SNP mapping of QTL affecting wool traits in a sheep backcross Sarda - Lacaune resource population.

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Abstract

A QTL detection experiment was organized in a backcross Sarda X Lacaune sheep resource population. The aim of this experiment was primarily the search for loci influencing milk production and several other traits including wool traits through a whole genome scan on 968 females from 10 sire families. Ten fleece characteristics: greasy fleece weight, length of long and fine wool as well as fibre diameter (mean and CV), fibre curvature (mean and CV) and medullation content (coarse and other medullated fibres) using OFDA 100 methodology were measured on 892 6-months old females. For QTL detection, the Illumina OvineSNP50 beadchip that provided 43,276 SNP markers after quality control was used. Within and across families analyses were performed with the QTLMAP software. The statistical techniques used were linkage analysis (LA), linkage disequilibrium analysis (LD) and joint linkage and association analysis (LDLA) using interval mapping. High significant QTL ($p<0.001$ at genome wide) affecting 7 wool traits: greasy fleece weight, fibre diameter (mean and CV), Fibre length, medullation content and CV of fibre curvature were found on chromosome 25 within a 2cM interval suggestting that one or some genes with major effect on fleece characteristics are located on this chromosomal segment. Other high significant QTL's ($p<0.001$ at genome wide) influencing medullation content and, fibre length on chromosome 20 and 15 respectively were also detected. Other putative QTL's ($p< 0.01$ at chromosome wide) were also observed on chromosome 3 and 6, 13 and 18, and 14 for greasy fleece weight, fibre length, and fibre curvature respectively. The linkage disequilibrium analysis and joint LDLA analysis confirmed the locations of the QTL mapped on OAR25, 20 15, 13 and 6 and all QTL found were discussed.

Introduction

A QTL detection experiment was organized in a backcross Sarda X Lacaune sheep resource population. The first aim of this experiment was the search for loci influencing milk production and several other traits difficult to measure through a whole genome scan (Carta and al, 2002). However Sarda and Lacaune sheep breeds differ for wool characteristics. The Lacaune sheep is a short wool breed while the Sarda is a long wool one with a fleece made of both long-coarse medullated fibre and short-finer wool fibre. The purpose of this paper is to give results about QTL detection on wool traits and fleece characteristics in this sheep population resource.

Methods

Experimental design.

In 1998, 14 elite Lacaune rams from France were mated in Italy by AI to 100 Sarda ewes to produces F1 rams. 10 sons of different Lacaune Sires were mated to 3000 Sarda ewes to procreate 967 backcross females born in 1999. Rearing conditions of animals have been earlier described (Carta et al, 2002).

Wool traits measurements.

In May 2000, a total of 892 females were shorn and mid side fleece samples were taken at 6 months of age. Greasy fleece weight (GFW) was recorded. The length of each main kind of fibre within the staple: long-wool staple length (LWL) and short-wool staple length (SWL) were measured. Then after a washing treatment, wool samples were analysed in a textile laboratory (IFTH, France) by Optical Fibre Diameter Analyser (OFDA) on 4000 fibre snippets for determining mean fibre diameter (MFD), coefficient of variation of fibre diameter (CVD), coarse medullated fibre content defined as the sum of both objectionable fibre content and flat fibre content and other medullated fibre content (MED), mean fibre curvature (MFC) and coefficient of variation of fibre curvature (CVC) using an OFDA100 apparatus according to IWTO-57-98 standard method (2005).

SNP Genotypes.

The whole back-cross population and the ten F1 sires were genotyped with the Illumina OvineSNP50 Beadchip.

SNPs showing Mendelian inconsistencies within the International Mapping Flock were discarded as well as SNP with a call rate <95%. A Minor allele frequency below 1% was applied and a test for Hardy-Weinberg disequilibrium within sire family was also considered ($p<10^{-6}$). Sexual chromosomes were not considered for analysis. Finally 967 backcross females and their sire and 43,276 autosomous markers remained for QTL analyses.

SNP positions were obtained from the sheep Genome Browser V3.1 on http://www.livestockgenomics.csiro.au/cgi-bin/gbrowse/oarv3.1/, (Archibald et al, 2010). For mapping purpose, 1 Mbp was considered as a proxy for 1 cM.

Statistical analyses.

Linkage Analysis.

Linkage analysis (**LA**) was performed with the 10-family SNP genotyped dataset. Within each sire family, the presence of a QTL was tested against the null hypothesis, which was absence of a QTL at every 0.1-cM interval (approximately 1 Mbp/1 cM), by likelihood computation using the QTLMAP software (Elsen et al., 1999). Chromosome-wise significance was determined by testing with 1,000 permutations for each chromosome-trait pair (Churchill and Doerge, 1994). To prevent any overestimations of thresholds due to the selective phenotyping occurring for some traits, permutations were restricted to animals that were both genotyped and phenotyped for the considered traits. These permutations were used to calculate the genome-wise suggestive threshold (1 false-positive result was expected for a whole genome scan) and genome-wise significant threshold (5% genome-wise significance threshold) as indicated in Lander and Kruglyak (1995). These genome-wise thresholds were obtained by applying the Bonferroni correction Pgenome-wise = 1 – (1 – Pchromosome-wise)^n, where n is the number of chromosomes (i.e. 26 in sheep; Knott et al., 1998). Confidence intervals were determined using the 2-LOD (i.e., logarithm of the odds) drop-off criterion (Ooijen, 1992) and assuming 1 LOD = 4.61 LRT (i.e., long terminal repeats; Lynch and Walsh, 1998). The QTL effects were expressed as average QTL substitution effect in phenotypic SD (**σp**). A *t*-test was performed to identify the 5% significant QTL effects within each sire family.

Association Analysis (LD) and Joint Linkage and AssociationAnalysis (LDLA).

The LD-decay model proposed by Legarra and Fernando (2009) was implemented in the QTLMAP software and applied to our data. In this application of the LD-decay model, observed phenotypes were regressed on the conditional probability of having inherited a 4-SNP haplotype from each of its 2 parents, the substitution effect of the sire haplotypes being weighted by the transmission probabilities. In addition, a joint association and linkage analysis (**LDLA**) was performed to take advantage of both LD and pedigree information in the experimental population (Legarra and Fernando, 2009). In this LDLA model, within sire QTL effects are added to the sire haplotypes effects of the LD-decay model to account for a possible between sire variability of the QTL effect beyond that reflected by the haplotype.

The chromosome-wise P values were estimated for each trait assuming the LRT statistics asymptotically followed a χ^2-distribution with *k* degrees of freedom, *k* being the number of QTL effects (Piepho, 2001). Hence, *k* was equal to the number of haplotypes plus the number of families minus 1 for LDLA. Genome-wise *P* values were derived by applying a Bonferroni correction as described above. Any association reaching the 1% genome-wise significant *P* value was declared significant. Associations reaching the 5% genome-wise significant threshold were only reported if a suggestive QTL had already been found for the same trait by LA analysis

For each, LA, LD and LDLA analyses, specific fixed effects for each wool trait were included in models. The main factors were age at shearing, dam parity and type of birth (single, double or triple). Single trait QTL analysis was performed by multi-marker regression (Knott et al, 1996; Elsen et al 1999) using QTLMAP software available online (www.inra.fr/qtlmap).

Results and discussion

Table 1 shows the mean, the standard deviation and the range of values for the different wool traits recorded on the 892 backcross animals of the experiment.

***Table 1**: Basic statistics of the different wools traits measured at 6 months of age in 892 Sarda- Lacaune backcross femelles.*

Trait	Mean	Standard Deviation	Minimum	Maximum
Greasy fleece weight (g)	635.9	136.0	252	1134
Mean fibre diameter (µm)	29.9	3.0	22.4	43.3
CV fibre diameter (%)	44.4	7.5	19.0	72.6
Length of outer long wool (mm)	90.0	20.4	45	155
Length of inner short wool (mm)	55.6	9.1	27.5	95
Objectionable Fibre Content (p 10,000)	102.1	151.9	0	2810
Flat fibre content (p 10,000)	84.6	85.2	0	842.5
Other medullated fibres (p 10,000)	339.4	218.4	35	2830
Mean fibre curvature (degree per mm)	65.6	9.3	38.8	97.4
CV fibre curvature (%)	90.6	7.6	69.7	127.2

QTLs affecting wool traits LA, LD and LDLA SNP analysis.

Results were only reported if significant QTL were observed conjointly for the three LA, LD and LDLA analysis. In total LA, LD and LDLA analysis jointly mapped for 13 QTLs regions and high significant QTLs at genome-wise ($p < 0.001$) were found on 6 different chromosomes for different wool traits and fleece characteristics. Each exhibiting a moderate to high effect (from 0.35 to 1.57 residual standard deviation). High significant QTLs were observed for greasy fleece weight, length of the outer long wool, mean fibre diameter, CV of fibre diameter, coarse medullated fibre content, other medullated fibre content, mean fibre curvature and CV of fibre curvature (table 2).

Table 2. *Genome-wise significant QTL (Pg<0.1%) for wool traits in LA, LD and LDLA analysis.*

Trait	OAR	Position Mb [CI] [a]	Significance	Average QTL effect [b]
Greasy fleece weight	6	14.2 [8.5 – 32.6]	**	0.41
Greasy fleece weight	25	6.1 [4.7 - 14.9]	**	0.43
Mean fibre diameter	25	6.3 [5.7 - 7.9]	***	0.82
CV fibre diameter	25	6.7 [6.2 - 7.2]	***	1.57
Length of long wool	13	46.2 [32.6 – 60.1]	*	0.37
Length of long wool	15	72.1 [69.5 – 73.5]	***	0.66
Length of long wool	18	64.9 [11.5 – 68.1]	*	0.35
Length of long wool	25	7.2 [4.8 - 8.0]	***	0.59
% coarse medul. fibres	20	50.0 [49.6 – 50.5]	***	0.55
% coarse medul. fibres	25	6.2 [5.7 - 6.6]	***	0,84
% other medul. Fibres	20	50.0 [48.8 - 50.5]	*	0.37
% other medul. fibres	25	8.1 [4.9 - 23.0]	***	0.47
CV fibre curvature	15	72.0 [71.8 – 75.0]	**	0.41
CV fibre curvature	25	8.0 [6.2 – 14.8]	***	0.64

[*] 5% genome-wise significant
[**] 1% genome-wise significant
[***] 0.1% genome-wise significant
[a] Confidence interval
[b] given in phenotypic SD

Seven huge significant QTLs at genome wise ($p<0.001$) were mapped on nearly the same region of chromosome 25 extended within 6. 1 and 8.2 Mb with a global confidence interval from between 4.9 and 23Mb. Interestingly, all effects observed on chromosome 25 are associated to haplotypes issued from the Lacaune grand sire with a decreasing on greasy fleece weigh, mean fibre diameter, CV of fibre diameter, length of the outer long wool, medullation content (both coarse medullated fibre and other medullated fibres) and CV of fibre curvature. The Lacaune sheep produces a lesser greasy fleece weight with a lower mean fibre diameter, CV of fibre diameter, meedullation content and CV of fibre diameter than the Sarde one. Such QTL's affecting wool traits on chromosome 25 have been previously reported on the same experimental design using microsatellite makers (Allain et al, 2006) and on mean fibre diameter, staple length and CV of fibre diameter in other sheep QTL experimental design (Allain et al, 1998; Ponz et al, 2001; Bidinost, 2008). It could be suggested that one or a few genes with major effects on wool traits and fleece characteristics are located on a small region chromosome 25. No candidate genes have been identified on this chromosome area. However new findings such as a selective sweep of 270kb size overlapping this $\text{QTL}_{\text{Oar25}}$ region (Kijas et al, 2012) and a potential causal mutation with the presence of an insertion segment (2Kb) polymorphism associated to the absence of long coarse hair in the birthcoat of the Romane breed which has been recently identified (Cano et al, 2013) suggest the presence of a good candidate gene in this chromosome area.

Other high significant QTLs affecting greasy fleece weight on chromosome 6, length of outer long wool on chromosome 13, 15 and 18, CV of fibre diameter on chromosome 15 and content of coarse medullated fibres on chromosome 20 (table 2). These QTLs exhibiting moderate to high effects (from 0.35 to 0.66 phenotypic standard deviation). But no candidate genes have been identified on these chromosome regions. QTLs affecting staple length obn chromosome 15 and 18 have been earlier reported (Allain et al, 2006).

Table 3. *Suggestive QTLs (Pc<0.1% at chromosome-wise) for wool traits in Linkage Analysis and confirmed in association analysis (Pg<5% at genome-wise).*

Trait	OAR	Position (Mb) [CI] [a]	Average QTL Effect [b]
Greasy fleece weight	3	11.4 [4.7 – 19.8]	0.38
Mean fibre curvature	13	41,9 [24,2 – 56,7]	0,28
CV fibre curvature	3	127.9 [123.8 – 139.7]	0,39

[a] Confidence interval
[b] given in phenotypic SD

Suggestive QTLs at chromosome-wise(p<0.001) affecting wool traits were observed for greasy fleece weight, mean fibre curvature and CV of fibre curvature on chromosome 3 and 13 (table 3). These suggestive QTLs in linkage analysis were confirmed in associations analyses. A previous study suggested a putative QTL on staple length on chromosome 3 close to KRT2 family genes (Allain et al, 1998; Ponz et al, 2001). This QTL on the length of wool was not confirmed in the present study but knowing close relationship between GFW and staple length, the existence of a QTL affecting wool traits in this chromosomal area cannot be excluded.

Four suggestive QTLs were observed in linkage analysis on chromosome 1, 9, 14 and 15 for coarse medullated fibre content, shortwool length, CV of fibre diameter and mean fibre curvature respectively. But only QTL affecting coarse medullated fibre content on chromosome 1 was confirmed as suggestive QTL on association analyses. Chromosome 1 harbors one of the keratin-associated-protein clusters (KAP6, KAP7 and KAP8 producing high-glycine tyrosine proteins deficient in sulphur) involved in the formation of matrix surrounding cortex wool microfibrils (McLaren et al 1997, Ede et al 1995, Parsons et al, 1993). A linkage between this keratin cluster gene and fiber diameter in a merino half-family was observed (Parsons et al, 1994) and thus would confirmed that a gene with a major effect on wool fibre characteristics could be located on chromosome 1 in the region of KAP cluster genes.

Conclusion

A significant QTL affecting several wool traits was found and suggest that a gene with major effect on fleece characteristics is located on chromosome 25. Other significant and putative QTL's were also detected on chromosome 1, 3, 6, 13, 15, 18 and 20. More investigations including both fine and comparative mapping as well as sequencing approaches need to be undertaken in order to find major genes controlling fleece characteristics which play an important role on both wool production and the protective aptitude of the fleece concerning heat loss when animals are raised under harsh environment and permanent exposure outdoors.

Acknowledgements

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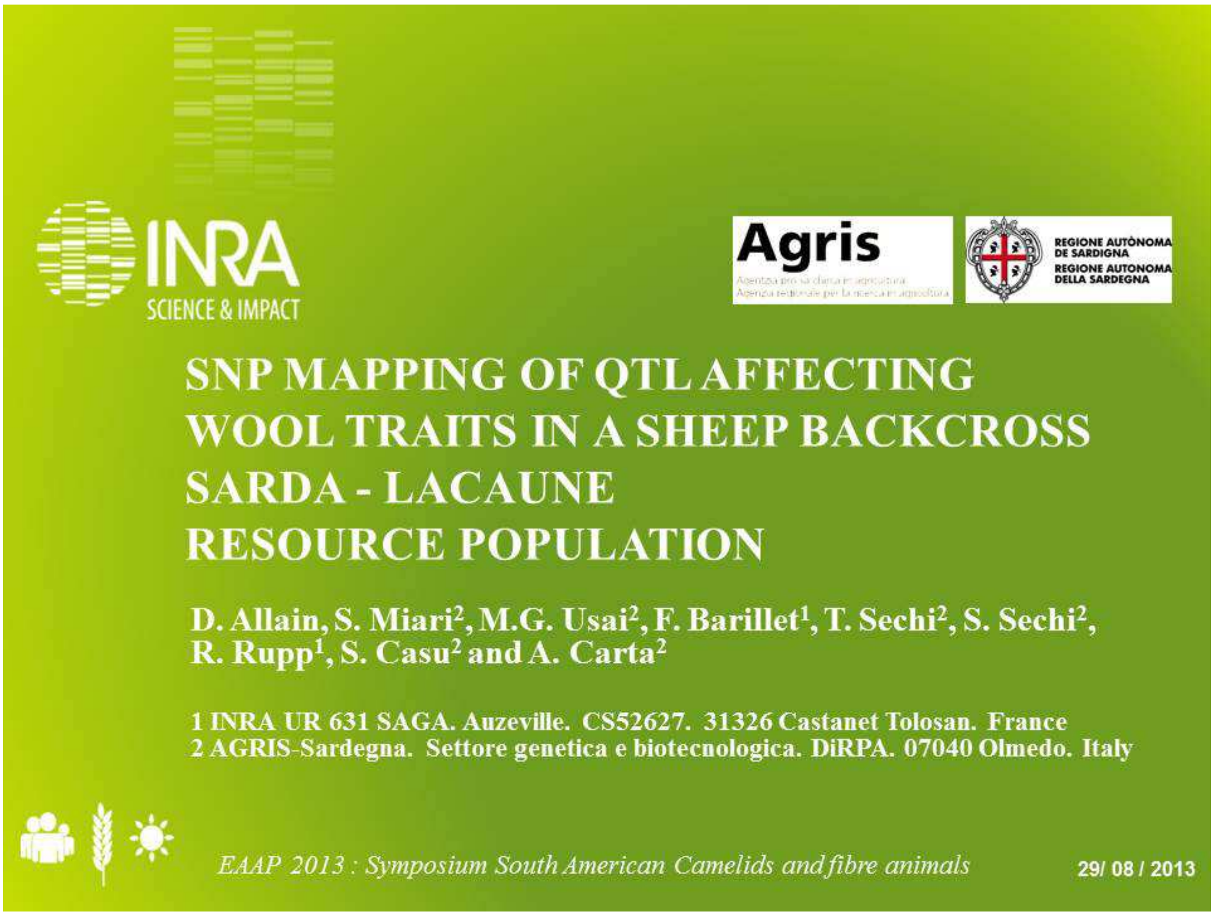

SNP MAPPING OF QTL AFFECTING WOOL TRAITS IN A SHEEP BACKCROSS SARDA - LACAUNE RESOURCE POPULATION

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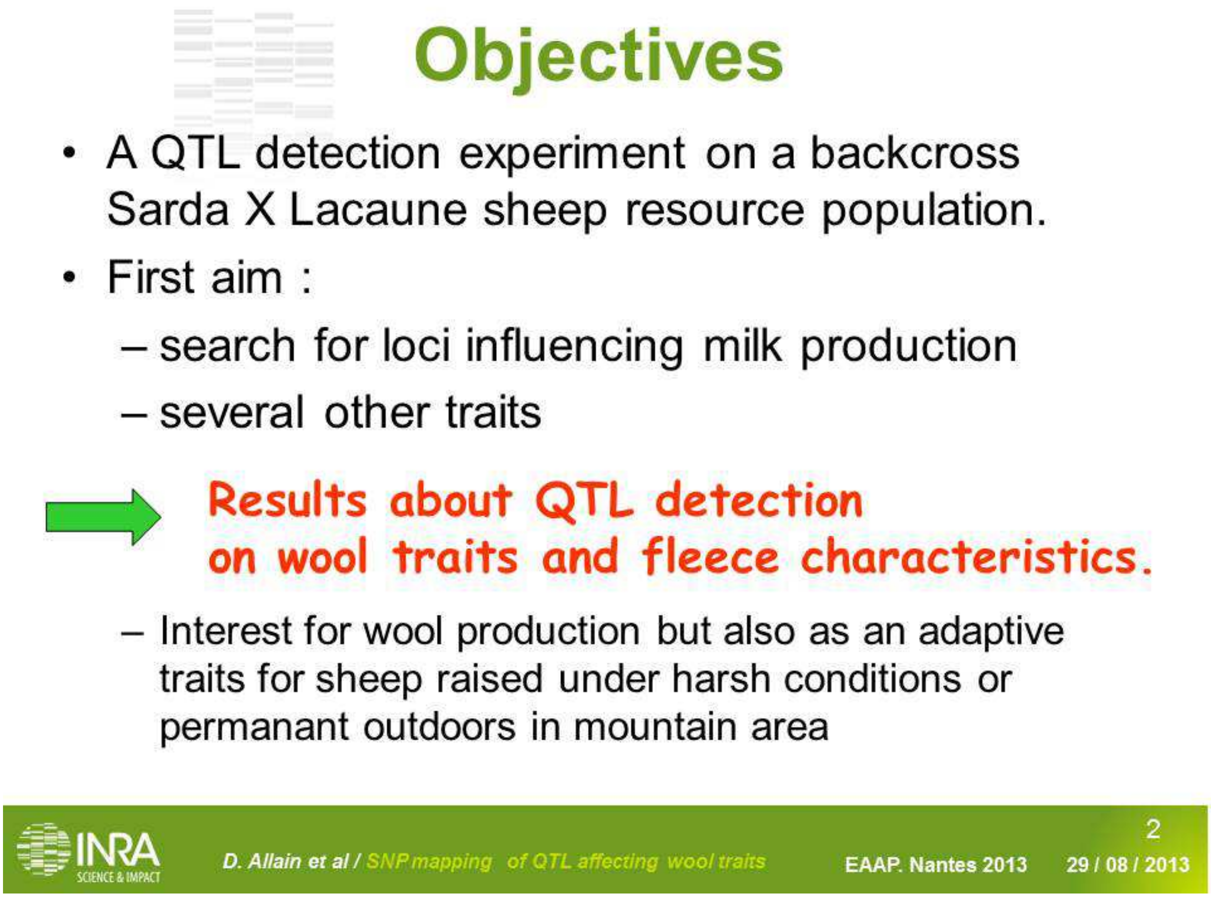

Objectives

- A QTL detection experiment on a backcross Sarda X Lacaune sheep resource population.
- First aim :
  - search for loci influencing milk production
  - several other traits

→ **Results about QTL detection on wool traits and fleece characteristics.**

- Interest for wool production but also as an adaptive traits for sheep raised under harsh conditions or permanant outdoors in mountain area

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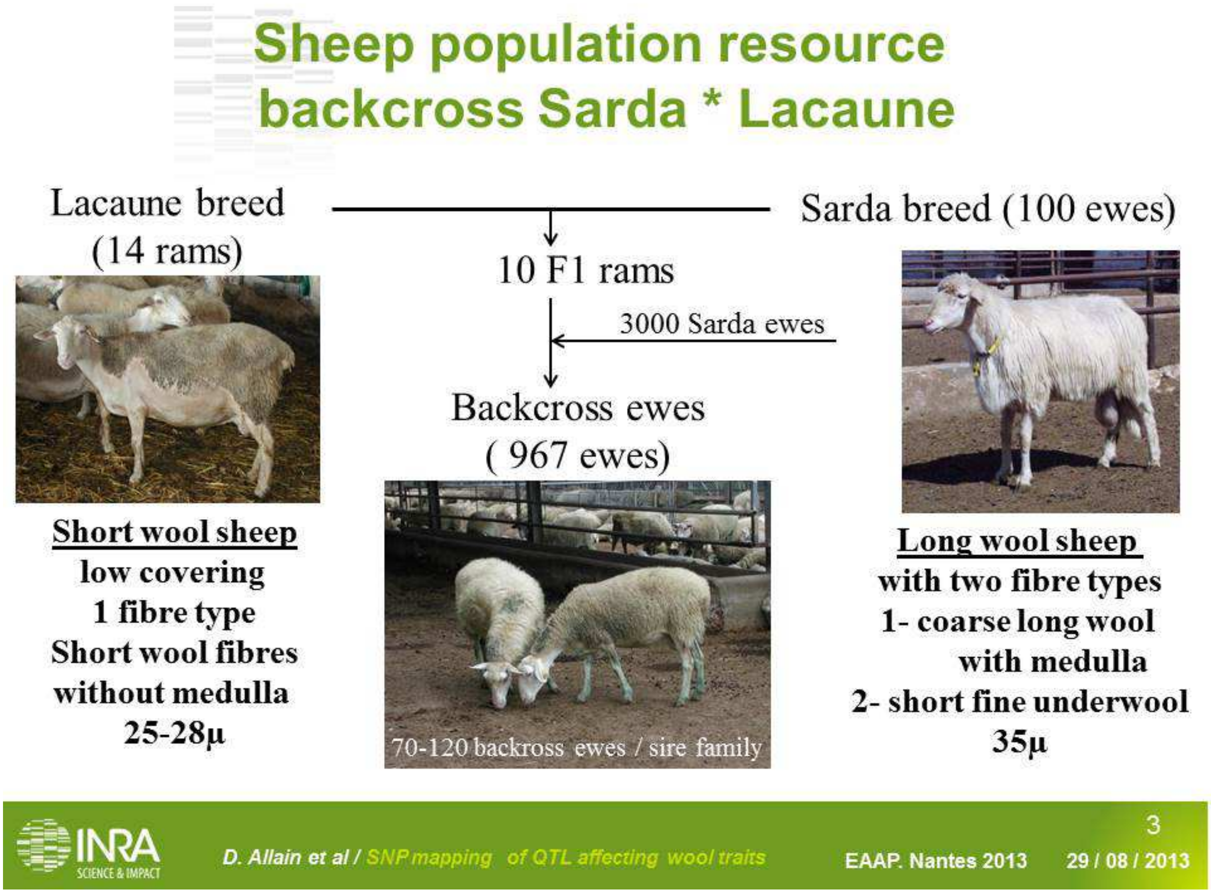

Sheep population resource backcross Sarda * Lacaune

Lacaune breed (14 rams)

Sarda breed (100 ewes)

10 F1 rams

3000 Sarda ewes

Backcross ewes (967 ewes)

70-120 backross ewes / sire family

Short wool sheep
low covering
1 fibre type
Short wool fibres
without medulla
25-28µ

Long wool sheep
with two fibre types
1- coarse long wool
with medulla
2- short fine underwool
35µ

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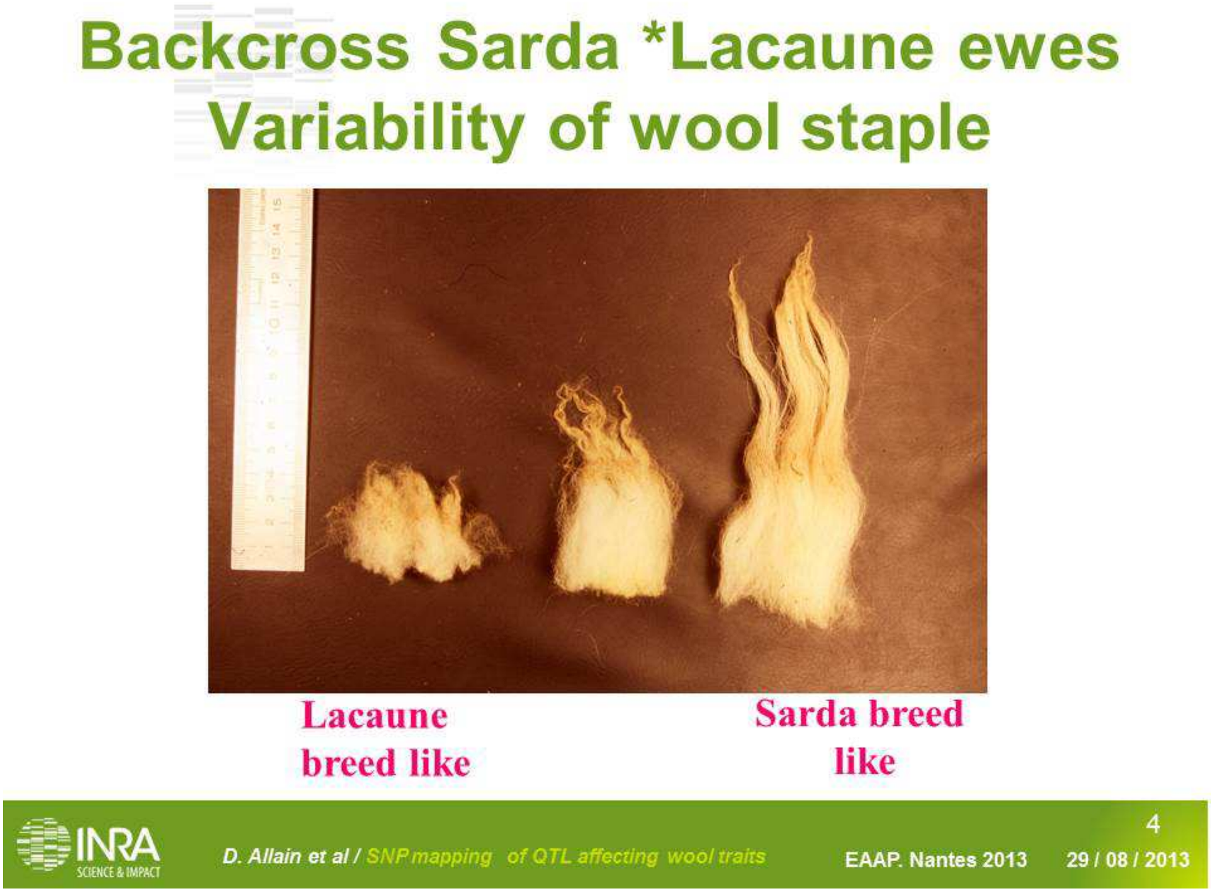

Backcross Sarda *Lacaune ewes Variability of wool staple

Lacaune breed like

Sarda breed like

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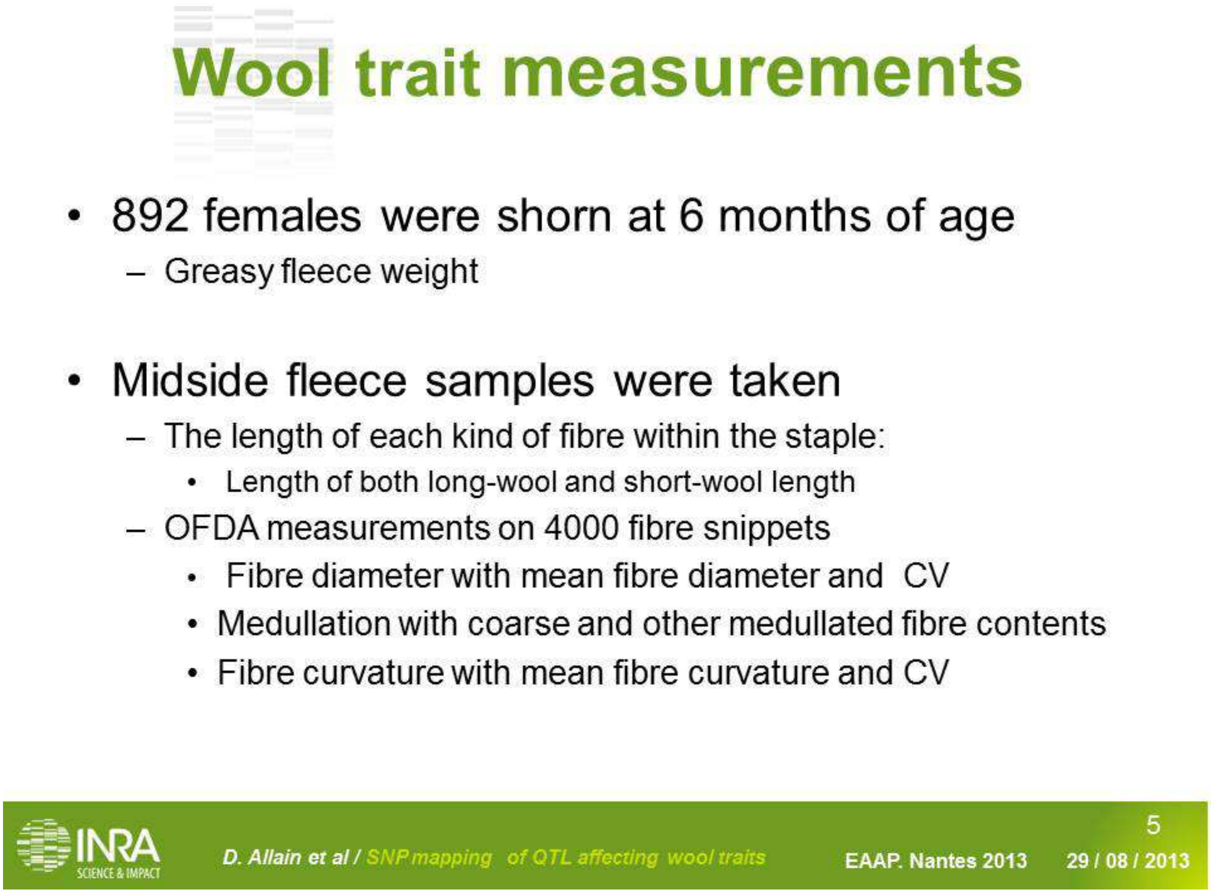

Wool trait measurements

- 892 females were shorn at 6 months of age
  - Greasy fleece weight
- Midside fleece samples were taken
  - The length of each kind of fibre within the staple:
    - Length of both long-wool and short-wool length
  - OFDA measurements on 4000 fibre snippets
    - Fibre diameter with mean fibre diameter and CV
    - Medullation with coarse and other medullated fibre contents
    - Fibre curvature with mean fibre curvature and CV

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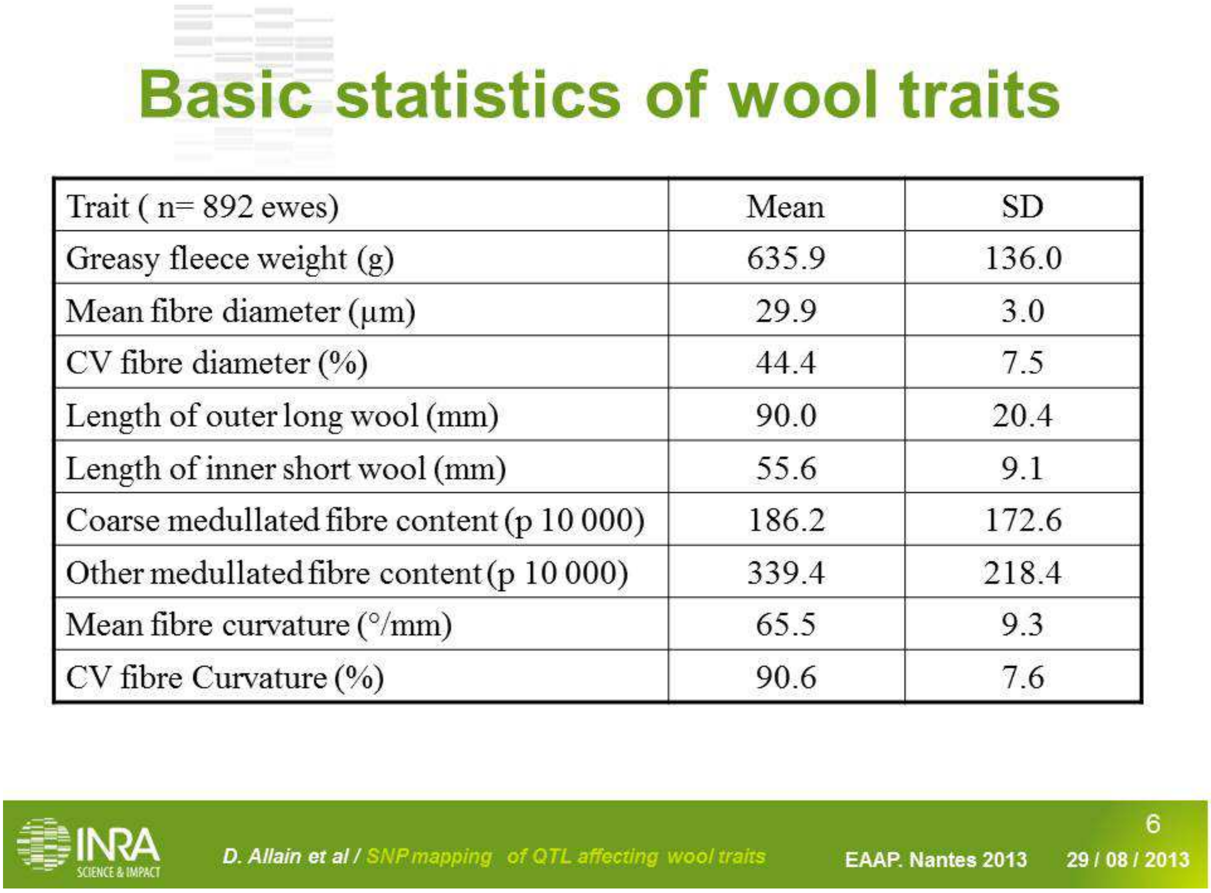

Basic statistics of wool traits

Trait (n= 892 ewes)	Mean	SD
Greasy fleece weight (g)	635.9	136.0
Mean fibre diameter (µm)	29.9	3.0
CV fibre diameter (%)	44.4	7.5
Length of outer long wool (mm)	90.0	20.4
Length of inner short wool (mm)	55.6	9.1
Coarse medullated fibre content (p 10 000)	186.2	172.6
Other medullated fibre content (p 10 000)	339.4	218.4
Mean fibre curvature (°/mm)	65.5	9.3
CV fibre Curvature (%)	90.6	7.6

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Methodology

- Genotyping with Illumina OvineSNP50 bead Chip
  - Filtering: call rate >95%; MAF>1%; HWE within family
    - 43 276 SNP used (~ 16 SNP / Mb)
- Data analysis
  - Single trait QTL analysis performed by multi-marker regression using QTLMAP software (Elsen et al. 1999, 2009)
    LA, LD, LDLA http://www.inra.fr/qtlmap
  - Nuisance fixed effects : age at shearing. dam parity. type of birth (single. double or triple)
  - Significance thresholds LA
    - through 1 000 permutations / chromosome all over genome
    - Bonferonni correction
    - Confidence interval using drop off criterion
  - Results only reported if QTL significant for LA, LD and LDLA analysis

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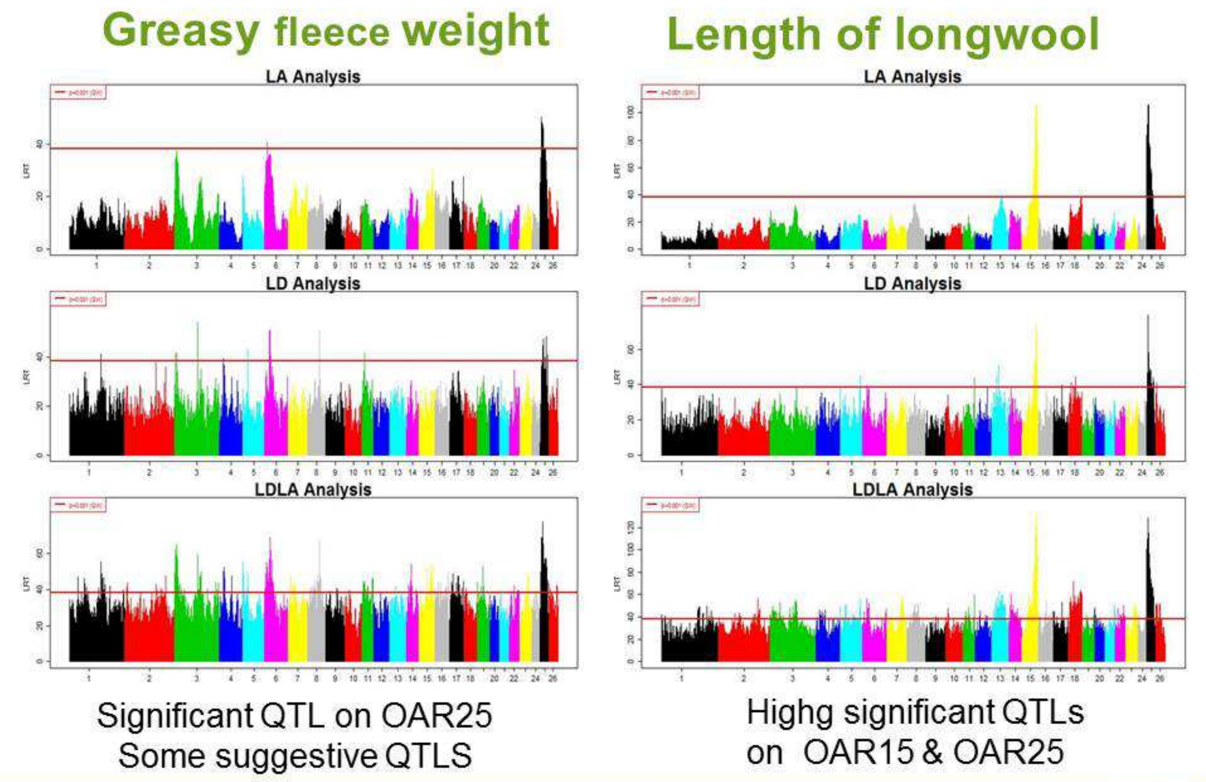

Greasy fleece weight

LA Analysis

LD Analysis

LDLA Analysis

Length of longwool

LA Analysis

LD Analysis

LDLA Analysis

Significant QTL on OAR25
Some suggestive QTLS

Highg significant QTLs
on OAR15 & OAR25

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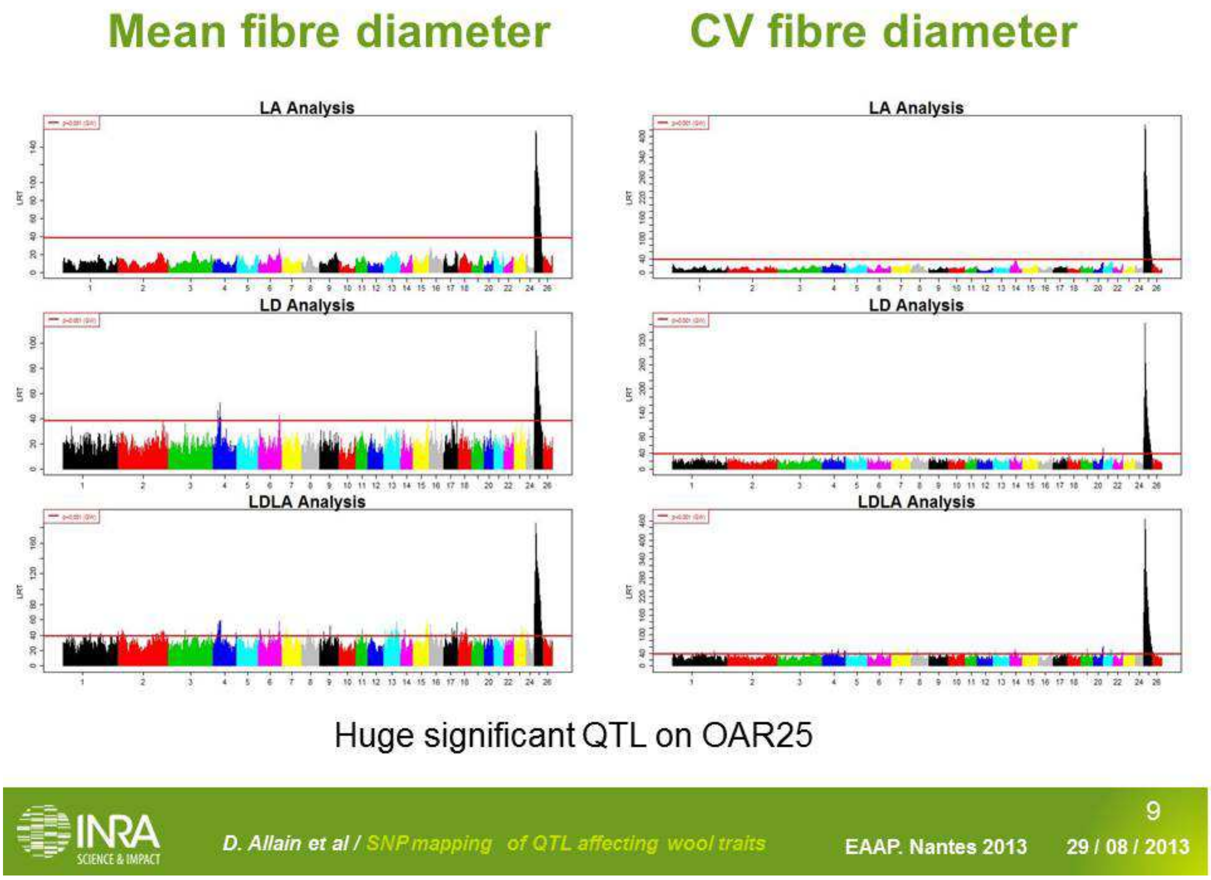

Mean fibre diameter

CV fibre diameter

Huge significant QTL on OAR25

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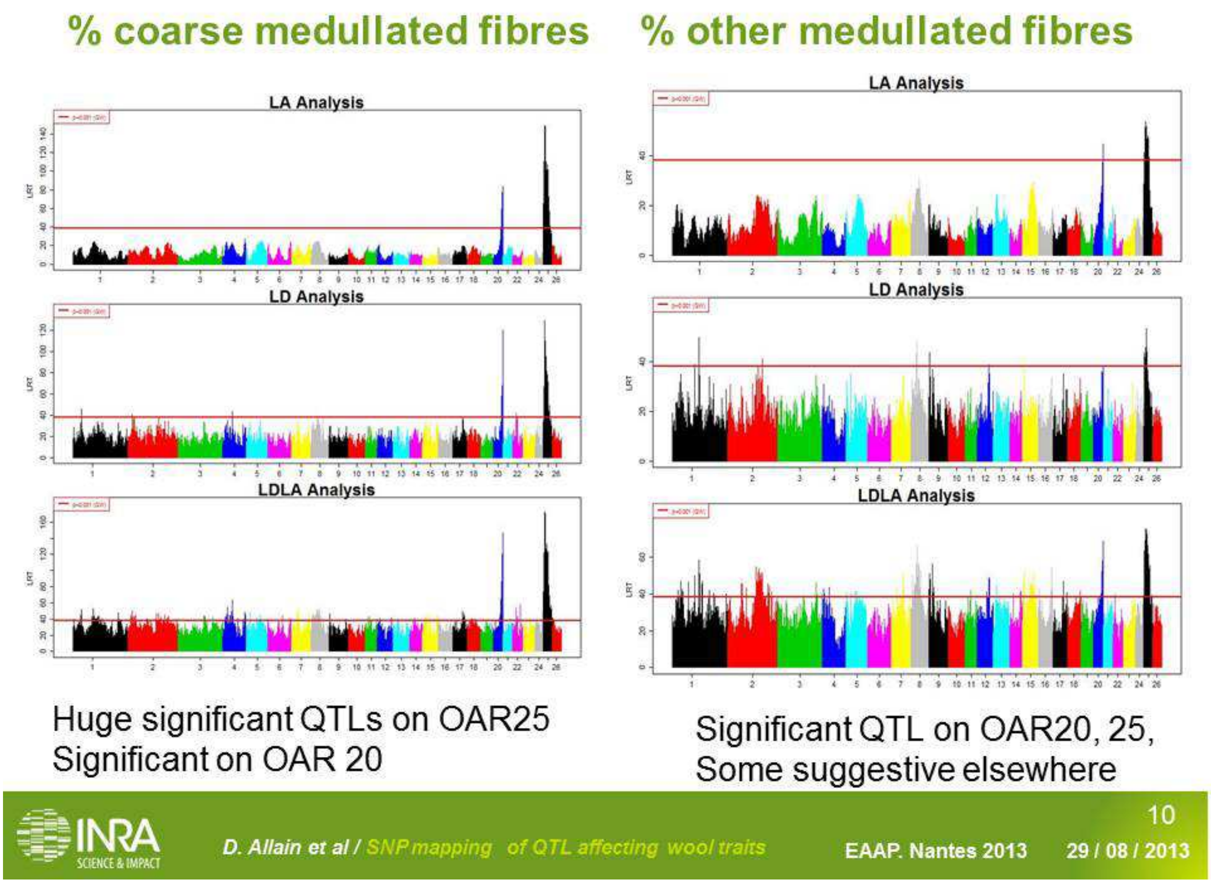

% coarse medullated fibres

% other medullated fibres

Huge significant QTLs on OAR25
Significant on OAR 20

Significant QTL on OAR20, 25,
Some suggestive elsewhere

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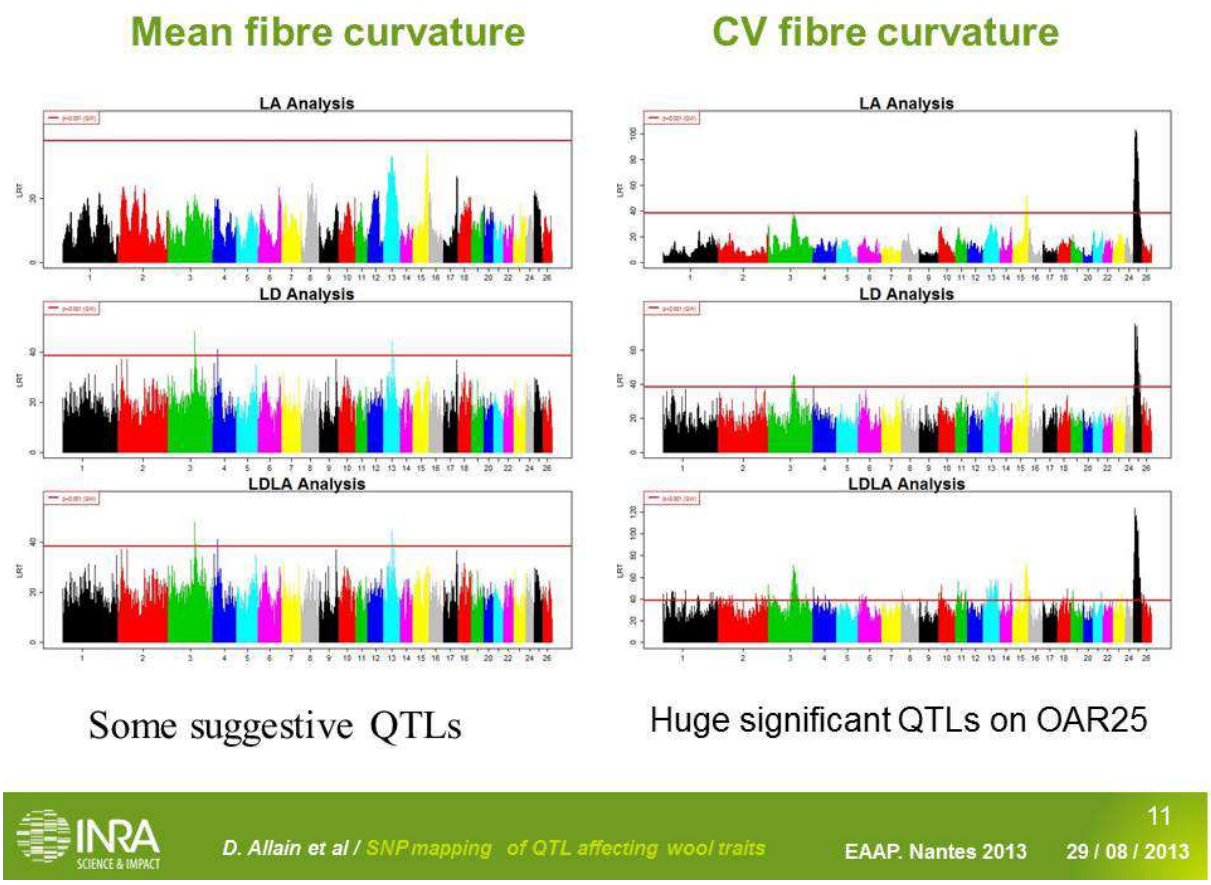
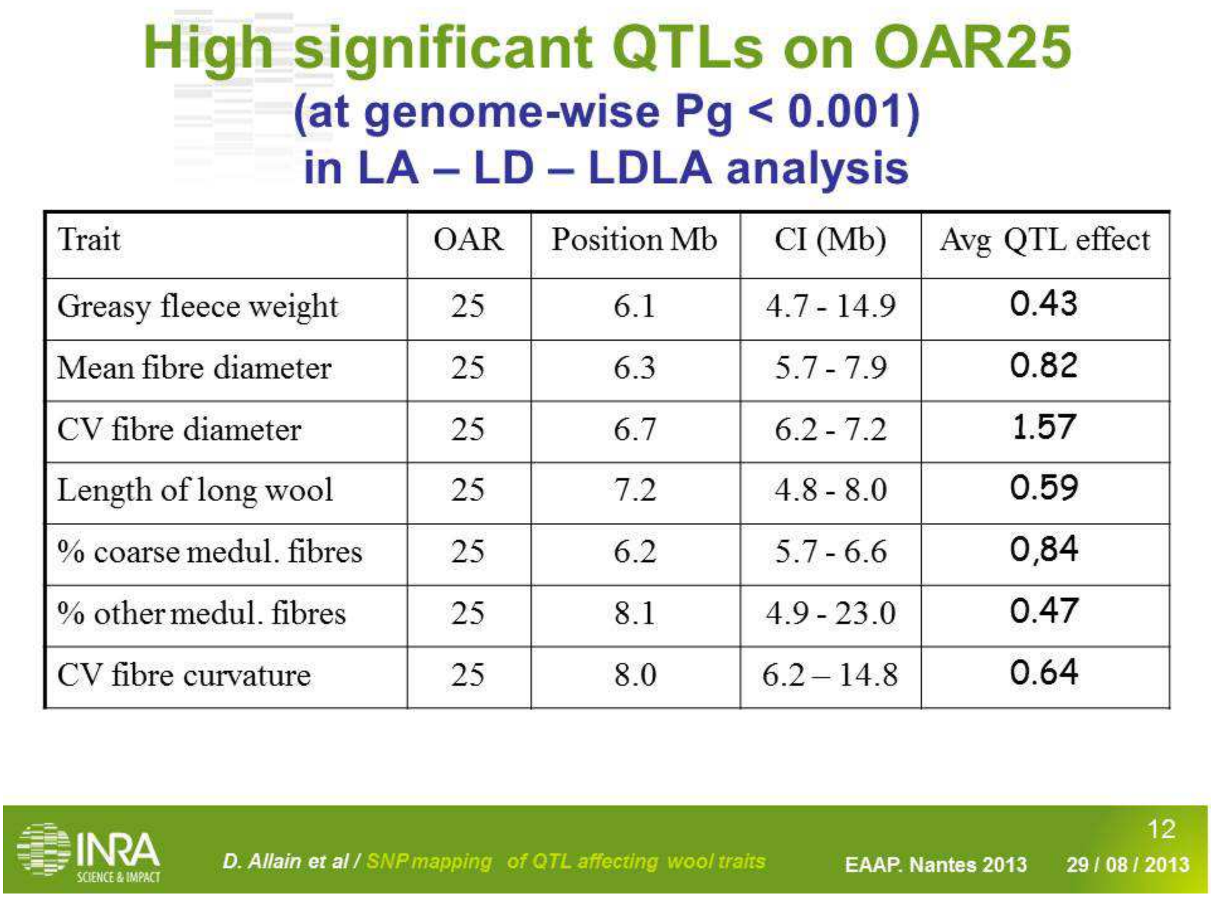


Mean fibre curvature

Some suggestive QTLs

CV fibre curvature

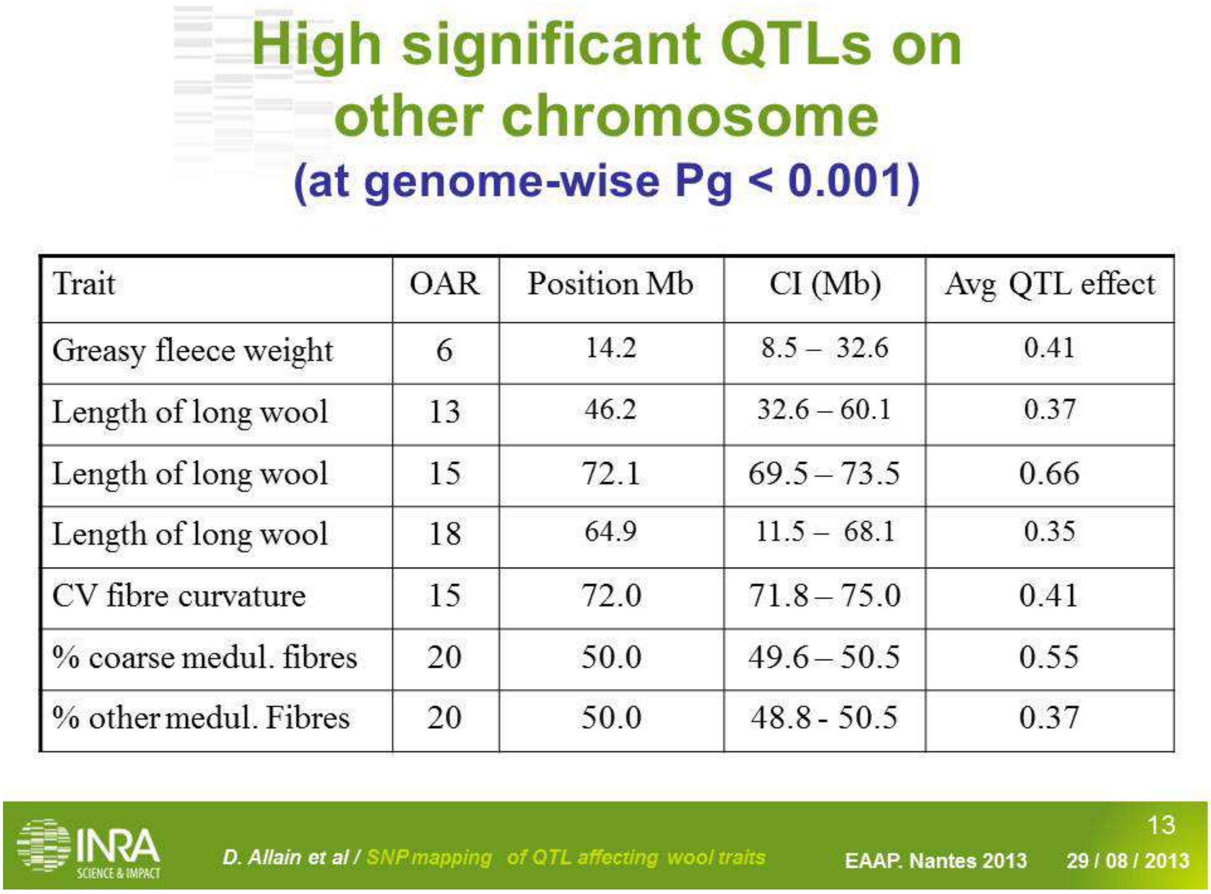
Huge significant QTLs on OAR25



High significant QTLs on OAR25

(at genome-wise Pg < 0.001) in LA – LD – LDLA analysis

Trait	OAR	Position Mb	CI (Mb)	Avg QTL effect
Greasy fleece weight	25	6.1	4.7 - 14.9	0.43
Mean fibre diameter	25	6.3	5.7 - 7.9	0.82
CV fibre diameter	25	6.7	6.2 - 7.2	1.57
Length of long wool	25	7.2	4.8 - 8.0	0.59
% coarse medul. fibres	25	6.2	5.7 - 6.6	0,84
% other medul. fibres	25	8.1	4.9 - 23.0	0.47
CV fibre curvature	25	8.0	6.2 – 14.8	0.64



High significant QTLs on other chromosome

(at genome-wise Pg < 0.001)

Trait	OAR	Position Mb	CI (Mb)	Avg QTL effect
Greasy fleece weight	6	14.2	8.5 – 32.6	0.41
Length of long wool	13	46.2	32.6 – 60.1	0.37
Length of long wool	15	72.1	69.5 – 73.5	0.66
Length of long wool	18	64.9	11.5 – 68.1	0.35
CV fibre curvature	15	72.0	71.8 – 75.0	0.41
% coarse medul. fibres	20	50.0	49.6 – 50.5	0.55
% other medul. Fibres	20	50.0	48.8 - 50.5	0.37

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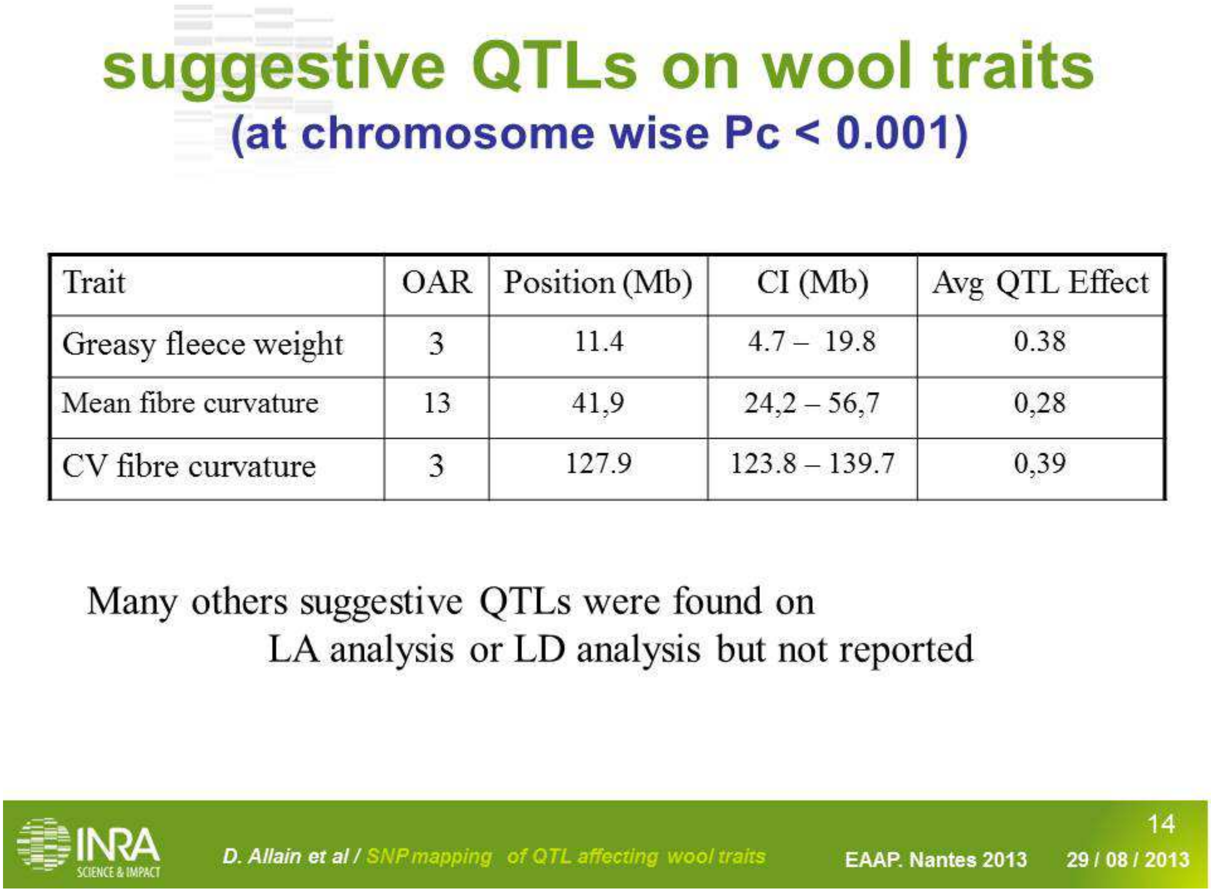

suggestive QTLs on wool traits

(at chromosome wise Pc < 0.001)

Trait	OAR	Position (Mb)	CI (Mb)	Avg QTL Effect
Greasy fleece weight	3	11.4	4.7 – 19.8	0.38
Mean fibre curvature	13	41,9	24,2 – 56,7	0,28
CV fibre curvature	3	127.9	123.8 – 139.7	0,39

Many others suggestive QTLs were found on
LA analysis or LD analysis but not reported

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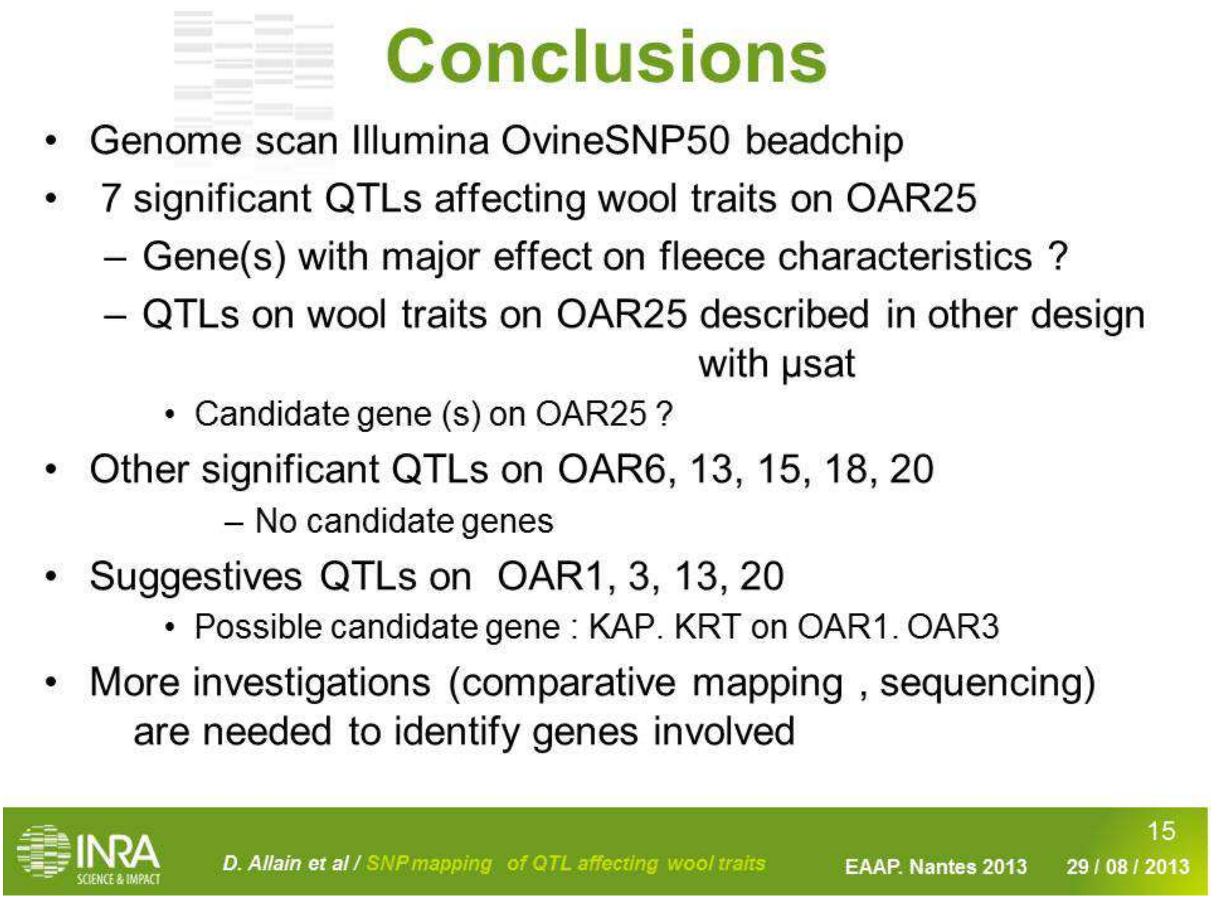

Conclusions

- Genome scan Illumina OvineSNP50 beadchip
- 7 significant QTLs affecting wool traits on OAR25
  - – Gene(s) with major effect on fleece characteristics ?
  - – QTLs on wool traits on OAR25 described in other design with µsat
    - Candidate gene (s) on OAR25 ?
- Other significant QTLs on OAR6, 13, 15, 18, 20
  - – No candidate genes
- Suggestives QTLs on OAR1, 3, 13, 20
  - Possible candidate gene : KAP. KRT on OAR1. OAR3
- More investigations (comparative mapping , sequencing) are needed to identify genes involved

Thank you for your attention

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