



Full Length Article

Evolution of Maize Landraces in Southwestern China: Evidence from B Chromosomes

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Abstract

To explore the evolution of maize landraces in Southwestern China, 30 maize landrace populations were examined to characterize the B chromosomes (Bs). Eighteen populations displayed numerical polymorphisms and a total of 487 Bs were identified. The number of Bs per individual varied from 0 to 2, especially 0 and 1. The percentage of individuals possessing Bs within populations ranged from 0 to 90%. Three types of B chromosomes were identified: a subtelocentric B (B_{ST}), a metacentric B chromosome (B_T) and a small B minichromosome (B_M). The C-banding of B_{ST} and B_T was highly heterochromatic and easily distinguished from A chromosomes (As) following the conventional C-banding methodology, whereas heterochromatin can be observed in a more condensed or dispersed state along both Bs and As. The number of C-bands in the As and numerical B polymorphisms were associated. The mean C-band number varied from 11.0 to 20.6 in the 0B class, 10.8–18.6 in the 1B class and 10.5–18.6 in the 2B class, showing a negative trend between the B chromosome and C-band number. Higher frequencies of B chromosomes, plants with Bs, and all three B chromosome variants were detected in Sichuan landrace populations, thus Sichuan is likely the origin of landraces in southwest China. © 2017 Friends Science Publishers

Keywords: *Zea mays*; Population; Polymorphism; C-band; Geographic centre

Introduction

The basic diploid chromosome of maize (*Zea mays* L.) is comprised of 20 A chromosomes (As). In addition to this normal chromosome complement, sometimes additional chromosomes are found, called B chromosomes (Bs). The differences between As and Bs are as follows: (i) Bs are highly heterochromatic and nondisjoin at the second pollen mitosis (Carlson and Chou, 1981; Cheng *et al.*, 2016), (ii) male gametes, containing Bs, preferentially fertilize the egg (Rosato *et al.*, 1998), (iii) B chromosomes do not exhibit a phenotype, except at high numbers (Huang *et al.*, 2016), (iv) and Bs enhance recombination as they accumulate in the genome (Lin, 1978; Ferro *et al.*, 2016).

Since the discovery of maize B chromosomes by Kuwada (1925), they have been intensively studied. Bs are distributed widely in native populations, commercial varieties, and inbred lines (Rosato *et al.*, 1998) where they can vary in frequency, size, and morphology. The standard Bs in maize are subtelocentric and smaller than any of the A chromosomes (Randolph, 1941). A large variety of maize populations have been identified to show from 0 to 6 of Bs, with numerical variants of Bs leading to differences in intraspecific genome-size (Yao *et al.*, 2015a). It is a matter of debate with respect to the maintenance of Bs in maize

(Huang *et al.*, 2016), as Bs are also called selfish entities, derived from As, and retain a polymorphism by a series of accumulation mechanisms such as nondisjunction, preferential fertilization, and enhanced pollen transmission (Chiavarino *et al.*, 2000). Rosato *et al.* (1998) reported that maize Bs accounted for approximately 4% of the total chromosome volume and an association exists between the number of Bs and the size of heterochromatic knobs, which can mask the contribution of Bs to total genome size. Negative correlations were found between the number of Bs and the amount of heterochromatin in both North American and Italian populations (Bianchi *et al.*, 1963). Cytogenetic studies conducted by Rosato *et al.* (1998) in 21 native populations from northwestern Argentina implied a positive correlation between altitude and the mean number of Bs per plant. In addition, Bretting and Goodman (1998) revealed a generally inverse correlation between Bs and altitude in 300 Mesoamerican populations, but Porter and Rayburn (1990) did not provide evidence for this association. With RAPD markers, Kao *et al.* (2015) and Liu *et al.* (2015) supported an A-chromosome origin of the B-chromosome.

Generally only one form of B chromosome is found, although variants can come in fairly frequently resulting in metacentric chromosomes, subtelocentric chromosomes, and minichromosomes (Jones and Houben, 2003). Ferro *et*

al. (2003) used four *Astyanax scabripinnis* populations to analyze B chromosome characteristics and identified three forms of Bs, a metacentric macrochromosome, a submetacentric, and a metacentric chromosome. On the basis of the FISH in B73 maize lines possessing Bs, Lamb *et al.* (2005) noted that normal Bs consist of a diminutive short arm, a centromere, a proximal heterochromatin block, a stretch of euchromatin, followed by four blocks of heterochromatin and the distal-most euchromatin. No difference was found in the buoyant densities of DNA from plants with and without Bs in maize, indicating a similar GC content (Chilton and McCarthy, 1973). Maize Bs are described as heterochromatic with many highly repetitive sequences, which includes transposons present in both As and Bs (Lamb *et al.*, 2007). Lin *et al.* (2014) suggested that the maize B-chromosome harbors few transcriptionally active sequences, although it may influence the transcription of As. Huang *et al.* (2016) suggested that as the maize B chromosome increases in copy numbers, it has a stronger influence on A-genome transcription. B chromosome behavior in maize exhibits great diversity among maize varieties (Jones, 2012; Yao *et al.*, 2015a).

Southwest China contains the main distribution of maize landraces in China. According to a field survey from 2005 to 2015, farmer-saved landraces have been cultivated mainly in the high-altitude areas of Sichuan, Chongqing, Yunnan, and Guizhou provinces (Yao *et al.*, 2015a). Variations in Bs are recognized as genetic diversity, and polymorphisms in maize Bs are one of the prominent components in germplasm characterization and conservation. Despite much molecular work on Bs, the significance of Bs in native populations remains unclear. The goals of this study were to (i) estimate B chromosome polymorphisms based on their occurrence, morphology, and frequency in maize landraces from Southwest China, (ii) provide evidence for the evolution of maize landraces from Southwest China, and (iii) infer the geographical origin of landraces in southwest China.

Materials and Methods

Plant Materials

Based on their geographical distribution, seeds of 30 maize landrace populations were sampled from Sichuan, Chongqing, Yunnan, and Guizhou province in southwestern China, which were used as the tissue source for all experiments. This sampling was done by the authors from native populations of maize landraces in 2005–2015. The geographical distribution of the samples are illustrated in Fig. 1. Native populations have been sustained by open pollination and individuals were randomly sampled from mixed populations. The seeds and voucher specimens were deposited in Crop Genetics and Breeding Research Centre, Yangtze Normal University. The numbers and localities of landrace populations are presented in Table 1.

Chromosomal Characterization and Banding

Root tips from 50 individual seedlings for each landrace population were pretreated in 0.1% α -bromonaphthalene at 25°C for 2 h followed by fixation in 1:3 (acetic acid: ethanol), and storage in 70% ethanol at 4°C. The fixed root tips were dipped in distilled H₂O at 5°C for 15 min for low permeability treatment before they were transferred to a digestion buffer (1% cellulose, 2% pectolyase, in 1 × citric buffer) and incubated in a water bath at 36°C for 45 min. The digested root tips were then rinsed in 70% EtOH, followed immediately by a replacement with 25 μ L of 100% acetic acid. Secondary root meristems with varying numbers of Bs were stained and crushed in 1% aceto-orcein.

Slides were C-banded using conventional Giemsa staining with modifications introduced by Porter and Rayburn (1990) and stained with 2% Giemsa solution in 0.01 phosphate buffer (pH 7.0). The slides were cleared in xylene for 15 min after drying overnight. Ten cells from 10 individuals per landrace population were observed cytologically and scored for the mean number of C-bands present.

Identification and Classification of B Chromosomes

The B chromosome may be cytologically identified as the smallest chromosome in addition to the normal karyotype, and has a size slightly larger than half of the smallest A complement, chromosome 10 (Carlson and Rosemon, 1992). Fifty individuals per landrace population were sampled, and 10 cells from the shoot growth area of root tips were scored for the presence of Bs under a microscope. A total of 15,000 cells (30 × 50 × 10) in mitotic metaphase were analyzed. If Bs were not found in 10 × 50 cells from a landrace population, it was defined as the 0B class i.e., a population without Bs. Accordingly, populations with 1B and 2Bs in a cell were placed in the 1B and 2B class, respectively (Li and Zhang, 1996).

Results

Forms and Size of B Chromosomes

The 30 populations of maize landraces from southwest China had a standard karyotype consisting of $2n = 20$ chromosomes with three metacentric, six submetacentric, and one subtelo centric chromosome pairs. Bs in maize landrace populations may be cytologically identified as they are smaller than any of the standard chromosome complements (As) (Longley, 1927; Randolph, 1941; Chiavarino *et al.*, 1995). Three forms of Bs were detected: a metacentric B chromosome (B_T), morphologically similar to first chromosomal pair of the standard karyotype (Fig. 2A), a subtelo centric B (B_{ST}) identical in size to B_T (Fig. 2B), and a small B minichromosome – B_M (Fig. 2C). Maize landrace populations from Sichuan possessed three forms of Bs.

Table 1: Locality, B chromosome frequency, and mean C-band numbers for landrace populations

NO.	Locality (County, Province)	The individual number with different B Nos.			Total	Individuals with Bs (%)	Mean no. of C-bands
		0	1	2			
CQ08	Fengdu, Chongqing, China	37	13	0	50	26	15.3
CQ22	Shizhu, Chongqing, China	11	39	0	50	78	13.5
CQ34	Wushan, Chongqing, China	18	30	2	50	64	13.8
CQ44	Fengdu, Chongqing, China	48	2	0	50	4	16.2
CQ61	Fengdu, Chongqing, China	50	0	0	50	0	18.2
CQ67	Chengkou, Chongqing, China	47	3	0	50	6	14.0
CQ83	Chengkou, Chongqing, China	50	0	0	50	0	13.3
SC09	Neijiang, Sichuan, China	46	4	0	50	8	10.8
SC11	Danba, Sichuan, China	8	31	11	50	84	12.4
SC17	Neijiang, Sichuan, China	22	28	0	50	56	12.8
SC35	Junlian, Sichuan, China	43	7	0	50	14	16.1
SC43	Qingshen, Sichuan, China	21	29	0	50	58	13.7
SC56	Junlian, Sichuan, China	50	0	0	50	0	15.6
SC57	Junlian, Sichuan, China	41	9	0	50	18	13.6
SC68	Dazhu, Sichuan, China	50	0	0	50	0	12.2
SC72	Pingshan, Sichuan, China	38	12	0	50	24	19.4
GZ03	Wengan, Guizhou, China	29	21	0	50	42	17.8
GZ08	Bijie, Guizhou, China	13	37	0	50	74	12.7
GZ17	Shiqian, Guizhou, China	50	0	0	50	0	18.5
GZ21	Panxian, Guizhou, China	50	0	0	50	0	15.6
GZ28	Huairan, Guizhou, China	50	0	0	50	0	17.3
GZ35	Wangmo, Guizhou, China	50	0	0	50	0	16.9
GZ39	Huairan, Guizhou, China	50	0	0	50	0	15.3
GZ52	Huairan, Guizhou, China	50	0	0	50	0	11.0
GZ57	Ziyun, Guizhou, China	50	0	0	50	0	20.6
YN05	Luxi, Yunnan, China	9	39	2	50	82	10.5
YN12	Xuanwei, Yunnan, China	12	36	2	50	76	18.6
YN26	Longchuan, Yunnan, China	5	39	6	50	90	13.9
YN51	Chengjiang, Yunnan, China	50	0	0	50	0	15.0
YN65	Chengjiang, Yunnan, China	8	42	0	50	84	13.2
Total		1056	421	23	1500		447.8

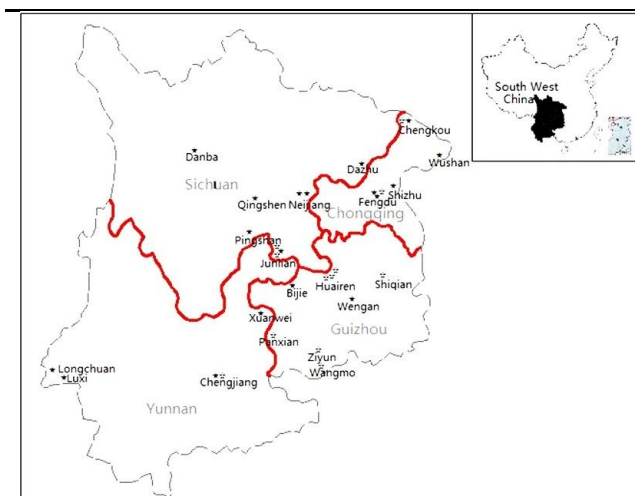


Fig. 1: Geographic distribution of the thirty populations of maize landraces from southwest China. ★ populations with Bs and ☆ populations without Bs

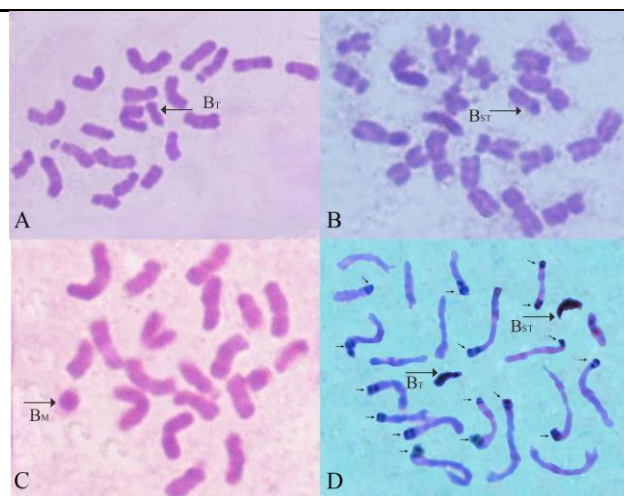


Fig. 2: Photomicrographs of mitotic chromosomes in maize landrace populations. A. A cell with a metacentric B chromosome (B_T); B. a cell with a subtelocentric B (B_{ST}); C. a cell with a small B minichromosome (B_M); D. C-bands in chromosomes of a cell with B_T and B_{ST}

In five populations of maize landraces from Yunnan both B_T and B_{ST} forms were found, while B_T and B_M were identified in seven populations of maize landraces from Chongqing. Only B_{ST} was found in the nine populations from Guizhou.

In comparison to the metacentric pair of the standard karyotype, measurements conducted on the 45 cells with Bs estimated a relative length of 34–52% for the B_T form, 32–58% for B_{ST} form, and 13–18% for the B_M form, and

relative lengths for B_T, B_{ST} and B_M were on average 43, 45 and 15%, respectively (Table 2). Size variation within the same B chromosome type is likely the result of differential chromosome condensation.

B Chromosome Frequency

As shown in Table 1, 18 of 30 populations of maize landraces from southwest China contained Bs, corresponding to 60% of the samples analyzed. A total of 487 Bs were identified in the samples from 30 populations of maize landraces. The number of Bs per individual varied from 0 to 2, with the predominant quantities being 0 and 1. The percentage of individuals possessing Bs among populations varied from 0 to 90%. B chromosome polymorphisms were also detected in the 30 populations. B_{ST} was the most frequent form accounting for 67% of the Bs in the populations, followed in turn by B_T and B_M forms corresponding to 19% and 14%, respectively. Landrace populations with Bs were distributed in all four regions (Fig. 1). Among the 18 populations with Bs, seven, five, four, and two were distributed in Sichuan, Chongqing, Yunnan, and Guizhou, respectively. In addition, the populations sampled from Sichuan, Chongqing, and Yunnan all had 2Bs, whereas only 1B chromosome was found in the Guizhou populations.

B Chromosome Structure

C-bands in As and Bs are diagramed in Fig. 2D, B_T and B_{ST} were highly heterochromatic and easily distinguished from A chromosomes with conventional C-banding, as described earlier (Porter and Rayburn, 1990). The heterochromatin was observed in a more condensed or more dispersed state along both Bs and As, since chromosomal condensation was variable. However, heterochromatin was difficult to visualize in the shorter B_M.

The number of C-bands in the A chromosome set were

detected to determine whether the variation of this structure can account for numerical polymorphism for Bs. The mean number of C-bands in the A chromosomes varied from 11.0 to 20.6 in 0B class, 10.8 to 19.4 in 1B class, and 10.5 to 18.6 in 2B (Table 1). There was a noticeable negative association with C banding as Bs increased in copy numbers.

Discussion

B Chromosome Numerical Polymorphism

A high frequency of individuals with Bs was identified in populations of maize landraces from southwest China. Out of a total of 1500 individuals, 421 possessed an average of 1.11 Bs ranging from 0 to 2, accounting for 28.07% of individuals. Eighteen of the 30 landrace populations studied exhibited a numerical polymorphism in B chromosome frequencies, while the five landrace populations from Yunnan had a maximum frequency of 80%. Longley (1938) identified 66 individuals with Bs from 431 individuals, the frequency of individuals with Bs was 15.3%. Numerical polymorphism for Bs in Mexican races of maize was analyzed by Kato (1976), who found that in 46 of 94 populations from 9 Mexican maize races had Bs, and Bs were present in 86 out of 531 individuals. When compared with the previous studies on numerical polymorphisms for Bs in native populations of maize, a higher frequency of Bs are found in the maize landrace populations from southwest China in this study, both in individuals and populations.

Polymorphism for B Chromosome

The three B chromosome forms B_T, B_{ST} and B_M were identified in the 30 populations of maize landraces, each of which was homogenous across the population in size, shape, and heterochromatic nature. The B_{ST} was the predominant form identified in landrace populations. B_{ST} were widely distributed in other maize population such as native

Table 2: B chromosomes compared with chromosome 1 of the A chromosome set in forty-five cells

S. No.	1 st A				Metacentric B				1 st A				Submetacentric B				1 st A				Spot-shape B			
	TL	TL	AR	RL	TL	TL	AR	RL	TL	TL	AR	RL	TL	TL	AR	RL	TL	TL	AR	RL	TL	TL	AR	RL
1.	8.10	2.92	1.20	36	6.45	3.30	1.95	51	6.00	0.90	1.00	15												
2.	5.32	2.45	1.16	46	5.29	2.11	1.89	40	5.21	0.92	1.00	18												
3.	5.90	2.23	1.24	38	7.42	3.56	1.80	47	7.02	0.88	1.00	13												
4.	6.48	2.95	1.20	46	6.05	3.13	1.96	52	6.75	0.91	1.00	14												
5.	5.45	2.24	1.08	41	5.26	2.54	1.77	48	5.53	0.86	1.00	16												
6.	5.82	1.96	1.10	34	6.67	2.64	1.84	40	5.73	0.90	1.00	16												
7.	6.34	3.02	1.27	48	4.57	2.39	1.93	52	5.68	0.89	1.00	16												
8.	7.41	3.10	1.22	42	7.37	3.21	2.13	44	6.38	0.90	1.00	14												
9.	6.70	3.31	1.25	49	7.15	2.57	2.06	36	6.47	0.91	1.00	14												
10.	7.12	3.28	1.15	46	6.81	2.20	2.12	32	5.90	0.90	1.00	15												
11.	8.05	4.21	1.17	52	6.75	2.79	2.20	41	5.92	0.91	1.00	15												
12.	6.48	2.75	1.06	42	6.82	2.60	2.18	38	6.37	0.88	1.00	14												
13.	6.30	2.27	1.17	36	5.85	3.06	1.90	52	7.05	0.91	1.00	13												
14.	5.77	2.28	1.21	40	5.46	3.14	1.88	58	5.60	0.90	1.00	16												
15.	7.56	3.30	1.30	44	6.60	2.47	2.14	37	6.91	0.90	1.00	13												
Mean	6.59	2.82	1.19	43	6.30	2.78	1.98	45	6.17	0.90	1.00	15												

1st A = the first A chromosome; TL, AR, and RL represent total length (μm), arm ratio, and relative length (%), respectively

populations from Northern Argentina, Latin American and Mexican races of maize, and the inbred line (Chien *et al.*, 2014; Houben *et al.*, 2014), implies a remote origin in maize species. It might be hypothesized that B_{ST} represents an ancestral B chromosome in maize, whereas the B_T and B_M are variants of the B_{ST} form (Chien *et al.*, 2014; Houben *et al.*, 2014). In this study, B_T and B_M were identified only in 19% and 14% of the populations, respectively. The low frequencies of the B_T and B_M forms, which were also exclusive forms in many other maize populations, indicate their recent origin.

B_{ST} and B_T were similar in size with a close relative length corresponding to the first metacentric pair of the karyotype with the mean relative length being 43 and 45%, respectively. On the basis of their C-band composition, the B_T and B_{ST} forms were both heterochromatic and GC-rich, indicating that B_{ST} shared a certain similarity with the ancestral form. However, the B_M was small and round, with a reduced relative length in comparison with that of the B_{ST} and B_T.

B Chromosome and C-band in A Chromosome Set

Bs do not pair with As at meiosis and are defined as non-homologous (Birchler and Han, 2013). Typically the C-band number is equal to double the total the knob number of chromosomes (Porter and Rayburn, 1990). A negative correlation between the B chromosome and knob number was reported by Longley (1938), who observed that a plant with more Bs had fewer knobs than plants with less Bs. But investigations conducted on 12 Arizona maize populations by Porter and Rayburn (1990) did not support such a correlation. On the whole, the 2B class was observed to possess fewer mean C-bands in As than both the 0B and 1B class in thirty 30 populations of maize landraces from southwest China. This negative correlation agrees with the correlation between the number of Bs and the amount of heterochromatin observed by Peng and Cheng (2011), although this correlation was not expected. In the GZ52 landrace population, 11 C-bands were seen in the A chromosome set, while Bs were not identified. On the contrary, 10.5 C-bands in As were detected in YN05 landrace with 82 Bs. This uniformity is probably due to the irregular inheritance of Bs and (or) a limited number of individuals sampled. The maize B chromosome has a selfish inheritance characterized by nondisjunction at the second pollen mitosis, univalent survival in meiosis, and preferential fertilization of the egg, which may be responsible for the different numbers of B chromosomes in maize populations (Masonbrink and Birchler, 2010; Masonbrink *et al.*, 2012, 2013).

Evolution of Maize Landraces in Southwestern China

A change in numbers and forms of parasitic Bs occurs concurrently with the host evolution. Through the analysis

of the form and number of Bs distributed over different territories, it is possible to get information on the origin and evolution of a species. Bs of maize were first discovered in the ancient races native to central Mexico. Focusing on chromosomal knobs and Bs, Kato and collaborators undertook a formal study of chromosome morphology and number among the maize races (Kato, 1976). Liu (2002) described the geographic distribution in North America, form as well as numerical polymorphisms of Bs in ancient races and their derivatives, noting that the central Mexico is a geographic center of maize. The B chromosome in maize has spread from Mexico through North America along three major paths: (1) the west path is the border of Mexico and Guatemala north to pacific coast, (2) the middle path starts from the central Mexico and goes north to the American border and (3) the east path spreads northward along the east coast of Mexico (Liu, 2002). During this migration, a loss of Bs in the ancient races was demonstrated due to the integration of exotic germplasm (Liu, 2002; Kato, 1976). Bs were distributed intensively in the central Mexico followed by declining frequencies of Bs in the derivatives during the migration.

Maize was recorded to be cultivated in China since 1511. There are two likely pathways for its introduction: migration from India to Sichuan Province via Tibet and an east coast migration from the southeast coastal area to inland regions in China (Liu, 2002). Evidence inferred from genetic diversity supports the hypothesis that maize landraces in southwestern China were first introduced to Sichuan (Yao *et al.*, 2015b). The B chromosome polymorphism analyses present supporting evidence for this origin and migration of landraces in southwestern China. First, a higher frequency of Bs was detected in landrace populations from Sichuan with seven out of nine populations containing Bs. Second, these populations also retained a relatively high frequency of plants with Bs compared with those in the other regions in southwestern China. Third, all the three types of Bs were found in the Sichuan populations. Hence, it can be deduced that Sichuan is the geographic origin of landraces in southwest China. It is likely that they were first introduced to Sichuan from India, through Tibet, and spread from Sichuan to the adjoining areas. During the migration from Sichuan, a portion of the Bs were lost, thus resulting in the intensive distributions of Bs in Sichuan and their discordant distributions in the other regions.

Conclusion

We analyzed 30 populations of maize landraces from southwest China for B chromosome polymorphisms. 487 Bs in total were identified in the samples with the number of Bs per individual varying from 0 to 2 and the percentage of individuals with Bs ranging from 0 to 86%. Three types of Bs were identified (B_{ST}, B_T and B_M). B_{ST} and B_T were similar in size with the mean relative length being 43 and

45%, respectively. They shared similarity with the ancestral form. The mean C-band number varied from 11.0 to 20.6 in the 0B class, 10.8 to 18.6 in the 1B class, and 10.5 to 18.6 in 2B class, thus showing a negative correlation between the B chromosomes and C-band number. It can be inferred that Sichuan is the geographic center of landraces from southwest China.

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