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ORIGINAL PAPER

Genetic mapping of the *labile* (*lab*) gene: a recessive locus causing irregular spikelet fertility in *labile*-barley (*Hordeum vulgare* convar. *labile*)

Helmy M. Youssef · Ravi Koppolu · Twan Rutten · Viktor Korzun · Patrick Schweizer · Thorsten Schnurbusch

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Abstract

Key message **The recessive *labile* locus mapped on chromosome 5HL causes irregular spikelet fertility and controls floret development as well as row-type in barley.**

Abstract The *labile*-barley displays a variable number of fertile spikelets at each rachis internode (0–3 fertile spikelets/rachis internode) which is intermediate between that observed in two- or six-rowed types. Previous re-sequencing of *Vrs1* in 219 *labile*-barley (*Hordeum vulgare* L. convar. *labile*) accessions showed that all carried a six-rowed specific allele. We therefore hypothesized that this seemingly random reduction in spikelet fertility is most likely caused by the *labile* (*lab*) locus, which we aimed to phenotypically and genetically define. Here, we report a detailed phenotypic analysis of spikelet fertility in *labile*-barleys in comparison to two- and six-rowed genotypes using scanning electron microscopy analysis. We found that the first visible morphological deviation occurred during the stamen primordium stage, when we regularly observed the appearance of arrested central floral primordia in *labile* but not in two- or six-rowed barleys. At late stamen and early awn primordium stages, lateral florets in two-rowed and only some in *labile*-barley showed retarded development and reduction in size compared with fully fertile lateral florets in six-rowed barley. We used two F_2 mapping populations to generate whole genome genetic linkage maps and ultimately locate the *lab* locus as a recessive Mendelian trait to a 4.5–5.8 cM interval at approximately 80 cM on chromosome 5HL. Our results will help identifying the role of the *lab* gene in relation to other spikelet fertility factors in barley.

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H. M. Youssef · R. Koppolu · T. Rutten · P. Schweizer · T. Schnurbusch (✉)
Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), 06466 Gatersleben, Germany
e-mail: thor@ipk-gatersleben.de

H. M. Youssef
Plant Physiology, Faculty of Agriculture, Cairo University, Giza 12613, Egypt

V. Korzun
Cereals Biotechnology, KWS LOCHOW GMBH, 37574 Einbeck, Germany

Introduction

The inflorescence of cultivated barley (*Hordeum vulgare* L.) is an indeterminate spike that produces three single-flowered spikelets at each rachis internode with one central and two lateral spikelets (Harlan 1914; Bonnett 1935; von Bothmer et al. 1985; Forster et al. 2007; Sreenivasulu and Schnurbusch 2012). Based upon lateral spikelet fertility, barley is classified into two- and six-rowed varieties (Mansfeld 1950). In two-rowed barley, to which wild barley (*H. spontaneum*) and some strains of cultivated barley belong, only the central spikelet is fertile and sets seed, while the florets of the two lateral spikelets remain empty. In six-rowed barley, all three spikelets are fertile and produce grains (von Bothmer et al. 1985).

Apart from two- and six-rowed barleys there is another row-type class, which is better known as *labile*-barley (*Hordeum vulgare* L. convar. *labile* (Schiem.) Mansf.) originally described as an irregular row-type of Abyssinian barley

(Åberg and Wiebe 1945). It was first identified in 1848 and regarded as a transition form between two- and six-rowed barley. Harlan (1914) as well as Åberg and Wiebe (1945) used the term '*irregular*' because these barleys showed irregular fertility of lateral spikelets along the spike, whereas infertile lateral spikelets were completely reduced to glumes without visible floral residues, rather resembling *deficiens* barleys (*H. vulgare* L. convar. *deficiens* (Schiem.) Mansf.). The *labile* row-type has been considered as a distinct spike character especially among Ethiopian barleys (Bjørnstad and Abay 2010) and has been grown in most of the barley cropping areas throughout Northern Ethiopia (Abay and Bjørnstad 2009; Hadado et al. 2009). Among all the naturally occurring row-type variants, the *labile*-barleys are genetically least described probably owing to their high phenotypic plasticity, which complicated their classification (Mansfeld 1950).

Genetic mapping and identification of genes controlling spikelet fertility and row-type are crucial for a better understanding of barley inflorescence development, including spikelet initiation, fertility and abortion. Until today, we know that the row-type phenotype is controlled by at least five independent loci that include *six-rowed spike1* (*vrs1*), *vrs2*, *vrs3*, *vrs4* and *Intermedium-c* (*Int-c*) mapping on barley chromosomes 2HL, 5HL, 1HS, 3HS and 4HS, respectively (Pourkheirandish and Komatsuda 2007). Variation at the *vrs1* locus, which belongs to the HD-ZIP I class of homeobox transcription factors, is sufficient to control complete lateral spikelet fertility (Komatsuda et al. 2007). The functional *Vrs1.b* acts as a negative regulator of lateral spikelet fertility resulting in a two-rowed phenotype, whereas the non-functional *vrs1.a* promotes lateral spikelet fertility resulting in a six-rowed phenotype. However, spikelet fertility in two- and six-rowed barley can be modified through the presence of different *Int-c* alleles. Ramsay et al. (2011) identified *Int-c* as an ortholog of the maize (*Zea mays* L.) domestication gene, *Teosinte branched1* (*ZmTB1*). They found that two-rowed barleys (*Vrs1*) usually possess the *int-c.b* allele, whereas six-rowed barleys (*vrs1*) often possess *Int-c.a*. Moreover, *Vrs1* also appears to be under the transcriptional control of *Vrs4*, which functions as a central regulator of spikelet meristem determinacy and row-type (Koppolu et al. 2013).

Djalali (1970) noted that, the *labile*-barleys display a continuous variation in the number of fertile lateral spikelets from genotype to genotype. Previous genetic studies suggested that the *labile* phenotype is a constant and heritable attribute (Engledow 1924) either derived from two- (Breitenfeld 1957) or six-rowed barleys (Nötzel 1952). For better understanding the inheritance of the *labile* phenotype, Djalali et al. (1970) tested the crosses between *labile* and two-rowed (*H. vulgare* L. convar. *distichon*) barley and reported that two genetic factors are necessary for the manifestation of the *labile* character, they include: the recessive allele for the six-rowed phenotype and the recessive allele at the *lab* locus for the *labile* character. In an attempt to reveal the haplotype structure at the *vrs1* locus in *labile*-barleys, Saisho et al. (2009) analyzed a set of 14 *labile* accessions, which showed reduction in lateral spikelet fertility and found that all carried the *vrs1.a* allele. They suggested that the complete six-rowed spike phenotype of *labile* resulted from a sequence variant in the HD-ZIP motif, whereas the irregular spikelet phenotype is controlled by another genetic factor. Also, *Vrs1* re-sequencing results in 219 *labile*-barley accessions from Ethiopia revealed two six-rowed alleles at *vrs1* (*vrs1.a1* and *vrs1.a3*), but reduced lateral spikelet fertility as well as the occasional missing of central florets (Youssef et al. 2012). We hypothesized that this reduction in lateral and central spikelet fertility in *labile*-barleys is most likely caused by the recessive *lab* locus (Youssef et al. 2012).

The generation of high-density genetic maps using markers such as single nucleotide polymorphisms (SNP) has greatly improved the ability to identify genes or QTLs (Stein et al. 2007). In the recent past, SNPs have become the markers of choice for genetic mapping because they are robust, simple to generate, co-dominant and highly reproducible (Manikanda 2012). For the barley research community, a very rich resource of SNP markers is available in the form of BOPA SNP markers (Close et al. 2009) and barley iSELECT chip (Comadran et al. 2012) for most of these SNPs chromosomal positions were already assigned.

In the present study, we used two mapping populations from crosses between *labile* and six-rowed barley to utilize the available SNP resources and to generate a whole genome genetic linkage map to genetically locate the *lab* locus onto a barley chromosome arm. The recessive *lab* locus mapped at approximately 80 cM on the long arm of chromosome 5H within a genetic interval of four to six cM. We also found that at late stamen and early awn primordium stages, lateral and occasionally central florets in *labile*-barleys showed retarded differentiation and reduction in size compared with fully fertile lateral florets in six-rowed barley. The long-term goal of our research in *labile*-barleys is to identify the underlying gene for the *lab* locus and elucidate its molecular function and relationship with other known *Vrs* genes that control barley spikelet fertility and row-type.

Materials and methods

Plant materials, growing conditions and spike phenotyping

Based upon our previous work (Youssef et al. 2012), crosses between different six-rowed barley cultivars and

labile accessions carrying *vrs1.a* and *Int-c.a* alleles at *vrs1* and *int-c* loci, respectively, were performed. F_1 plants from these crosses were tested for heterozygous plants using SSR markers according to Li et al. (2003). True F_1 plants were grown under greenhouse conditions at IPK, Gatersleben; 12/12 h (day/night) light and 14/12 °C (day/night) and F_2 seeds were harvested. Two segregating F_2 populations consisting of 130 individuals derived from the cross between Morex × HOR2573 (M/H2) and 96 individuals derived from the cross between Shimabara × HOR5465 (SH/H5) were used for linkage analysis. The F_1 and F_2 plants were scored for spike phenotypes (either six-rowed or *labile* phenotype) after anthesis.

Scanning electron microscopy (SEM)

For SEM analysis, immature barley spikes at triple mound, lemma, stamen and awn primordium stages (Kirby and Appleyard 1987) were collected from *labile* and wild-type plants (WT, i.e. Morex, six-rowed; Bowman, two-rowed). Plants were grown under greenhouse conditions as described previously. Immature spikes were fixed with 4 % formaldehyde in 50 mM phosphate buffer, pH 7.0 overnight. After dehydration in a graded ethanol series and critical point drying in a Bal-Tec critical point dryer (Bal-Tec AG, Balzers, Switzerland), spikes were gold sputtered in an Edwards S150B sputter coater (Edwards High Vacuum Inc., Crowley, West Sussex, UK) and examined in a Hitachi S-4100 SEM (Hisco Europe, Ratingen, Germany) at 5 kV acceleration voltage. Digital recordings were made and stored as Tiff-image files.

Genomic DNA isolation

For DNA extraction, leaf samples from the two mapping populations and respective parental genotypes were collected from single plants at the three to five leaf stage. Total genomic DNA was extracted according to Doyle and Doyle (1990). DNA quality and quantity were checked on 0.8 % agarose gels. For PCR amplification, DNA concentration was adjusted to 50 ng/μl.

SNP selection and marker development

Two different VeraCode SNP oligo pools comprising of 384 BOPA SNP markers mapped at regular intervals on seven barley chromosomes (see supplementary data) were custom designed for Illumina GoldenGate genotyping on the Bead express reader. The SNP markers with minor allele frequencies (MAF) ≥2.0 were selected to maximize the polymorphism rate (Close et al. 2009). The raw data from the SNP GoldenGate assay were analyzed using GenomeStudio v2010.3. For further marker development in the defined *labile* map interval (based on VeraCode SNP genotyping data), we relied on the barley genome zipper (Mayer et al. 2011). Gene sequences from syntenic interval were extracted from *Brachypodium* genome browser server (http://www.phytozome.net/cgi-bin/gbrowse/brachy/). Syntenic *Brachypodium* gene sequences were BLASTed against IPK Barley BLAST server (http://webblast.ipk-gatersleben.de/barley/viroblast.php) to obtain barley sequences for respective *Brachypodium* genes. Primers designed from the barley sequences all had annealing temperatures of 60 ± 1 °C according to Gawroński and Schnurbusch (2012).

PCR amplifications were carried out in 25 μl reaction volume containing 20 ng of DNA, 2.5 μl of PCR buffer (10X) (Qiagen, Hilden, Germany), 5 mM dNTPs, 5 μl of Q-solution (Qiagen, Hilden, Germany), 5 pM primers, and 1U of *Taq* polymerase (Qiagen, Hilden, Germany) using a thermal cycler (SensoQuest Thermal Cycler, USA). The PCR profile included an initial denaturation step for 3 min at 94 °C followed by 45 cycles of 94 °C for 40 s denaturation and an annealing step with constant annealing temperature of 60 °C for 40 s and an extension step at 72 °C for 2 min, followed by a final extension for 10 min at 72 °C. PCR products were tested on 1.2 % agarose gels. For Sanger-sequencing, PCR products were purified using MinElute 96UF PCR purification kit (Qiagen, Hilden, Germany) and sequenced with BigDye Terminator v3.1 cycle sequencing Kits (Applied Biosystems, USA). DNA sequence analysis, quality score assignments and construction of contigs were done with Sequencher 4.7 DNA sequence assembly software. SNP polymorphisms identified from sequencing data were converted to restriction enzyme-based CAPS markers (Vincze et al. 2003) (http://tools.neb.com/NEBcutter2/). For mapping the *lab* locus, the *labile* phenotype was scored as a monogenic Mendelian trait, and linkage analysis of the phenotype with polymorphic markers was carried out using JoinMap3.0 (Van Ooijen 2006).

Results

Spikelet and floret development for the *labile* row-type

SEM image analysis at triple mound, lemma, stamen and awn primordium stages revealed that up until the lemma primordium stage no morphological differences among the three tested row-types became apparent, suggesting that two-rowed, six-rowed and *labile*-barleys initially go through a very similar succession of spike developmental processes (Fig. 1a, b). The first visible morphological deviation between two- and six-rowed cultivars was found in late stamen primordium and early awn primordium stages

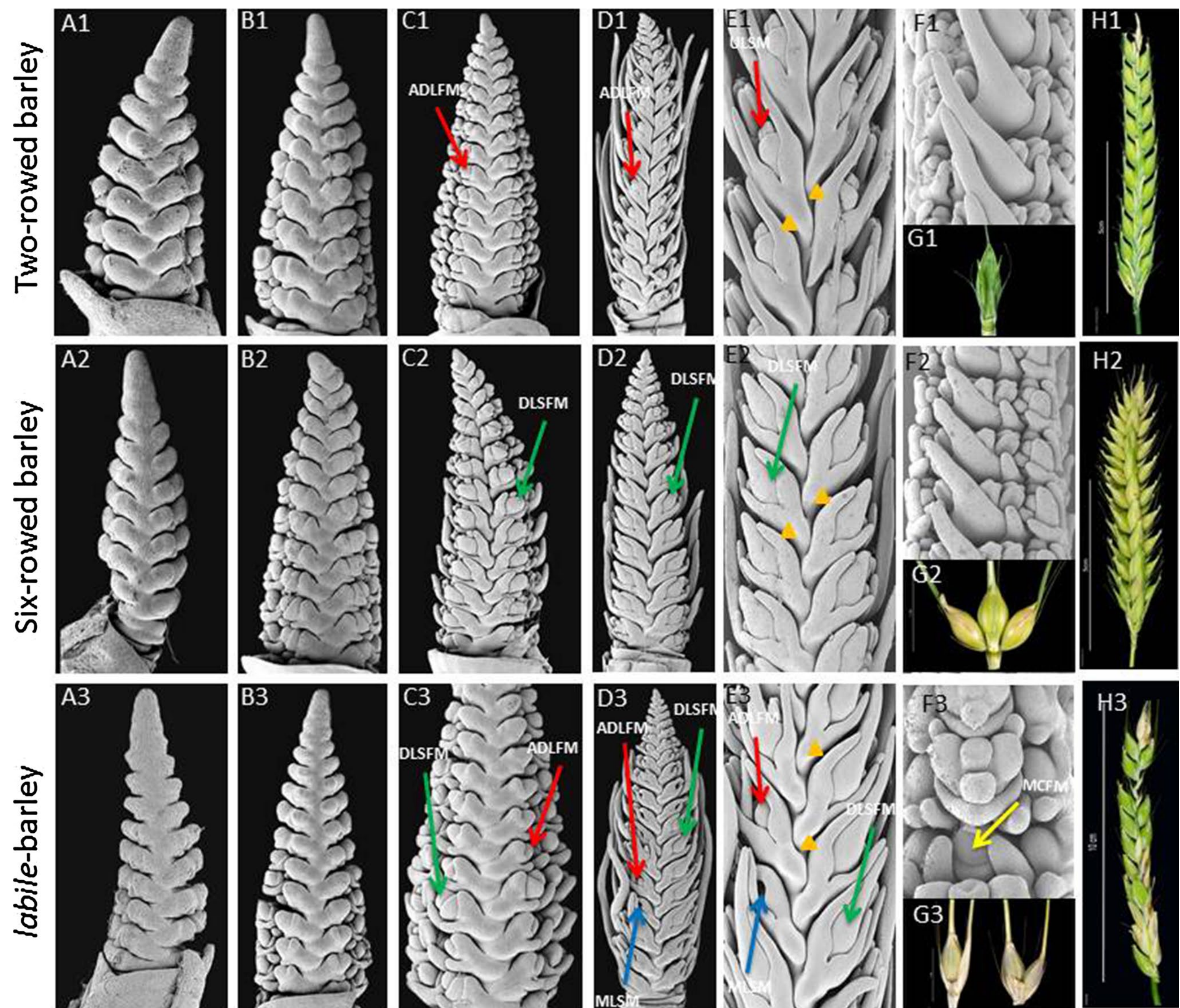

Fig. 1 SEM analysis of two-rowed, six-rowed and *labile*-barley spikes. (*A1-3 and B1-3*) Immature spikes at lemma primordium and early stamen primordium stages without visible differences. *C* Lateral view of inflorescences at early awn primordium stage; **C1** two-rowed spike shows arrested development of lateral floret meristem (ADLFM) *red arrows*, **C2** six-rowed spike shows developed lateral spikelet and floral meristems (DLSFM) *green arrows*, **C3** *labile* spike shows DLSFM and ADLFM, *D* lateral view of spikes at late awn primordium stage; **D1** two-rowed spike shows clearly ADLFM, **D2** six-rowed spike shows DLSFM, **D3** *labile* spike shows DLSM and ADLFM in addition to missing lateral floret meristem (MLFM) *blue arrows*, *E* high magnification of (**D**) photos shows clearly ADLFM, DLSFM and MLFM in *labile* spikes comparing with two-rowed and six-rowed barley spikes at late awn primordium stage. At this stage, glume primordium (*GP orange arrows heads*) were developed in two-rowed, six-rowed and *labile* spikes. (*F*) dorsal view of spikes at late awn primordium stage shows no differences between two- and six-rowed barley (**F1** and **F2**). (**F3**) *labile* spike with missing central floret meristem (MCFM) *yellow arrow*. **G** Number of set seeds per rachis internode; **G1** in two-rowed barley only the central spikelet is setting seed. **G2** in six-rowed three spikelets set seeds (one central and two lateral), **G3** *labile*-barley spikelets setting from 0 to 3 seeds per rachis internode. **H** Spikes of two-rowed, six-rowed and *labile*-barley; **H1** two-rowed spike, **H2** six-rowed spike, **H3** *labile* spike

(i.e. staging according to the central spikelet and floret development!), when lateral florets in two-rowed showed retarded development and reduction in size compared with lateral florets in six-rowed barley (Fig. 1c1, c2). The clearly observed developmental difference in lateral florets for these two row-type classes is diagnostic for the allelic differences at the *vrs1* locus. In *labile*-barley at stamen primordium stage, however, we regularly observed the occurrence of arrested central floral primordia (Fig. 1f3), a feature generally not found in two- and six-rowed barleys (Fig. 1f1, f2). Next to that, at late stamen primordium and early awn primordium stages, we found that only a few lateral florets showed retarded differentiation and reduction in size, producing an irregular pattern of spikelet fertility

Table 1 Spike phenotypes in F_1 and F_2 crosses of Morex × HOR2573 and Shimabara × HOR5465

	labile phenotype	Six-rowed phenotype	Total	% of the *labile* phenotype[a]	χ^2/P value for 3:1
F_1 (Morex × HOR2573)	–	30	30	0	–
F_1 (Shimabara × HOR5465)	–	8	8	0	–
F_2 (Morex × HOR2573)	29	101	130	22.3	0.50/0.48
F_2 (Shimabara × HOR5465)	22	74	96	22.9	0.50/0.47

[a] *labile* barleys show an irregular spike phenotype with either missing, undeveloped, and sterile central and lateral florets along the spike

along the spike (Fig. 1c3). Importantly, glume primordia developed normally in all three row-types at these stages (Fig. 1d1–d3), indicating that all row-types are not affected in their spikelet development. At the awn primordium stage, the *labile* spike displayed a mosaic of lateral spikelet fertility, eventually setting seeds in lateral florets (Fig. 1g3); however, fertile lateral florets in *labile*-barley did not differ compared to those in six-rowed barley (Fig. 1e2, g2). Moreover, glumes appeared to be always present regardless of floral status (i.e. fertile or sterile floret), clearly indicating that the *lab* locus is primarily affecting floret meristem development in a random fashion (Fig. 1e3). In two-rowed barley, all lateral florets had stopped differentiating at the awn primordium stage (Fig. 1e1–g1). Most interestingly, in *labile*-barleys, arrested floral development was not restricted to the lateral florets. These morphological features make the *labile* spike (Fig. 1h3) a mosaic form between the two- (Fig. 1h1) and six-rowed spike (Fig. 1h2), but also showed that spikelet fertility in *labile*-barley seems to be generally affected and is not restricted to lateral floral meristems as reported previously (Djalali 1970; Takeda and Saito 1988; Saisho et al. 2009).

Phenotypes of F_1 plants and F_2 populations

Phenotyping of 38 true F_1 plants obtained from the crosses, Morex × HOR2573 (M/H2) and Shimabara × HOR5465 (SH/H5) showed a complete six-rowed phenotype in all F_1 plants, indicating that *labile* is a recessive trait. The F_2 populations of the respective crosses (130 M/H2 plants and 96 SH/H5 plants) segregated for two different spike forms, i.e. either *labile* or six-rowed spike. The *labile* spike phenotype was found in 29 (22.3 %) plants ($\chi^2 = 0.50$) of M/H2 and 22 (22.9 %) plants ($\chi^2 = 0.50$) of the SH/H5 populations (see Table 1). This near to 1:3 segregation ratio of *labile* versus six-rowed spike phenotype in F_2 confirmed that the *lab* locus segregated as a monogenic recessive gene.

Genetic mapping of the *labile* (*lab*) locus

To identify the *lab* locus, a set of 381 selected SNP markers were used to perform whole genome mapping in barley. To this end, eight linkage groups were built based on 173 polymorphic markers, which were mapped on the seven barley chromosomes (one linkage group for chromosomes 1H to 6H and two for chromosome 7H) (Table 2). Mapping of the *labile* phenotype from the F_2 populations located it on chromosome 5H. The *lab* locus mapped in the genomic region between two linked markers ge00218s01 and ge00066s01 (23.2 cM) (Fig. 2).

We further narrowed down the mapping interval containing *lab*, using 50 primer pairs designed from 18 barley genes, which are in synteny with *Brachypodium* chromosome 4. The syntenic genes were extracted based on the virtual gene order reported in the barley genome zipper (Mayer et al. 2011). The 18 genes selected for marker design were spaced at a regular interval of 1.3 cM according to genome zipper. Genetic mapping results localized the *lab* locus at approximately 80 cM on the long arm of chromosome 5H to an interval of 5.7 cM in the M/H2 population and 4.6 cM in the SH/H5 population between the closely linked markers BAR and ge00066s01 (Fig. 3). Five common markers ge00355s01, ABC1, BAR, ge00066s01 and ge00186s01 were mapped in both populations in the *labile* genomic region (Fig. 3).

Discussion

Possibly due to their high phenotypic row-type plasticity and restricted regional occurrence, *labile*-barleys (Mansfeld 1950) are genetically least described among all the naturally occurring row-type variants. This study is the first showing that the *lab* locus can be mapped as a distinct Mendelian trait located on the long arm of chromosome 5H at approximately 80 cM to an interval of 4.5–5.8 cM. The segregating F_2 populations showed either the *labile* or six-rowed spike phenotype. This segregation pattern (1:3) in conjunction with reports by Djalali (1970) confirmed that the reliable detection of the *labile* character is primarily dependent upon two conditions: (1) the six-rowed spike phenotype (i.e. genetically constituted as *vrs1.a* + *Int-c.a*), and (2) the recessive allele at the *lab* locus for the *labile* character. Furthermore, we show that the newly identified

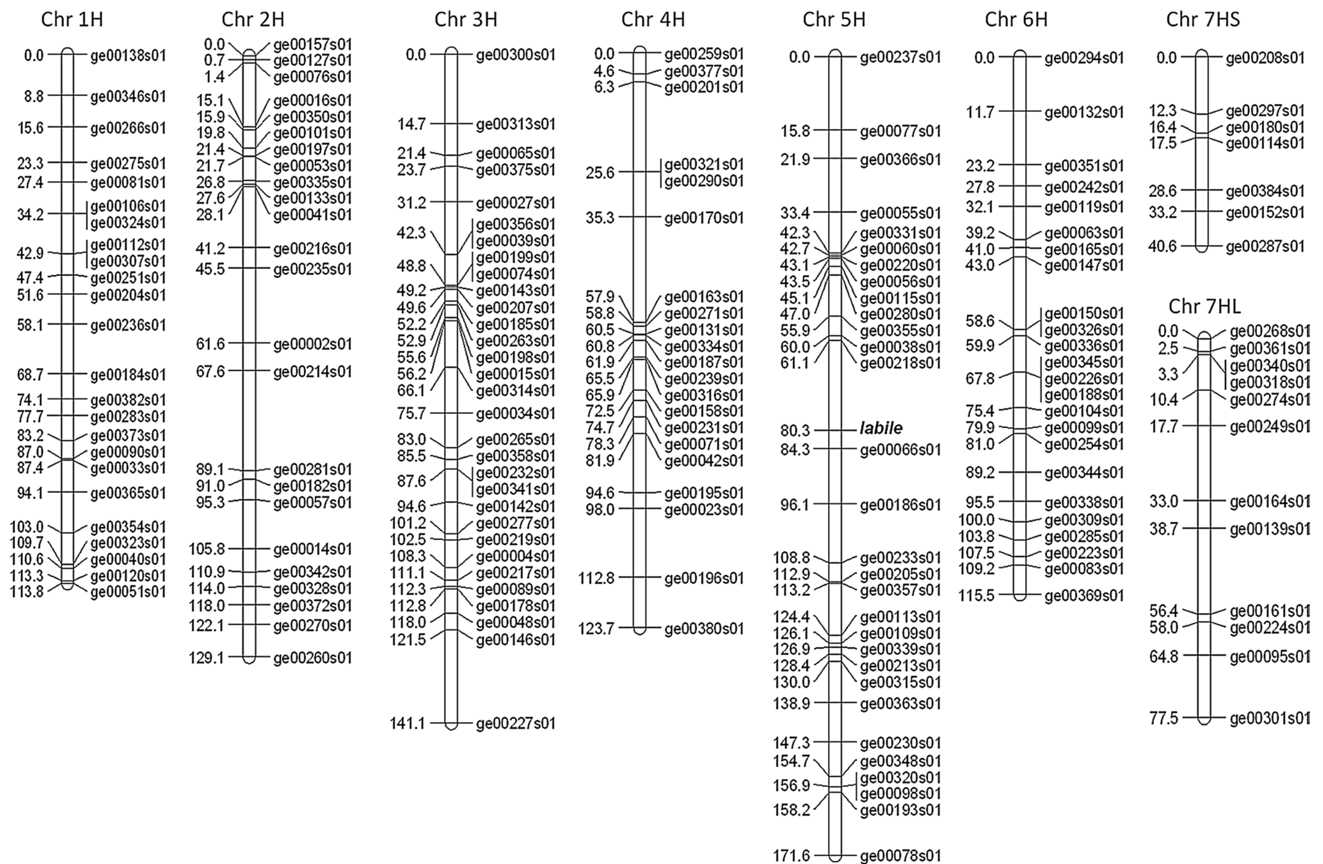

Fig. 2 Whole genome mapping of the *labile* phenotype in the F_2 population derived from Morex × HOR2573

Table 2 The whole barley genome genetic linkage analysis

	No. of selected markers	No. of polymorphic markers	Length of linkage group (cM)	Average marker interval (cM)
Chromosome 1H	43	24	113.8	4.7
Chromosome 2H	64	24	129.1	5.4
Chromosome 3H	54	31	141.1	4.6
Chromosome 4H	47	21	123.7	5.9
Chromosome 5H	73	30	171.6	5.7
Chromosome 6H	56	24	115.5	4.8
Chromosome 7HL	21	12	77.5	6.5
Chromosome 7HS	23	7	40.6	5.8
Total/average[a]	381	173	912.9	5.4

[a] The numbers for No. of selected markers, No. of polymorphic markers, Length of linkage group (cM), represent total values for the seven chromosomes, whereas the number for Average marker interval (cM) represents average value for all chromosomes

lab locus is genetically distinct from previously known loci conferring the six-rowed spike phenotype in barley (i.e. *vrs1*, *vrs2*, *vrs3*, *vrs4* and *int-c* on chromosomes 2HL, 5HL, 1HS, 3HS and 4HS, respectively; Pourkheirandish and Komatsuda 2007); but resides close to the *vrs2* locus, which is located in between the flanking markers ge00066s01 and ge00186s01 on the same chromosome arm (data not published). The *vrs2* mutant shows occasional lateral spikelet fertility without any missing central or lateral florets, the characteristic features of *labile* spikes. Moreover, the *vrs2* mutant phenotype does not require the presence of the six-rowed genetic background to become apparent. So, these clear differences between *vrs2* and *labile* mutants strongly suggest that they are two independent genetic loci located on the same chromosome arm (Youssef et al. 2013).

Among all row-type mutants, the *labile*-barleys are unique in their spike architecture showing a mosaic of six- and two-rowed spike phenotypes (irregular spikelet

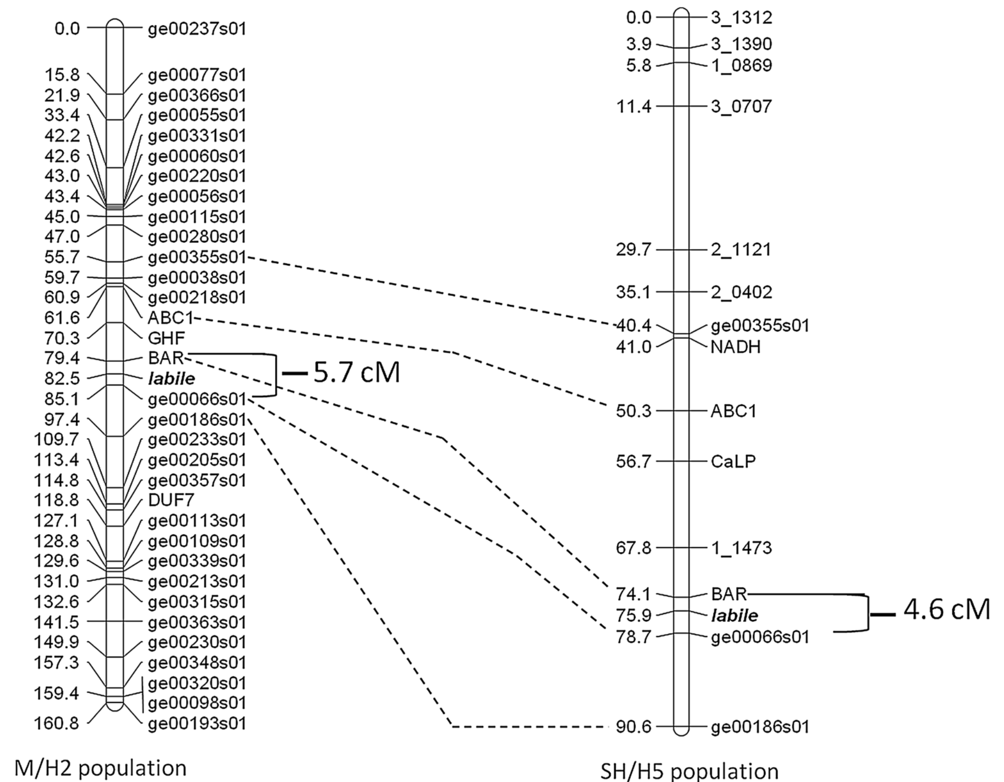

Fig. 3 Genetic linkage maps of the *labile* (*lab*) locus on barley chromosome 5H. Linkage analysis was performed on 130 and 96 F_2 plants from the crosses, Morex × HOR 2573 and Shimabara × HOR5465, respectively

fertility). The analysis of our scanning electron micrographs revealed that up until the lemma primordium stage there were no visible differences in spike development between two-rowed, six-rowed and *labile* spikes. During these early stages, the central floral primordia were more developed than those of the lateral floral primordia (see also Komatsuda et al. 2007). At late stamen and early awn primordium, first morphological differences in spike development became apparent. In the case of six-rowed barleys, central and lateral spikelets/florets displayed complete development, whereas in two-rowed barleys, a clearly retarded development was consistently observed in all lateral florets. Komatsuda et al. (2007) provided the first step in the elucidation of lateral floret fertility and showed that loss-of-function of the wild-type *Vrs1* gene (responsible for the two-rowed phenotype) resulted in complete fertility of lateral florets displaying the six-rowed spike phenotype. The *Vrs1* gene belongs to the HD-ZIP I class of homeobox transcription factors. Loss-of-function of the VRS1 protein in lateral floral primordia enabled complete fertility, suggesting that VRS1 suppresses the development of lateral florets. In contrast to two-rowed barleys, infertile lateral florets of *labile*-barleys are completely reduced without any floral development except glumes (Fig. 1d3, e3), rather resembling the *deficiens* phenotype (Mansfeld 1950). Moreover, *labile*-barleys showed another interesting feature whereby some central spikelets also remained reduced only to glumes without any floral meristem development (Fig. 1f3). These *labile*-specific features resulted in a variable number of fertile lateral (Djalali et al. 1970; Takeda and Saito 1988) and central (Youssef et al. 2012) spikelets at each rachis internode (0–3 per rachis internode). This unique spikelet fertility phenotype only observed in *labile*-barleys clearly suggests that the *labile* gene seems to be important for floral meristem identity and development.

The development of six-rowed spikes is often controlled by a non-functional *Vrs1*, (Komatsuda et al. 2007) complemented by *Int-c.a* (Ramsay et al. 2011). The spatial and temporal specificity of *Vrs1* gene expression suggests that VRS1 is involved in the development (i.e. suppression) of lateral florets complemented by the presence of the *int-c.b* allele in two-rowed barley (Komatsuda et al. 2007; Ramsay et al. 2011). We established that in both two-rowed and *labile*-barley this suppression of lateral spikelet development starts in late stamen primordium (see Fig. 1c1, c3). According to Komatsuda et al. (2007), loss-of-function in *Vrs1* during early spike development leads to the formation of the six-rowed spike. Our previous study revealed that *labile*-barleys carry six-rowed alleles (*vrs1.a, Int-c.a)* at *vrs1* and *int-c* loci (Youssef et al. 2012), displaying a mosaic spike phenotype between the two- and six-rowed condition. Apparently, the lack of *Vrs1* gene function in combination with *Int-c* may be sufficient to explain the lateral spikelet fertility in *labile*-barleys, but seems rather insufficient to clarify the random floral sterility seen in lateral as well as central spikelets. Thus, identification of the underlying gene

for the *lab* locus, using a map-based and mutant analysis approaches seems promising. Molecular genetic results in combination with the examination of detailed lateral and central spikelet development in *labile*- and other row-types may help elucidate the role of the *lab* gene in relation to other floret development and fertility factors in barley.

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Conflict of interest The authors declare that they have no conflict of interest.

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