Mol Breeding (2012) 29:159–171
DOI 10.1007/s11032-010-9534-x

Meta-QTL analysis of the genetic control of crop height in elite European winter wheat germplasm

Simon Griffiths · James Simmonds · Michelle Leverington · Yingkun Wang · Lesley Fish · Liz Sayers · Leodie Alibert · Simon Orford · Luzie Wingen · John Snape

Received: 13 September 2010 / Accepted: 11 November 2010 / Published online: 2 December 2010

Abstract In bread wheat (*Triticum aestivum* L.), crop height is an important determinant of agronomic performance. The aim of this study was to identify genes controlling variation in crop height segregating in elite European winter wheat germplasm. Four doubled haploid populations derived from the crosses Avalon × Cadenza, Savannah × Rialto, Spark × Rialto and Charger × Badger were selected, representing wide diversity in European winter wheat breeding programmes. Genetic maps based on simple sequence repeat (SSR) and Diversity Arrays Technology (DArT) markers were constructed for each population. One hundred and four significant quantitative trait loci (QTL) were identified in the four populations. A meta-analysis was conducted and the effects condensed into sixteen meta-QTL on chromosomes 1A, 1B, 1D, 2A (two meta-QTL), 2B, 2D, 3A, 3B, 4B, 4D, 5A, 5B, 6A, 6B and 6D. These include QTL with additive effects equivalent to *Rht-D1* and a potentially new allele of *Rht8*. The description of these effects offers new opportunities for the manipulation of crop height, biomass and yield in wheat breeding programmes.

Keywords Wheat · Height · QTL · Meta QTL

Introduction

Crop height is an important trait for the performance of a wheat crop (*Triticum aestivum* L.). In particular, tall plants are much more susceptible to lodging (Berry et al. 2003), so crop height reduction has been an important target for wheat breeding programmes for many decades. A large number of major dwarfing genes have been identified, including natural variants, induced mutations (Konzak 1988) and effects identified using aneuploid lines (Snape et al. 1977). However, efforts to breed for reduced crop height are complicated by the tight coupling of stem extension with other developmental and physiological processes. Reduced crop height is often associated with a reduction in grain yield (Law et al. 1978) or earlier ear emergence, so the identification of genes with alleles that reduce crop height, without reducing grain yield potential, is important for wheat breeding. Genes in this category include the major gibberellic acid (GA)-insensitive dwarfing genes *Rht-D1b* and *Rht-B1b*, the height-reducing alleles of which actually increase grain yield in most environments (Flintham et al. 1997). Other height-reducing effects widely

Electronic supplementary material The online version of this article (doi:10.1007/s11032-010-9534-x) contains supplementary material, which is available to authorized users.

S. Griffiths (✉) · J. Simmonds · M. Leverington · Y. Wang · L. Fish · L. Sayers · L. Alibert · S. Orford · L. Wingen · J. Snape
Crop Genetics, John Innes Centre, Norwich Research Park, Colney, Norwich NR4 7UH, UK
e-mail: simon.griffiths@bbsrc.ac.uk

deployed in world agriculture include *Rht8* on 2DS (Korzun et al. 1998), and the photoperiod-insensitive alleles of the ear emergence time genes *Ppd-D1* on 2DS and *Ppd-B1* on 2BS which have pleiotropic effects on crop height (Borner et al. 1993).

In addition to the major crop height genes, quantitative trait loci (QTL) for crop height have been identified in a number of studies (Ahmed et al. 2000; Cadalen et al. 1998; Kato et al. 1999; McCartney et al. 2005; Quarrie et al. 2005; Sourdille et al. 2003). Together, these studies provide an invaluable survey of the genetic control of crop height in wheat. However, there is relatively little data available that shows which genes are still segregating for variation in crop height in modern elite Western European winter wheat germplasm. Wheat yields in Western Europe are amongst the highest in the world and the rate of progress in yield potential made by Western European wheat breeding companies is the highest in the world. In spite of this, crosses between modern elite UK winter wheat varieties usually exhibit significant segregation for crop height, even though the populations are fixed for the major semi-dwarfing genes. It is not known whether the allelic variation responsible for this variation is maintained in elite germplasm, because it has insignificant, neutral or beneficial effects on crop performance.

Here we aim to identify QTL responsible for crop height variation segregating in four doubled haploid populations derived from six winter and one alternative wheat varieties that represent a broad cross-section of elite Western European germplasm.

Methods

Plant materials and development of genetic maps

The doubled haploid wheat populations and genetic maps used in this study have been described previously (Griffiths et al. 2009). They are: Charger × Badger (C × B), 93 doubled haploid lines; Spark × Rialto (S × R), 129 double haploids lines, Savannah × Rialto (Sv × R), 126 doubled haploid lines, and Avalon × Cadenza (A × C), 202 doubled haploids. The parents of these populations represent a broad spectrum of the variation present in the UK elite winter germplasm pool, and are generally crosses between varieties developed by different plant breeding companies.

Framework genetic maps were primarily developed using publicly available single sequence repeat (SSR) markers aiming for a marker density of one every 10–20 cM. Primer sets were used from JIC (*psp*), IPK Gatersleben (*gwm/gdm*), Wheat Microsatellite Consortium (*wmc*), Beltsville Agricultural Research Station (*barc*) and INRA (*cfd/cfa*) collections; see GrainGenes website (http://www.wheat.pw.usda.gov/). Targeted markers were selected to provide good genome coverage using published consensus maps (Somers et al. 2004), and for their ease of scoring. DNA fragments were amplified with PCR and run on 5% polyacrylamide gels for separation. The silver staining technique was used to visualise fragments (Bassam et al. 1991). To further improve map density, DNAs of the S × R, A × C and Sv × R populations were subjected to Diversity Arrays Technology (DArT) genome profiling (Wenzl et al. 2004) at Triticarte Pty Ltd, Australia (http://www.triticarte.com.au). Single strand conformation polymorphism (SSCP) analysis was carried out as described by Bertin et al. (2005).

Joinmap v3.0 (Stam 1993) was used for genetic linkage map construction, set at the default settings with the Kosambi mapping function. Linkage groups were selected at a minimum LOD of 3 for reliable associations.

Field trials

Field trials were conducted at five sites: Norwich, Norfolk, UK; Sandringham, Norfolk, UK; Balmonth, Fife, UK; Bohnshausen, Langenstein, Germany; and Froissy, near Amiens, France. Experimental details are shown in Table 1. The populations S × R, C × B and Sv × R were part of parallel experiments grown in the same years; A × C data was collected later but is included here because it is now the UK reference population under the UK Department of Environment Food and Rural Affairs (DEFRA) Wheat Genetic Improvement Network (WGIN http://www.wgin.org.uk/). Each line was grown in three replicate, 5.5-m^2 plots, in a randomised block design, grown according to standard agronomic practice including the use of chemical plant growth regulators. Crop height was measured from soil level to the collar of

Table 1 Populations used for the detection of height QTL and environments tested

Population	Abbreviation	Individuals	Environments
Avalon × Cadenza	A × C	202 DH	CF_05, CF_06, CF_07, CF_08
Charger × Badger	C × B	93 DH	CF_01, CF_02, CF_03, San_02 San_03, Fr_03
Spark × Rialto	S × R	129 DH	CF_01, CF_02, CF_03, San_01, San_03, Fr_03
Savannah × Rialto	Sv × R	126 DH	CF_02,CF_03, CF_04, CF_07, CF_08

Numerical suffixes show the years in which each experiment was carried out

CF Church Farm, Norwich, UK; *Fr* Froissy, near Amiens, France; *San* Sandringham, Norfolk, UK; *DH* doubled haploid

each wheat ear; the mean of two measurements was taken for each plot.

Statistical analysis

Basic statistical analyses were carried out using Minitab v15. Analysis of variance was used to demonstrate the genetic contribution to variation in crop height for each population and site. Mean values from the three replicates on each site were used to calculate correlations of crop height between environments and for the detection of QTL. QTL effects were estimated using the single marker analysis and composite interval mapping functions of QTL Cartographer v2.5 (Basten et al. 1994) using default settings. QTL with LOD scores greater than 2 were taken further for inclusion in the meta-analysis. Additive effect and percentage of total variation for each QTL identified was calculated using the multiple interval mapping (MIM) function of QTL Cartographer. Epistatic interactions were detected using the 'Refine MIM model' and 'QTL interactions' options in the QTL Cartographer MIM module.

Meta-QTL analysis was performed using Biomercator software v2.1 (Arcade et al. 2004). The genetic linkage maps of the four populations were projected onto the published consensus map (Somers et al. 2004) joined with S × R and A × C WheatDArTmaps v1.2 (http://www.triticarte.com.au). QTL and confidence intervals (CI) were projected together with the genetic linkage maps; CI were approximated by the software following Darvasi and Soller (1997). Meta-analysis was carried out separately for all chromosomes with three and more QTL. The number of meta-QTL present was determined as the model which minimised the Akaike criterion (AIC).

Alternative methods of QTL detection designed for multi-trait multi-environment (MTME) data (Malosetti et al. 2008) were also employed. Mixed model multi-environment QTL analysis was carried out for each population separately in the GenStat 12.1 (VSN international) QTL suite. Mean phenotypic data from the different environments and the respective population map and genotype data were used. The best suitable variance–covariance structure was detected for each of the four populations. Genetic predictors were computed for a step size of 4 cM. The genetic model was built using the suggested candidate QTL from single QTL scans. QTL significance levels and effects were determined by a final backward selection step at a significant level of 0.05.

Results

Extent of variation in crop height

All populations exhibited significant genetic variation for crop height within each year/environment combination (ANOVA not shown). The distribution of doubled haploid lines into crop height classes in each environment studied is shown in Fig. 1. Crop height for each population was highly correlated between environments, never falling below a r^2 value of 0.69 (0.81–0.95 for A × C; 0.69–0.88 for C × B; 0.83–0.94 for S × R; and 0.89–0.96 for Sv × R).

Identification of QTL controlling crop height

Analysis of the data using QTL Cartographer with the threshold criteria described identified a total of 104 QTL. The closest genetic marker, estimated additive effect and portion of variation accounted for by each QTL are shown in Electronic Supplementary Material Table S1. If the assumption is made that QTL identified in the same genetic interval in one

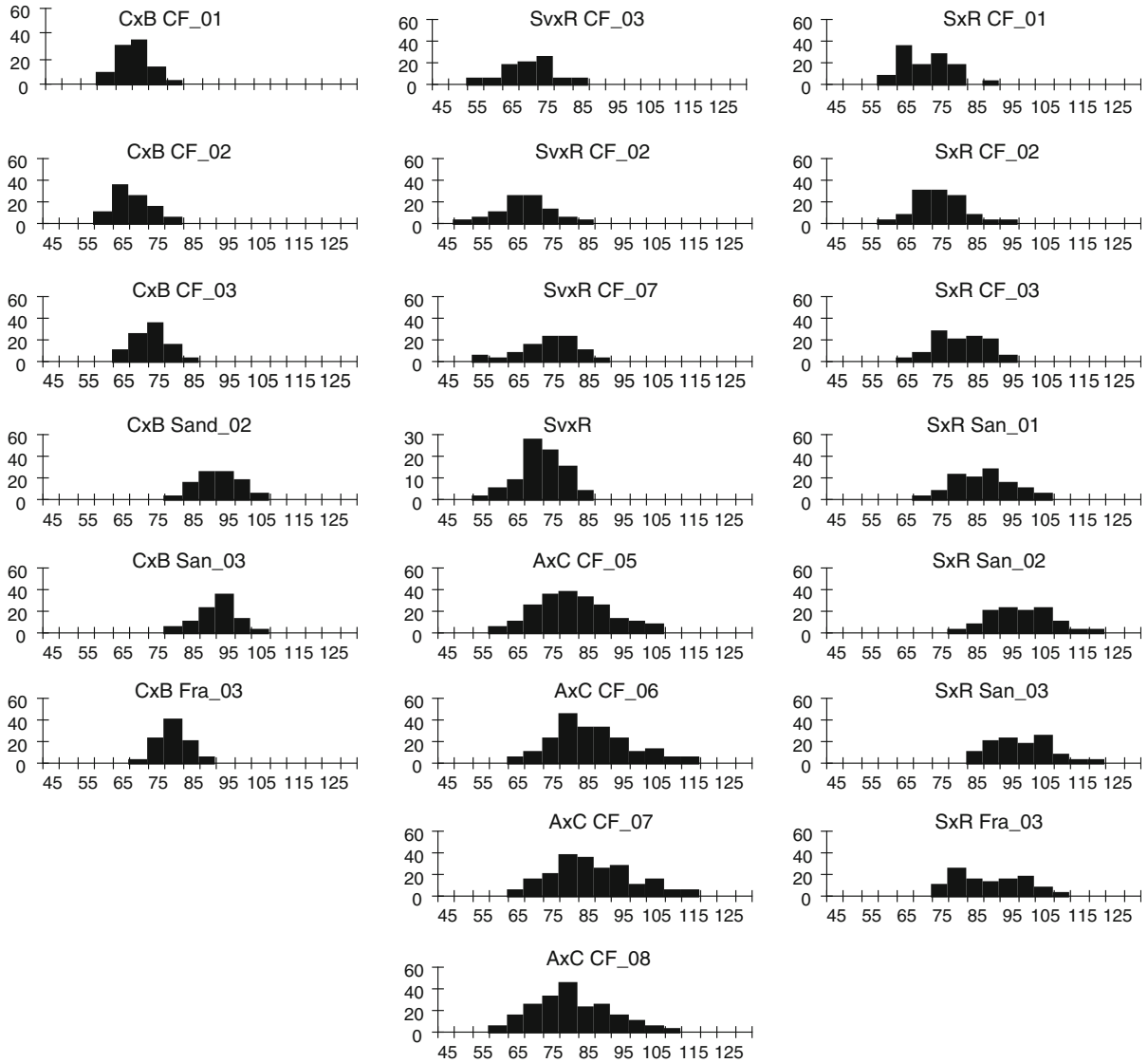


Fig. 1 Distribution of crop height in different environments for the A × C, C × B, Sv × R, and S × R doubled haploid populations used in this study

population, across multiple environments, are due to the same genes then the numbers of independent QTL can be reduced to ten in A × C, seven in S × R, seven in C × B and seven in Sv × R (Fig. 2). Common markers allow the alignment of the genetic maps used in this study and the projection of the QTL onto a consensus linkage map showing sixteen meta-QTL on chromosomes 1A, 1B, 1D, 2A (two meta-QTL), 2B, 2D, 3A, 3B, 4B, 4D, 5A, 5B, 6A, 6B and 6D (Tables 2 and S2). The MTME approach was used to complement this analysis. In all cases this approach identified fewer QTL; six in A × C, three in C × B, four in S × R and nine in Sv × R. In general this is due to differences in threshold criteria; MTME analysis detects the QTL but rejects them. However, in other cases MTME analysis does increase the significance of QTL located on 1D in S × R; 2B in C × B and Sv × R; and 7D in Sv × R. MTME QTL locations are shown in Fig. 2 and associated statistics are shown in Table S3. The effects identified using QTL Cartographer are now described in more detail, for each homoeologous chromosome group.

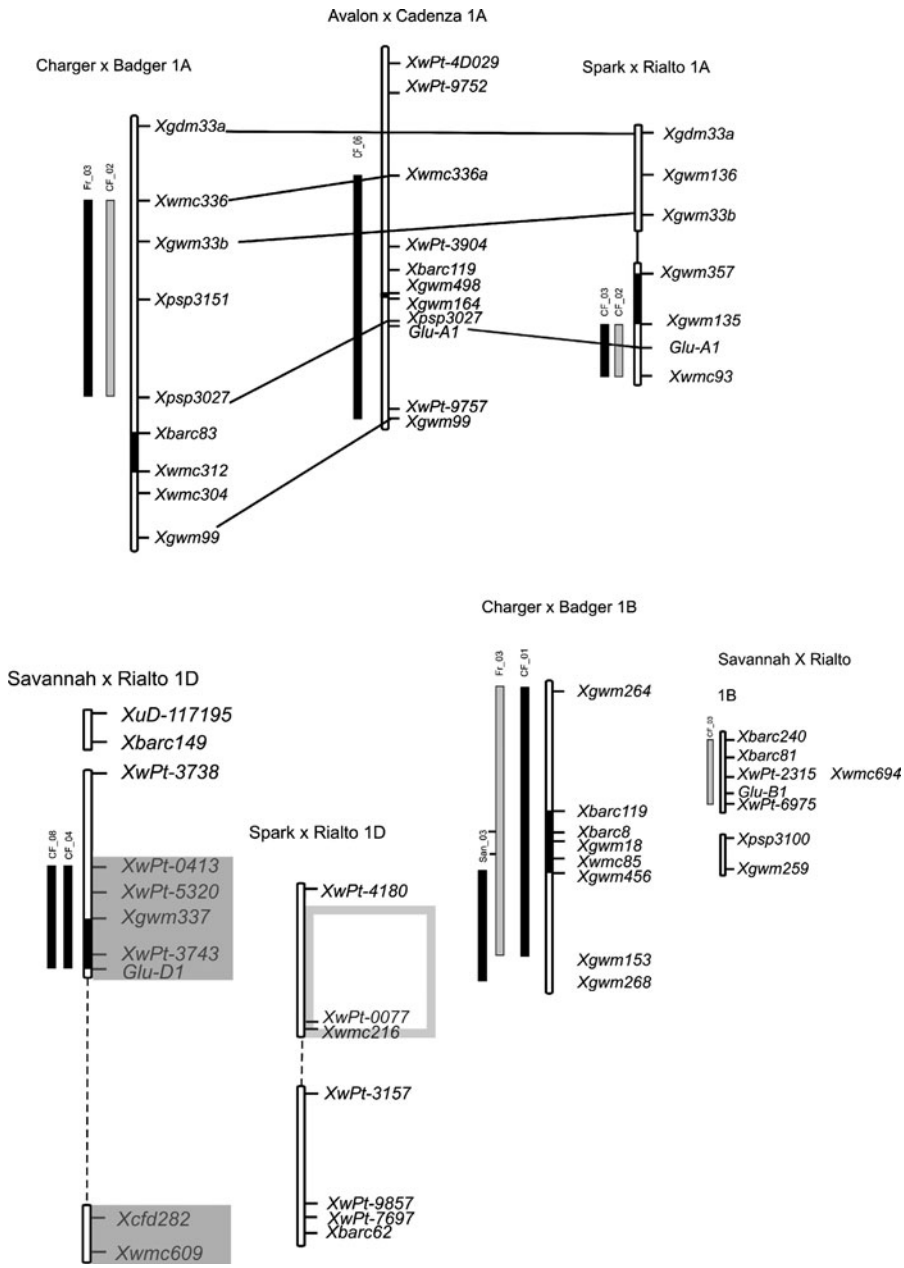
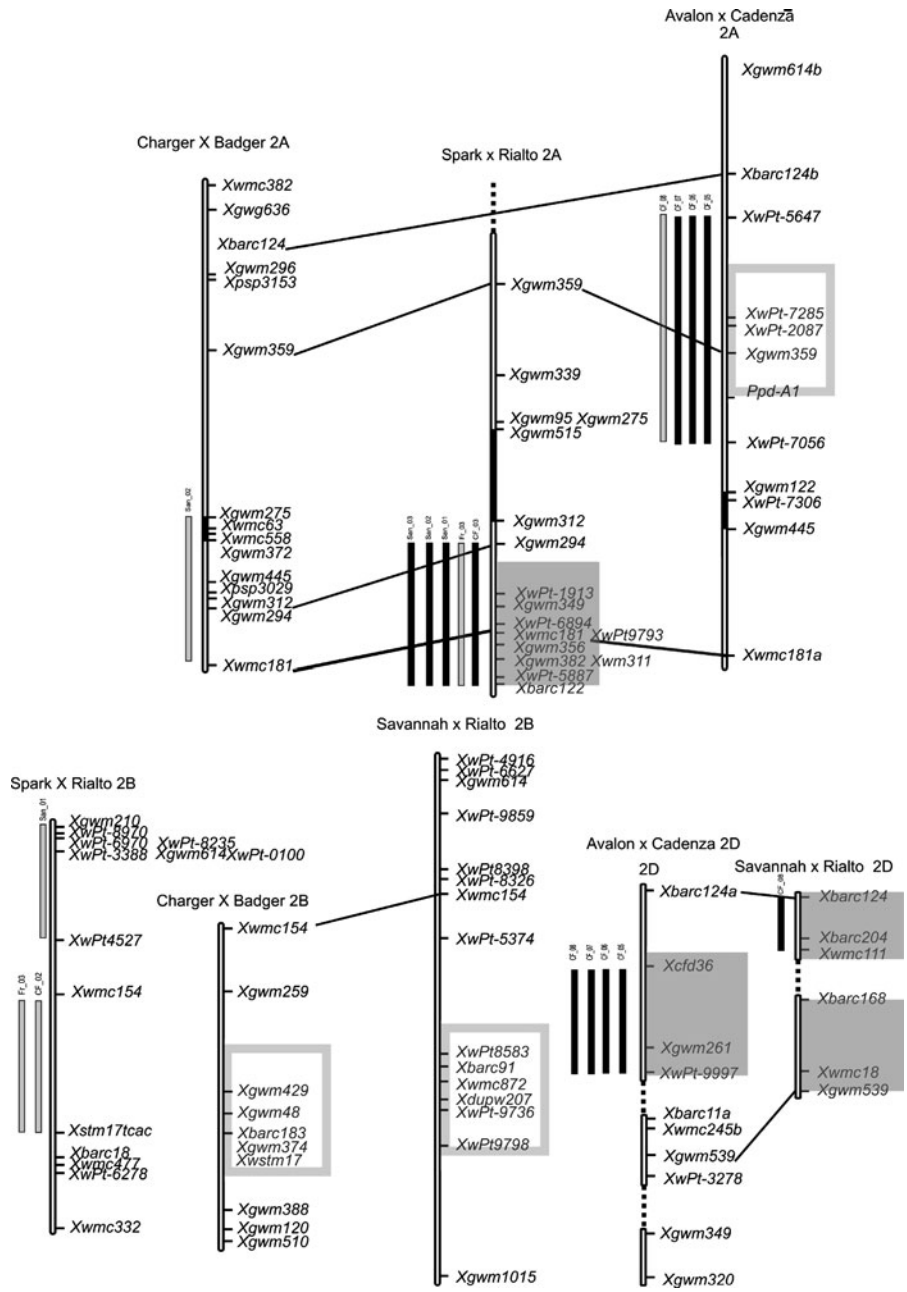


Fig. 2 Chromosomal location of significant height QTL identified. Chromosomes are shown as *hollow bars*, centromere containing intervals are *solid bars*. Bars to the *left* of each linkage group correspond to marker intervals containing QTL defined using QTL Cartographer software, and are coloured *grey* if LOD is between 2 and 3, and *black* if greater than 3. *Boxes* around markers correspond to QTL peaks defined by MTME; the boxes are not filled if increasing alleles are from the female parent (Savannah, Spark, Avalon, Charger) and opaque if from the male parent (Rialto, Rialto, Cadenza, Badger). Common markers between maps are connected. Sections of a wheat consensus map (Somers et al. 2004) are included where it aids map alignment. Linkage groups from the same chromosome are connected by a *dashed line*

Homoeologous Group 1

Crop height effects were detected on 1AS in C × B (*Xwmc336–Xpsp3027*) in two of the six environments that were tested, with an additive effect between 0.8 cm (Fr_03) and 1.4 cm (CF_02). However, the direction of the effect is different in each environment; in France the increasing allele came from Charger but on Church Farm (UK) from Badger. In A × C an effect was detected in the corresponding location in one (CF_06) of the four environments tested; it has an additive effect of 2 cm with the increasing allele coming from Avalon. A third effect on 1AS was identified in S × R, in the interval *Xwmc336–Xpsp3027*, and detected in two of the six environments tested. The additive effect was between 1.3 cm

Fig. 2 continued

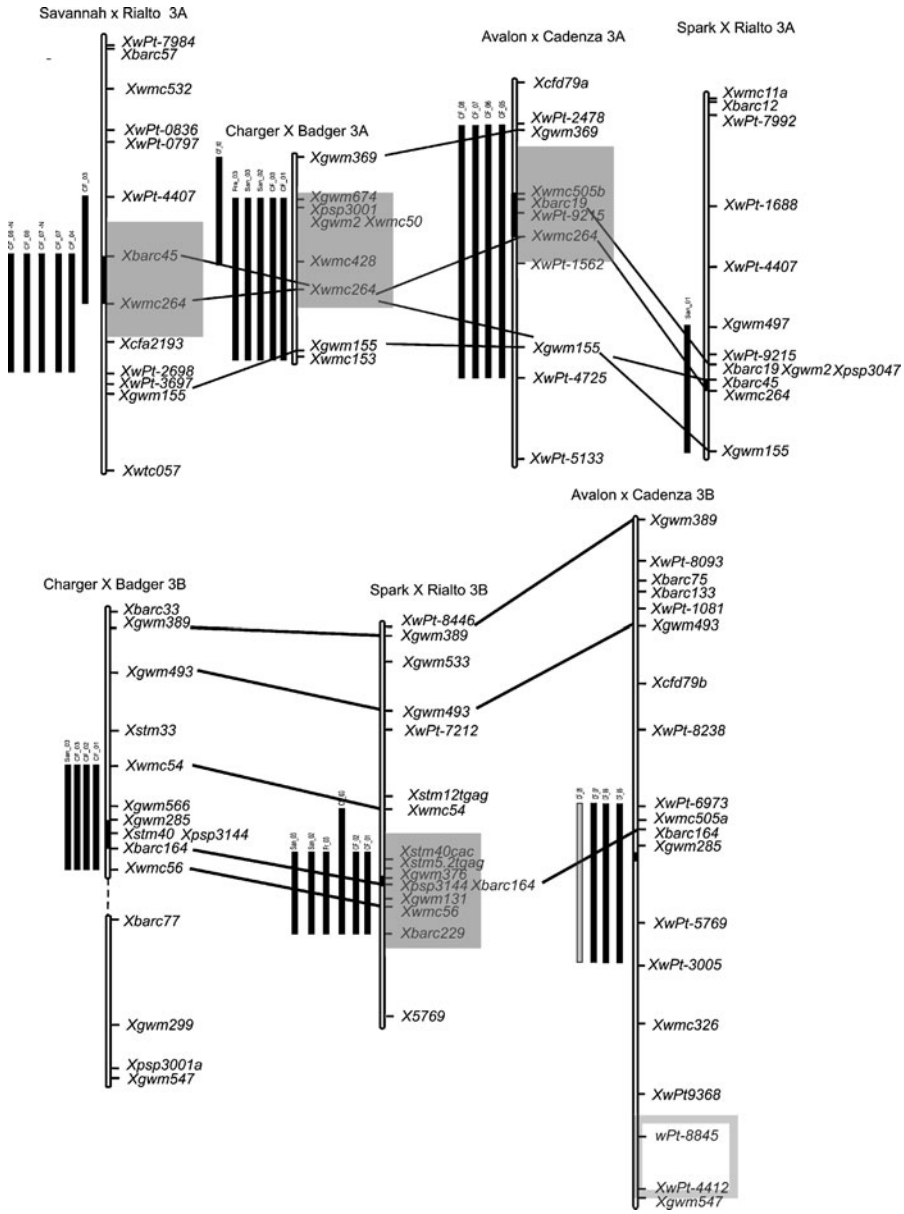


(CF_02) and 1.8 cm (CF_03) with the increasing allele coming from Rialto.

An effect was detected on 1B in three of the six environments tested for C × B (*Xgwm264–Xgwm268*); the additive effect ranged from 1.3 cm (CF_01) to 2.2 cm (San_03) with the increasing allele coming from Charger. For Sv × R a single effect was detected in the interval *Xbarc240–XwPt-6975* on 1B (CF_03) with an additive effect of 1.5 cm and the increasing allele coming from Savannah.

The only crop height effects located on 1D were identified in Sv × R in the interval *XwPt-0413–Glu-D1* in two of the four environments tested. The additive effect ranged from 1.6 cm (CF_08) to 1.7 cm (CF_04) with the increasing allele coming from Rialto.

Fig. 2 continued



Homoeologous Group 2

Crop height effects were identified on 2AS (*XwPt-5647–XwPt-7056*) in A × C in all of the environments tested. The additive effect ranged from 2.2 cm (CF_08) to 3.3 cm (CF_06) with the increasing allele coming from Avalon. An effect was identified on 2AL in one (San_02) of six environments for C × B (*Xgwm275–Xwmc181*) with an additive effect of 1.8 cm and the increasing allele coming from Badger. In S × R a 2AL effect (*Xgwm294-Xbarc122*) was identified in five of six environments tested, with additive effects ranging from 1.3 cm (Fr_03) to 3.3 cm (San_02) and the increasing alleles coming from Rialto.

In S × R separate effects were identified on 2B. In the interval *Xstm17tcac–Xwmc154* significant QTL were detected in CF_02 and Fr_03 with additive effects of 1.2 and 2 cm respectively, with the increasing allele coming from Spark. In the interval *Xgwm210–XwPt4527* an effect identified in one of

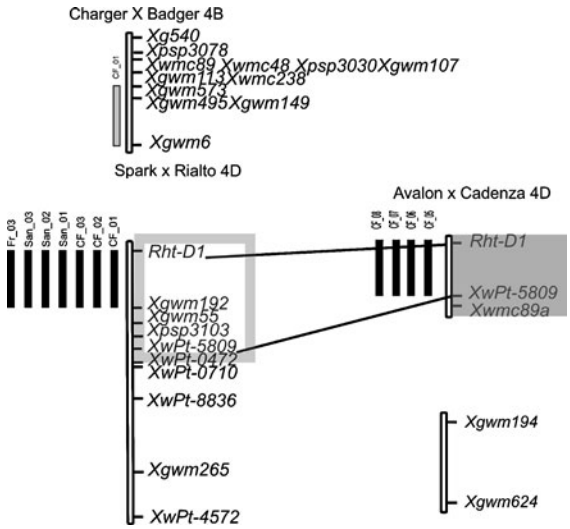


Fig. 2 continued

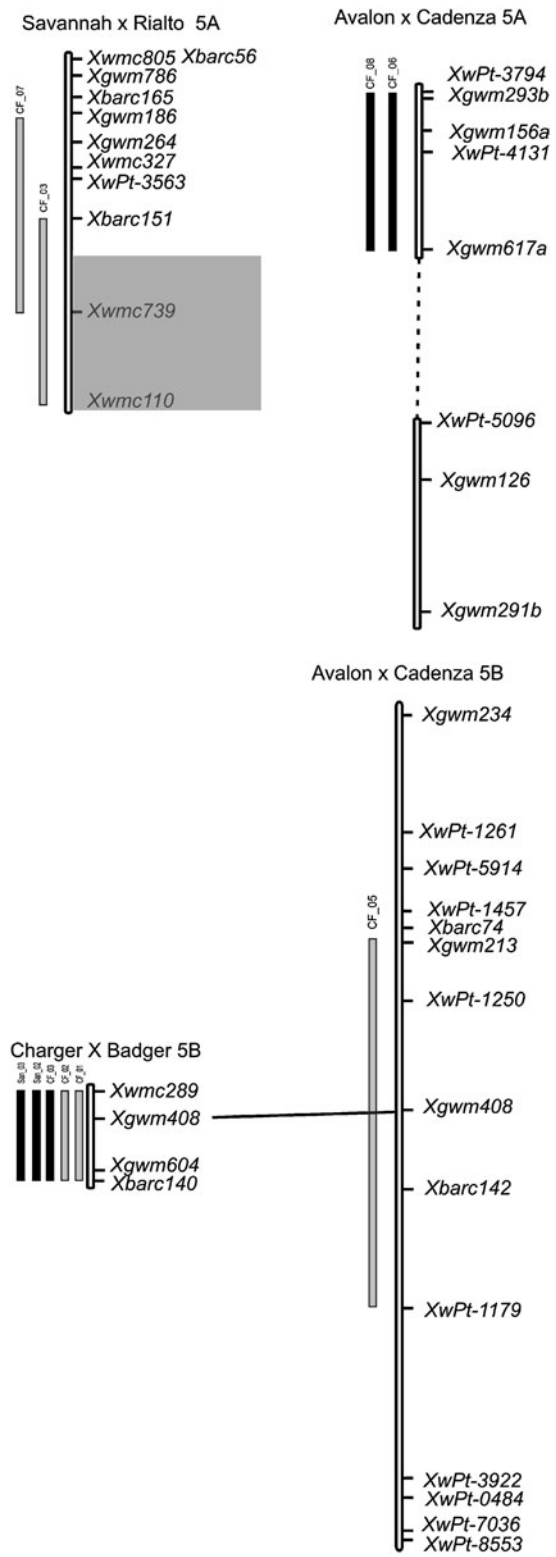


Fig. 2 continued

the six environments tested had an additive effect of 1.6 cm with the increasing allele coming from Spark.

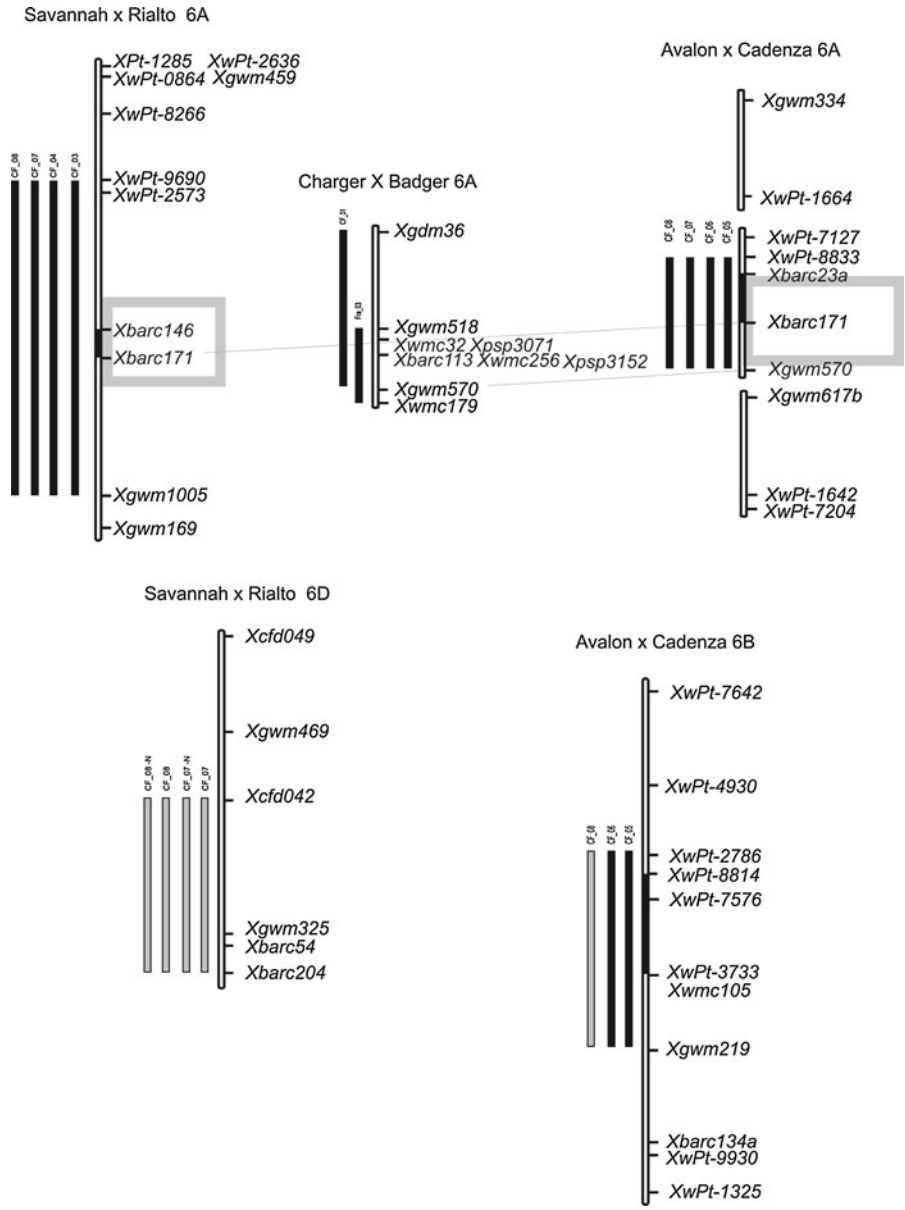
Crop height effects were identified on 2DS (*Xcfd36–XwPt-9997*) in all environments tested for A × C and in one (CF_08) for Sv × R (*Xwmc111-Xbarc124*). For A × C the additive effect ranged from 4.3 (CF_06) to 6.3 cm (CF_07) with the increasing allele coming from Cadenza. For Sv × R the additive effect is 1.5 cm and the increasing allele is from Rialto.

Homoeologous Group 3

Crop height effects were identified in the centromeric region of 3A in all four populations studied. In Sv × R (*XwPt-2698–XwPt-4407*), C × B (*Xgwm369–Xwmc153*) and A × C (*Xgwm369–XwPt-4725*), the QTL were significant in all environments tested; for S × R (*Xgwm497–Xgwm155*) in just one of the six environments. Additive effects ranged from 3.1 cm (CGF_06) to 4.3 cm (CF_07) for A × C, 1.5 cm (CF_01) to 3.6 cm (San_02) for C × B, and 3 cm (CF_08) to 4.1 cm (CF_03) for Sv × R. Increasing alleles were from Rialto, Badger and Cadenza. For the single effect of S × R the additive effect was 1.7 cm, with the increasing allele from Spark.

For 3B, crop height QTL were also detected in the centromeric region for C × B (*Xwmc54–Xwmc56*),

Fig. 2 continued



S × R (*Xwmc54–Xbarc229*) and A × C (*XwPt-6973–XwPt-3005*). For A × C these QTL were significant in all of the environments tested. For C × B and S × R the effects were detected in four of the six or all environments tested repectively. Additive effects ranged from 1.3 cm (CF_01) to 2.6 cm (San_02) for S × R, 1.5 (CF_08) cm to 2.9 cm for A × C (CF_07), and 1.3 cm (CF_02 and CF_03) to 1.9 cm (CF_01) for C × B. Increasing alleles were from Rialto, Cadenza and Charger.

Homoeologous Group 4

Populations S × R and A × C are both segregating for *Rht-D1b*. A crop height effect was detected in the region of *Rht-D1* in both populations in all environments tested. The additive effect in S × R ranged from 4.4 cm (CF_02) to 7.2 cm (Fr_03), and in A × C from 2.5 cm (CF_07) to 4.8 cm (CF_06). The increasing (gibberellin-sensitive) allele came from Spark and Cadenza.

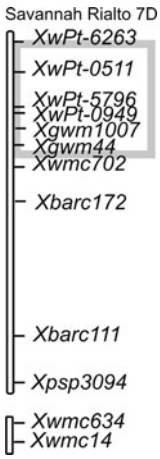


Fig. 2 continued

Table 2 Meta-QTL calculated from four populations used in this study. Positions refer to consensus genetic map (see Electronic Supplementary Material Table S1)

Meta-QTL	Chromosome	Position	Flanking markers
QTL_height_1A_1	1A	42.7	wPt9317–wmc93
QTL_height_1B_1	1B	57.8	gwm456–gwm124
QTL_height_1D_1	1D	59.2	gwm337–wmc36
QTL_height_2A_1	2A	30	wPt6207–wmc827
QTL_height_2A_2	2A	111	cfd86–barc76
QTL_height_2B_1	2B	42	wPt4526–wmc261
QTL_height_2D_1	2D	123.6	gwm320–529tc
QTL_height_3A_1	3A	50.4	barc67–wmc269
QTL_height_3B_1	3B	75.7	wmc307–gwm853
QTL_height_4B_1	4B	42	wmc617–wPt8292
QTL_height_4D_1	4D	12	wmc285–Rht2
QTL_height_5A_1	5A	60.3	cfa2104–wmc475
QTL_height_5B_1	5B	116.4	wmc289–barc140
QTL_height_6A_1	6A	32.2	wmc182–psp3029
QTL_height_6B_1	6B	35.8	wmc486–wmc417
QTL_height_6D_1	6D	70.3	cfd19–barc96

A crop height effect was detected on 4B (*Xgwm57–-Xgwm6*) in C × B in one of the environments tested.

Homoeologous Group 5

Crop height effects were identified on 5A in Sv × R (*Xgwm186–Xwmc110*) and A × C (*Xgwm293b–Xgwm617a*). Additive effects for Sv × R ranged from 1.1 cm (CF_03) and 1.4 cm (CF_07) and the increasing allele came from Savannah. In A × C QTL were identified in CF_06 and CF_08 with additive effects of 1.9 and 2.0 cm, with the increasing allele from Cadenza.

On 5B QTL were identified in five of the six environments tested for C × B (*Xwmc289–Xbarc140*). Additive effects ranged from 1.1 cm (CF_01) to 2.2 cm (San_03), with the increasing allele coming from Badger. In A × C an effect was detected in just one of the environments tested with the increasing allele of Cadenza giving an additive effect of 1.6 cm.

Homoeologous Group 6

Crop height effects were identified in the centromeric region of 6A in all the environments tested for Sv × R (*XwPt-9690–Xgwm1005*) and A × C (*XwPt-8833–Xgwm570*), and two of the six environments for C × B (*Xgdm36–Xwmc179*). The ranges of additive effects were 3.2 cm (CF_08) to 3.9 cm (CF_03) for Sv × R; 2.7 cm (CF_06) to 3.3 cm (CF_08) for A × C; and 1.6 cm (Fr_03) to 2.1 cm (CF_01) for C × B. The increasing alleles came from Savannah, Avalon and Badger. Independent effects were identified in Sv × R on 6D (*Xcfd42–Xbarc204*) at CF_07 and CF_08 with the increasing allele from Savannah and in A × C on 6B (*XwPt-2786–Xgwm219*) at CF_05, CF_06 and CF_08, with the increasing allele coming from Cadenza.

Homoeologous Group 7

No significant QTL were identified on group 7 chromosomes in this study using QTL Cartographer.

Additional QTL identified by MTME analysis

MTME analysis identified QTL on 2B in (C × B and Sv × R) and 7D in Sv × R. The 2B C × B QTL had an additive effect up to 1.9 cm (Fr_03) and was closest to *Xgwm388,* with the increasing allele from Badger. The 2B Sv × R QTL was estimated to have an additive effect of 1.49 cm in all seven environments, the closest marker was *Xdupw207* and the increasing allele came from Savannah The 7D Sv × R QTL had an additive effect between

0.59 cm (CF08) and 2.4 cm (CF_07) with the increasing allele coming from Savannah; the closest marker was *Xwmc702*.

Discussion

Implications for the genetic manipulation of crop stature in wheat

The best characterised crop height effects in wheat are the GA-insensitive dwarfing alleles of *Rht-1*: *Rht-D1b* and *Rht-B1b*. *Rht-D1b* is prevalent in UK winter wheat varieties. *Rht-D1* is segregating in S × R showing additive effects of 4.4 cm (CF_02) to 7.2 cm (Fr_03), and in A × C from 2.5 cm (CF_07) to 4.8 cm (CF_06). This work confirms that, of the crop height genes which are commonly segregating in UK germplasm, *Rht-1* generally has the largest additive effect. However, a number of previously undescribed QTL identified in this study have large additive effects and a major impact on crop height variation in segregating material of UK wheat breeding programmes. As confirmed by MTME analysis in this study, the height QTL shown to have a large effect in any one environment tend to be expressed in the widest range of environments. The MTME analysis provides a good framework for further investigation of QTL × environment interactions. However, this discussion will focus on crop height QTL, identified using QTL Cartographer, that have an additive effect greater than 2.5 cm. It is worth noting that all of these QTL were detected with the application of plant growth regulator (PGR) so the effects identified are of the same magnitude as experienced by wheat breeders, agronomists and farmers. The additive effects are likely to be accentuated in material not treated with PGR.

In A × C a QTL on 2DS had an additive effect up to 6.4 cm, 3.8 cm greater than *Rht-D1* in the same population and environment. This effect was only detected in A × C, showing that the parents of other crosses surveyed are likely to carry the same alleles at this locus, probably the short allele. The 2DS QTL LOD peak coincides with *Xgwm261,* which has been shown to be tightly linked to the GA-sensitive semi-dwarfing gene *Rht8* (Korzun et al. 1998). The height-reducing allele of *Rht8* from the variety Mara is usually associated with a 192-bp allele of *gwm261*, although the 192-bp allele is not universally diagnostic for the height-reducing allele of *Rht8*, especially from varieties not derived from Mara (Ellis et al. 2007). In A × C, the short allele of Avalon is linked to a 174-bp allele of *Xgwm261* and the height-increasing allele of Cadenza to a 196-bp allele. It is possible that this A × C crop height QTL is an allele of *Rht8*. Future work will show if this is the case, and whether the Cadenza allele is a height-increasing allele or, alternatively, that Avalon carries the height-reducing allele brought into coupling with the 174-bp allele of *Xgwm261* by historical recombination. It is intriguing that the Cadenza allele (196 bp) is rare in winter wheat germplasm collections and that the increased height associated with this allele is also associated with increased yield (unpublished data). Another QTL unique to A × C was identified on 2AS in the region of *Xgwm359*, 10 cm distal to *Ppd-A1*. This is a potentially homoeologous location to the 2D effect.

In contrast to the 2AS and 2DS QTL of A × C, some effects appeared to be segregating in the majority of populations studied. A QTL for crop height was segregating in the centromeric region of 3A in all populations studied, in a similar location on 3B in C × B, S × R and A × C, and on 6A in Sv × R, C × B and A × C. This shows that allelic variation for genes controlling crop height is common at these loci. The summed additive effects are large. For example, in A × C in environment CF_07 the substitution effect of tall for short alleles at 2A, 2D, 3A, 3B and 6A but excluding *Rht-D1* adds up to 39.6 cm. By applying marker-assisted selection at these few loci, wheat breeding programmes could manipulate the stature of varieties by a defined genetic route, as they have done for *Rht-1* since the discovery of the GA sensitivity test (Gale and Marshall 1973). In recent years the general correlation of crop height and yield (Law et al. 1978) has been dissected into single QTL effects (e.g. Maccaferri et al. 2008; Zhang et al. 2004), and it has been shown that some crop-height-increasing effects also increase grain yield while others have a neutral effect. There are likely to be optimal combinations of these alleles for any particular target environment, balancing grain yield potential against standing ability and source limitation. Prior to the introduction of GA-insensitive semi-dwarfing genes, an important element of the 'green revolution', breeding for this

balance was more complex and entirely empirical. The first GA-insensitive semi-dwarfs in the UK were shorter than their modern counterparts, which can be thought of as 'tall dwarves'. Increased yield potential in these varieties is associated with their increased biomass (Shearman et al. 2005), which often brings with it an increase in crop height.

In the wider context of global wheat breeding, the genes identified here also have a role to play. For example, *Rht-1* semi-dwarf alleles are widely deployed and confer a yield advantage in many environments. However, the beneficial effects of *Rht-1* are not expressed in all environments, for example some non-irrigated low rainfall areas (Chapman et al. 2007) and where nitrogen fertiliser inputs are low (Laperche et al. 2008). The genetic characterisation of crop-height-controlling genes from Western European wheat varieties described here makes their export to other international breeding programmes via marker-assisted selection a possible mechanism to enrich germplasm already adapted to other mega-environments.

Coincidence of QTL for crop height and ear emergence

The meta-QTL for crop height identified on 3A, 3B and 6B are coincident meta-QTL for ear emergence identified in the same populations (Griffiths et al. 2009). It is possible that the observed differences in crop height and ear emergence are pleiotropic effects of the same genes, as is the case for *Ppd-1* in wheat (Borner et al. 1993) and *sdw1/denso* in barley (Bezant et al. 1997). Closer inspection shows that the relationship between crop height and ear emergence QTL in the populations studied here is not simple. The 3A crop height QTL is calculated from effects identified in A × C, Sv × R, S × R and C × B. Coincident ear emergence QTL were identified in A × C, Sv × R and S × R but not C × B. The 3B crop height meta-QTL derived from effects identified in C × B, S × R and A × C. For ear emergence, the 3B meta QTL was from C × B and S × R, with no effect identified in A × C. Finally, for 6A, a crop height meta-QTL was derived from effects identified in Sv × R, C × B and A × C. For ear emergence, 6A meta-QTL were derived from A × C and S × R data only; no effect was detected in Sv × R and C × B. In spite of this, the direction of the effects for the six loci in which heading date and height effects were coincident were the same, with early and tall alleles going together in all cases, thus providing some evidence for consistent pleitropic effects.

This data shows that the apparent coincidence of these effects could be a consequence of the level of genetic resolution in the segregating populations used, so that linked QTL occur together. This is more likely to occur in proximal regions where the reduced level of recombination means that the ratio of physical to genetic distance is high. For the same reason, the condensation of effects identified in different populations into single meta-QTL is a statistical tool that should be used with caution. In some cases alleles of positive and negative effect might be linked. Knowledge of their genetic location will allow the identification of recombinants that break this linkage or confirm that the two effects are mediated by the same genes.

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