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Sub-arm location of prolamin and EST-SSR loci on chromosome 1H^{ch} from *Hordeum chilense*

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Abstract *Hordeum chilense* Roem. et Schult. is a diploid wild South American barley that contains genes of interest for cereal breeding, many of them located on chromosome 1H^{ch}. In the current study, two *H. chilense*-wheat addition lines with deletions in the 1H^{ch} chromosome were used for sub-arm localization of five prolamin (glutenin and gliadin) loci and 33 EST-SSR marker loci on chromosome 1H^{ch}. The two sets of markers were distributed across five sub-arm chromosome regions. Three glutenin loci (*Glu-H^{ch}2*, *Glu-H^{ch}3*, *Glu-H^{ch}4*) together with the gliadin locus *Gli-H^{ch}1* were located on the distal 20% of the 1H^{ch}S arm, whereas the glutenin locus *Glu-H^{ch}1* was on the proximal 88% region of 1H^{ch}L. Among 33 EST-SSR marker loci, 7 (21.2%) were on the 1H^{ch}S arm and, of them, 3 (9.1%) were on the distal 20% end and 4 (12.1%) on the proximal 80% region. The 26 loci (78.8%) on 1H^{ch}L were distributed across three different regions: 18 (78.8%) in the proximal 88%, 3 (9.1%) in the distal 12% and 5 (15.2%) in a region less than 12% from the distal end. The deletions in the 1H^{ch} chromosome added to the common wheat background were thus shown to be useful for determining the sub-arm location of EST-SSR and prolamin loci. This could facilitate the identification of molecular markers linked to genes of agronomic interest and the isolation of such genes for use in common wheat improvement.

Keywords Chromosome mapping · Genetic markers · Gliadin · Glutenin · Wheat

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Introduction

Hordeum chilense Roem. et Schult. is a diploid South American wild barley containing genes potentially useful for wheat breeding. Genes for several agronomically important traits such as those controlling tolerance to salt (Forster et al. 1990), resistance to the root-knot nematode *Meloidogyne naasi* (Person-Dedryver et al. 1990) and resistance to greenbug (*Schizaphis graminum*) (Castro et al. 1994) are located on chromosome 1H^{ch}. In addition to contributing to abiotic and biotic stresses, *H. chilense* could widen the genetic basis for grain quality traits of common wheat (*Triticum aestivum* ssp. *aestivum* L. em. Thell.) and durum (*T. turgidum* ssp. *durum* Desf. em. M.K.) since the H^{ch} genome has an effect on gluten strength similar to that of the D genome of *Aegilops tauschii* Coss. (Alvarez et al. 1999). This trait is related to the prolamins (glutenins and gliadins) that are the major storage proteins synthesized in the seeds of cereals and other grasses (Payne 1987). The glutenins are the main factor responsible

for the rheological properties of wheat flour (Wrigley et al. 2006). Most of the prolamins from *H. chilense* are synthesised by loci on chromosome $1H^{ch}$ (Payne et al. 1987; Tercero et al. 1991) and there are as many as five prolamin loci on this chromosome (Alvarez et al. 2004).

H. chilense crosses readily with many species belonging to genera in the *Triticeae* tribe (Fedak 1992). Its high crossability with common and durum wheat makes it suitable for introgression of favourable traits into cultivated wheats (Martín et al. 1998). It is important to identify the position of loci and/or markers controlling key agronomic traits for marker-assisted introgression of small segments of the $1H^{ch}$ chromosome into both common wheat and durum. The availability of expressed sequence tag (EST) data has facilitated the development of microsatellite or simple sequence repeat (SSR) markers in a number of plant species groups, including cereals (Varshney et al. 2002). As they are based on expressed genes, EST-SSR markers are more conserved across species than genomic microsatellites and hence more transferable.

The current study focussed on the $1H^{ch}$ chromosome from *H. chilense* with the aims of determining the sub-arm chromosome regions containing loci for grain quality, such as glutenins (*Glu-H^{ch}1*, *Glu-H^{ch}2*, *Glu-H^{ch}3* and *Glu-H^{ch}4*) and gliadins (*Gli-H^{ch}1*), increasing the molecular markers available for this chromosome, and identifying their locations in specific sub-arm regions.

Materials and methods

Plant material

The study was based on *H. chilense* (lines H1 and H7), common wheat cv. Chinese Spring (CS), wheat-*H. chilense* disomic addition line for complete chromosome $1H^{ch}$ in CS (named CS + $1H^{ch}$), the wheat-*H. chilense* ditelosomic addition line for the short arm of $1H^{ch}$ (named CS + $1H^{ch}$S) and two homozygous terminal deletion lines involving chromosome $1H^{ch}$ added to CS. One of these lines carried a double terminal deletion for both 20% of the short and 12% of the long arm of chromosome $1H^{ch}$ (called CS + del$1H^{ch}$-1), and the other line carried a translocation $T7H^{ch}L{\cdot}1H^{ch}L$ in which the $1H^{ch}$L arm had lost 12% of the distal region (called CS + del$1H^{ch}$-2).

The wheat-*H. chilense* addition line for chromosome $1H^{ch}$ and the two terminal deletion lines were obtained by pollinating tritordeum line HT31 (amphiploid *H. chilense* and durum wheat, $AABBH^{ch}H^{ch}$, $2n = 6\times = 42$) with a CS disomic addition line for chromosome 2C from *Ae cylindrica* Host and F_1 plants ($AABBDH^{ch}$ + 2C) monosomic for the gametocidal 2C were backcrossed with CS followed by five generations of selfing (Cifuentes et al. 2005; Cabrera et al. unpublished results). Tritordeum line HT31 is a secondary amphiploid, having both H1 and H7 lines in its pedigree. The wheat-*H. chilense* (H1) ditelosomic addition $1H^{ch}$S was kindly provided by Dr. S. Reader, JI Centre, Norwich, UK.

Prolamin extraction and electrophoretic analysis

Proteins were extracted from crushed endosperm according to the protocol described by Alvarez et al. (2001). Gliadins were separated by Acid-PAGE at 6.7% (C: 3.6%) with low catalyst (ferrous sulphate and hydrogen peroxide) levels to increase gel firmness (Khan et al. 1985). Electrophoresis was carried out at 20 mA/gel at 18°C. Reduced and alkylated glutenin subunits were fractionated by electrophoresis in vertical SDS-PAGE slabs in a discontinuous tris–HCl-SDS buffer system (pH: 6.8/8.8) at a polyacrylamide concentration of 10% (w/v, C: 1.28). The tris–HCl/glycine buffer system of Laemmli (1970) was used. Electrophoresis was carried out at 30 mA/gel and 18°C for 45 min after the tracking dye had migrated off the gel. Gels were stained overnight with 12% (w/v) trichloroacetic acid solution containing 5% (v/v) ethanol and 0.05% (w/v) Coomassie Brilliant Blue R-250. De-staining was carried out with tap water.

EST-SSR molecular analysis

H. chilense (line H1), *H. vulgare* cv. Betzes, and common wheat CS were used for the initial transferability study. A set of 14 EST-SSR markers (coded k0) developed by Nasuda et al. (2005) and located on *H. vulgare* chromosome 1H were tested for amplification of *H. chilense* DNA. The CS + $1H^{ch}$ line was used to locate markers showing polymorphism between *H. chilense* and hexaploid wheat on chromosome $1H^{ch}$,

and the wheat-*H. chilense* 1H^{ch}S line was used to allocate markers to the short arm of chromosome 1H^{ch}. The sub-arm location of polymorphic markers was determined by noting presence and absence of each EST-SSR marker allele on the two (CS + del1H^{ch}-1 and CS + del1H^{ch}-2) terminal deletion lines. In addition, we tested 29 EST-SSR primer pairs (coded BAWU) that had previously been assigned to chromosome 1H^{ch} (Hagras et al. 2005), but not to their respective chromosome arms.

Total genomic DNA was isolated from young frozen leaf tissue using the Plant DNAzol® method (Invitrogen) following the protocol of Lin and Kuo (1998). The concentration of each sample was estimated using a NanoDrop 1000 Spectrophotometer (Thermo Scientific).

Amplifications were carried out using a TGradient Biometra® PCR thermocycler (Biometra GmbH, Göttingen, Germany). PCR was performed in 96-well plates, each well containing 10 µl of reagent mixture composed of 30 ng of template DNA, 0.5 µM of forward and reverse EST-SSR primers, 1 µl of 10× buffer, 0.8 µl of dNTP mixture (2.5 mM each), 0.25 U of *Taq* DNA Polymerase (Promega Madison, WI, USA) and 2.0 mM $MgCl_2$. PCR conditions for EST-SSR markers followed the touchdown protocol of Nasuda et al. (2005) and Hagras et al. (2005).

Amplified products were separated in 2% agarose gels. Electrophoresis was performed at 110 V and maximum current for 3 h. Gels were stained with ethidium bromide and photographed under UV light using Kodak Digital Science 1D software (version 2.0). The molecular weights of the markers were checked by the comparative molecular-weight-marker ϕX-174 DNA/*Bsu*RI (*Hae*III) Marker, 9, purchased from Fermentas Life Sciences (Hanover, USA) also using Kodak Digital Science 1D software (version 2.0). All primers used in this study were synthesized by Sigma-Genosys, Pampisford, UK.

Results

Sub-arm location of prolamin genes

Figure 1 shows the glutenin (a) and gliadin (b) electrophoregrams of the lines evaluated. Proteins derived from the *H. chilense* parent were detected in the CS + 1H^{ch} addition line (Fig. 1, lanes 2 and 3, respectively). B-LMW glutenins coded at the *Glu-H^{ch}2* and *Glu-H^{ch}3* loci, and C-LMW glutenins coded at the *Glu-H^{ch}4* locus derived from the *H. chilense* line H7 (Fig. 1, lane 5) were absent in the CS + del1H^{ch}-1 line (Fig. 1a, lane 4). The ω-gliadins synthesised at the *Gli-H^{ch}1* locus were also absent in this line (Fig. 1b, lane 4). Thus, these four prolamin loci are physically located in the distal 20% region of 1H^{ch}S (Table 1).

The absence of the HMW glutenin coded at the *Glu-H^{ch}1* locus in the CS + 1H^{ch}S ditelosomic addition line and its presence in the CS + del1H^{ch}-1 deletion line (Fig. 1) showed that *Glu-H^{ch}1* is located in the proximal 88% of 1H^{ch}L (Table 1). The CS + del1H^{ch}-2 deletion line showed patterns of separation of all glutenin subunits on SDS-PAGE identical to that obtained with the CS + del1H^{ch}-1 deletion line and therefore was not included in Fig. 1.

Barley EST-SSR transferability and sub-arm location

Among 14 barley EST-SSR markers (coded k0) located on chromosome 1H (Nasuda et al. 2005), 10

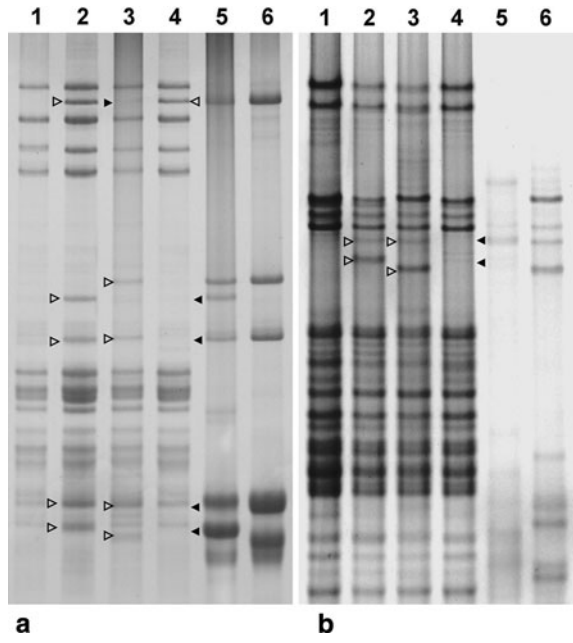

Fig. 1 **a** Separation of glutenin subunits on SDS-PAGE. **b** Acid-PAGE separation of the gliadin fraction of the same lines. *Lanes* are as follows: *1* CS, *2* CS + 1H^{ch}, *3* CS + 1H^{ch}S, *4* CS + del1H^{ch}-1, *5 H. chilense* line H7, *6 H. chilense* line H1. *White arrows* indicate presence of *H. chilense* protein; *black arrows* the absence of the same proteins

Table 1 PCR and SDS-PAGE analyses showing the presence (+) or absence (−) of EST-SSR markers and prolamin genes on chromosome $1H^{ch}$ of *H. chilense*

Marker/gene	$1H^{ch}$	$1H^{ch}S$	CS + del$1H^{ch}$-1	CS + del$1H^{ch}$-2	Sub-arm location
BAWU136	+	+	−	−	$1H^{ch}S$ (20% distal)
BAWU343	+	+	−	−	$1H^{ch}S$ (20% distal)
k02512	+	+	−	−	$1H^{ch}S$ (20% distal)
Gli-H^{ch}1	+	+	−	−	$1H^{ch}S$ (20% distal)
Glu-H^{ch}2	+	+	−	−	$1H^{ch}S$ (20% distal)
Glu-H^{ch}3	+	+	−	−	$1H^{ch}S$ (20% distal)
Glu-H^{ch}4	+	+	−	−	$1H^{ch}S$ (20% distal)
BAWU616	+	+	+	−	$1H^{ch}S$ (80% proximal)
BAWU719	+	+	+	−	$1H^{ch}S$ (80% proximal)
BAWU842	+	+	+	−	$1H^{ch}S$ (80% proximal)
k04065	+	+	+	−	$1H^{ch}S$ (80% proximal)
BAWU12	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU17	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU25	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU162	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU211	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU216	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU316	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU541	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU574	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU585	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU735	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU760	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU785	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU917	+	−	+	+	$1H^{ch}L$ (88% proximal)
k00183	+	−	+	+	$1H^{ch}L$ (88% proximal)
k04031	+	−	+	+	$1H^{ch}L$ (88% proximal)
k04150	+	−	+	+	$1H^{ch}L$ (88% proximal)
k04686	+	−	+	+	$1H^{ch}L$ (88% proximal)
Glu-H^{ch}1	+	−	+	+	$1H^{ch}L$ (88% proximal)
BAWU235	+	−	+	−	$1H^{ch}L$ (12% distal)
BAWU756	+	−	+	−	$1H^{ch}L$ (12% distal)
k04239	+	−	+	−	$1H^{ch}L$ (12% distal)
BAWU299	+	−	−	−	$1H^{ch}L$ (<12% distal)
BAWU532	+	−	−	−	$1H^{ch}L$ (<12% distal)
k03876	+	−	−	−	$1H^{ch}L$ (<12% distal)
k04015	+	−	−	−	$1H^{ch}L$ (<12% distal)
k04311	+	−	−	−	$1H^{ch}L$ (<12% distal)

(71%) gave reliable amplifications in *H. chilense* and all were polymorphic between *H. chilense* and common wheat. All 10 markers amplified a single product in *H. chilense*, but did not amplify in common wheat. These polymorphic EST-SSR markers amplified in the same homoeologous linkage group as in *H. vulgare* as revealed by the analysis of the CS + $1H^{ch}$ addition line (Table 1). Therefore, these markers

were suitable for *H. chilense* chromosome $1H^{ch}$/wheat introgression.

Of the 29 EST-SSR markers (coded BAWU) previously identified in 1H chromosome (Hagras et al. 2005), we successfully amplified 23 from chromosome $1H^{ch}$, but failed to confirm the remaining six because there was no clear PCR amplification in *H. chilense* and/or the $1H^{ch}$ addition line. Using the 10 EST-SSR k0 and 23 BAWU EST-SSR primer sets, we conducted PCR analysis for the presence or absence of the 33 EST-SSR markers in the CS + $1H^{ch}S$ ditelosomic addition line. Seven (2 k0 and 5 BAWU) (21%) and 26 (8 k0 and 18 BAWU) (79%) markers were located on the $1H^{ch}S$ and on the $1H^{ch}L$ arms, respectively (Table 1).

The sub-arm positions of the seven EST-SSR loci on $1H^{ch}S$ were determined using the CS + del$1H^{ch}S$-1 line with a 20% terminal deletion. Three of the seven markers failed to amplify a product showing they are located in the terminal region. The remaining four markers did amplify product on the CS + del$1H^{ch}$-1 deletion line and hence they are located on the proximal 80% region of $1H^{ch}S$.

Sub-arm positions of the EST-SSR markers in $1H^{ch}L$ were determined using the CS + del$1H^{ch}$-1 and CS + del$1H^{ch}$-2 deletion lines. The deleted distal fragments in the $1H^{ch}L$ arm in these two lines were estimated to represent 12% of the arm. Among the 26 EST-SSR markers located on $1H^{ch}L$, 18 amplified products in both CS + del$1H^{ch}$-1 and CS + del$1H^{ch}L$-2 showing that these loci are located in the proximal 88% region of the long arm (Table 1). Three markers (BAWU235, BAWU756 and k04239) amplified products in the CS + del$1H^{ch}$-1 line, but were absent in CS + del$1H^{ch}L$-2. Although the $1H^{ch}L$ long arm in the two deletion lines are not distinguishable cytologically, the deleted fragment in CS + del$1H^{ch}$-1 must be less than 12%. Five markers were absent from both deletion lines and hence they are located less than 12% from the distal end of $1H^{ch}L$. The sub-arm distribution of all 33 EST-SSR

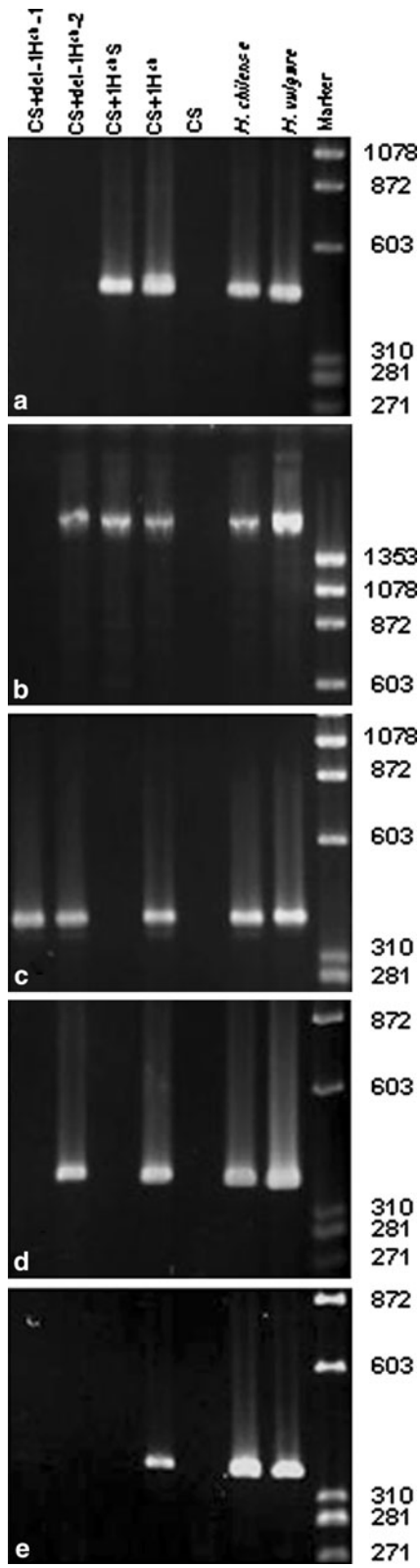

Fig. 2 PCR amplification profiles used for sub-arm locations of five EST-SSR markers on *H. chilense* chromosome $1H^{ch}$. **a** BAWU343 located in the 20% distal region of the short arm, **b** BAWU719 located in the 80% proximal region of the short arm, **c** k04150 located in the proximal 88% region of the long arm, **d** BAWU756 located in the 12% distal end of the long arm, **e** k04311 located the distal region of the long arm slightly less than 12%

markers on five different regions of chromosome $1H^{ch}$ is given in Table 1. Examples of amplification products of EST-SSRs in different $1H^{ch}$ sub-arm regions are shown in Fig. 2.

Discussion

The *H. chilense* cytogenetic stocks used in this study enabled the locations of 38 (5 prolamin and 33 EST-SSR) marker loci to be allocated to sub-arm regions of chromosome $1H^{ch}$. Glutenin (*Glu-H^{ch}2*, *Glu-H^{ch}3*, *Glu-H^{ch}4*) and gliadin (*Gli-H^{ch}1*) loci were located in the distal 20% region of $1H^{ch}$S. In wheat, by physically mapping gene markers on an array of wheat chromosome deletion lines, it was shown that loci for glutenins (*Glu-3*) and gliadins (*Gli-1* and *Gli-2*) were present in a region around fraction length (FL) 0.80 of the short arm of wheat homoelogous group 1 chromosomes (Sandhu and Gill 2002). The present results indicated that these loci are physically located at similar homoeologous positions in wheat and *H. chilense* and that synteny in grain quality genes is conserved between the two species. Similarly, high molecular weight glutenin subunits encoded at the *Glu-1* loci were physically mapped in a region around FL 0.70 of the long arms of homoelogous wheat chromosomes 1A, 1B and 1D (Erayman et al. 2004). In barley, *Hor-3* was physically mapped in a region between FL 0.47 and FL 0.72 of the 1HL arm (Taketa et al. 2002). Compared to homoeologous genes in wheat (*Glu-1*) and barley (*Hor-3*), the position of *Glu-H^{ch}1* in the proximal 88% region of the $1H^{ch}$L arm indicates synteny between *H. chilense* and both wheat and barley for these prolamin loci.

In the current study, 71% of the barley chromosome EST-SSR 1H markers produced amplicons in *H. chilense* and all detected polymorphic loci in chromosome $1H^{ch}$ added to common wheat. The level of transferability of barley EST-SSR markers observed in this study is similar to that found by Castillo et al. (2008) who reported 66% transferability of barley EST-SSRs to *H. chilense*. The present level of polymorphism detected with EST-SSR is higher than with genomic SSRs (Said and Cabrera 2009; Castillo et al. 2010), confirming the general observation that among PCR-based methods, locus-specific EST-SSR markers are highly transferable across species (Thiel et al. 2003; Varshney et al. 2005). From this study, the number of molecular markers available for chromosome $1H^{ch}$ was increased by 10 polymorphic EST-SSR. They are high quality, reproducible markers producing intense amplification using agarose gels and are therefore suitable for rapid detection of the $1H^{ch}$ chromosome or segments of it.

A total of 33 EST-SSR (10 coded k0 and 23 coded BAWU) marker loci were assigned to different chromosome regions of chromosome $1H^{ch}$. Seven markers (21.2%) were allocated to the $1H^{ch}$S arm and, of these, three (9.1%) were in the distal 20% region and four (12.1%) were on the proximal 80% region. The 26 loci (78.8%) allocated to $1H^{ch}$L were distributed across three different regions: 18 (78.8%) in the proximal 88%, 3 (9.1%) in the distal 12%, and 5 (15.2%) in a region between the other two.

In conclusion, deletions in the $1H^{ch}$ chromosome added to common wheat were shown to be useful for determining the sub-arm locations of EST-SSR and prolamin loci. Although, additional deletion lines are needed for more precise localization of marker loci, the division of the $1H^{ch}$ chromosome into five different sub-arm regions could facilitate the identification of molecular markers linked to genes of agronomic interest and isolation of these genes for use in crop improvement. Such lines may also enable transfer of potentially useful genes to wheat.

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