et al. (1999)	Liveweight	Finnish Ayrshire
Farnir et al. (2002)	Milk production	Holstein -Friesian
Freyer et al. (2002)	Milk yield and contents	German Holstein-Friesian
Georges et al. (1995)	Milk production	US Holstein
Grosz and MacNeil (2001)	Birth weight	Hereford x Composite
Harada et al. (2001)	BMS	Japanese Black (Wagyu)
Heyen et al. (1999)	Milk production and health	North American Holstein -Friesian
Hirano et al. (2002)	BMS	Japanese Black (Wagyu)
Inoue et al. (2001)	BMS	Japanese Black (Wagyu)
Jansen et al.(1998)	Milk production	Dutch Holstein -Friesian
Keele et al. (1999)	Longissimus tenderness	Brahman x Hereford
Kim and Georges (2002)	Milk production	Dutch Holstein -Friesian
Kobayashi et al. (2002)	BMS	Japanese Black (Wagyu)
Komatsu et al. (2002)	Growth	Japanese Black (Wagyu)
Li et al. (2002)	Growth	Beefbooster Angus M1 and M3
Lien et al. (2000)	Twinning rate	Norwegian cattle
Lipkin et al.(1998)	Milk protein percentage	Israeli Holstein
Looft et al. (2001)	Milk production	Holstein -Friesian
MacNeil and Grosz (2002)	Carcass	Hereford x Composite backcross
Mizoguchi et al. (2001a)	Fat necrosis	Japanese Black (Wagyu)
Mizoguchi et al. (2001b)	BMS, Carcass weight	Japanese Black (Wagyu)
Napolitano et al. (2001)	Beef conformation	Piedmontese x Chianina
Ogura et al. (2002)	Intramuscular fat melting point	Japanese Black (Wagyu)
Ron et al. (1994)	Dairy traits	Holstein -Friesian
Stear et al. (1989a)	Reproduction	Angus, Brown Swiss, Charolais,
Stear et al. (1989b)	Growth	Hereford, Limousin, Simmental
Spelman et al. (1996)	Milk production	Dutch Holstein-Friesian
Stone et al. (1999)	Growth and carcass	Bos indicus x Bos taurus
Taylor et al. (1998)	Growth and carcass	Angus x Brahman backcross
Velmala et al. (1999)	Milk production	Finnish Ayrshire
Vilkki et al. (1997)	Milk production	Finnish dairy cattle
Zhang et al. (1998)	Milk production and health	Holstein

Table 2. Some detected QTL of beef traits and their estimated chromosomal locations

Trait(s)	Chromosome No.	Location (cM) *	Reference
Liveweight	17	52 (35-69)	MacNeil and Grosz (2002)
Marbling	2	122 (112-132)	MacNeil and Grosz (2002)
Rib-eye area	12	34-36	MacNeil and Grosz (2002)
Fat depth	16	66-72	MacNeil and Grosz (2002)
Dressing percentage	16	22-26	MacNeil and Grosz (2002)
Birth weight	5	0-30	Li et al. (2002)
Preweaning average daily gain	5	55-70	Li et al. (2002)
Average daily gain	5	70-80	Li et al. (2002)
Birth weight	2	114	Grosz and MacNeil (2001)
Fat depth	5	62-72	Casas et al. (2000)
Retail product yield	5	62-72	Casas et al. (2000)
Yield grade	5	62-72	Casas et al. (2000)
Birth weight	6	48-51	Casas et al. (2000)
Yearling weight	6	48-51	Casas et al. (2000)
Longissimus muscle area	6	48-51	Casas et al. (2000)
Hot carcass weight	6	48-51	Casas et al. (2000)
Fat depth	14	15	Casas et al. (2000)
Marbling score	17	21	Casas et al. (2000)
Marbling score	27	60	Casas et al. (2000)
Warner-Bratzler shear force	29	56-65	Casas et al. (2000)
Rib bone	5	50-80	Stone et al. (1999)
Dressing percentage	5	50-80	Stone et al. (1999)
Tenderness	15	28 (17-40)	Keele et al. (1999)
Liveweight	23	25	Elo et al. (1999)
Calf mortality	23	6	Elo et al. (1999)
Veterinary treatment	23	38	Elo et al. (1999)
Muscle hypertrophy	2	4 (2-6)	Casas et al. (1998)
Birth weight	5	90	Davis et al. (1998)
Birth weight	6	48	Davis et al. (1998)
Birth weight	14	42	Davis et al. (1998)
Birth weight	18	116	Davis et al. (1998)
Birth weight	21	4	Davis et al. (1998)

* Figures in brackets indicate 95% confidence interval locations

Table 3. Some detected QTL of dairy traits and estimated chromosomal locations or LOD scores

Trait(s)	Chromosome No.	Location (cM)*/LOD score	Reference
Milk yield	6	49	Freyer et al. (2002)
Fat yield	6	70	Freyer et al. (2002)
Protein yield	6	70	Freyer et al. (2002)
Protein content	6	46	Freyer et al. (2002)
Fat percentage	14	2 (0-7)	Heyen et al. (1999)
Fat yield	14	1 (0-51)	Heyen et al. (1999)
Protein percentage	3	3 (0-97)	Heyen et al. (1999)
Protein yield	3	16 (2-125)	Heyen et al. (1999)
Fat percentage	3	22 (0-64)	Heyen et al. (1999)
Milk yield	14	47	Coppieters et al. (1998a)
Protein percentage	14	70	Coppieters et al. (1998a)
Fat percentage	14	2	Coppieters et al.(1998a)
Protein percentage	6	48	Coppieters et al. (1998b)
Milk fat	14	7	Farnir et al. (2002)
Milk yield	14	25.1 (Lod score)	Kim and Georg es (2002)
Fat yield	14	20.9 (Lod score)	Kim and Georges (2002)
Protein yield	14	11.0 (Lod score)	Kim and Georges (2002)
Fat percentage	14	85.7 (Lod score)	Kim and Georges (2002)
Protein percentage	14	17.4 (Lod score)	Kim and Georges (2002)
Milk yield	14	48	Looft et al. (2001)
Fat yield	14	22	Looft et al. (2001)
Protein yield	14	75	Looft et al. (2001)

* Figures in brackets indicate 95% confidence interval locations