

Distribution of the photoperiod insensitive *Ppd-D1a* allele in Chinese wheat cultivars

F. P. Yang · X. K. Zhang · X. C. Xia · D. A. Laurie · W. X. Yang · Z. H. He

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Abstract Photoperiod response is of great importance for optimal adaptation of bread wheat cultivars to specific environments, and variation is commonly associated with allelic differences at the *Ppd-D1* locus on chromosome 2D. A total of 926 Chinese wheat landraces and improved cultivars collected from nine

wheat growing zones were tested for their genotypes at the *Ppd-D1* locus using allele-specific markers. The average frequency of the photoperiod-insensitive *Ppd-D1a* allele was 66.0%, with the frequencies of 38.6 and 90.6% in landraces and improved cultivars, respectively. However, the *Ppd-D1a* allele was present in all improved cultivars released after 1970 except for spring wheats in high latitude northwestern China, and winter wheats in Gansu and Xinjiang. The presence of the *Ppd-D1a* allele in landraces and improved cultivars increased gradually from north to south, illustrating the relationship between photoperiod response and environment. *Ppd-D1a* in Chinese wheats is derived from three sources, Japanese landrace Akagomughi and Chinese landraces Mazhaimai and Youzimai. The current information is important for understanding the broad adaptation of improved Chinese wheat cultivars.

F. P. Yang and X. K. Zhang contributed equally to this work.

F. P. Yang · W. X. Yang
Crop Research Institute, Gansu Academy of Agricultural Sciences, Lanzhou 730070, Gansu, China

F. P. Yang · X. K. Zhang · X. C. Xia (✉) · Z. H. He (✉)
Institute of Crop Science, National Wheat Improvement Center/The National Key Facility for Crop Gene Resources and Genetic Improvement, Chinese Academy of Agricultural Sciences (CAAS), 12 Zhongguancun South Street, Beijing 100081, China
e-mail: xiaxianchun@caas.net.cn

Z. H. He
e-mail: z.he@cgiar.org

X. K. Zhang
College of Agronomy, Northwest Sci-Tech University of Agriculture and Forestry, Yangling, Shaanxi 712100, China

D. A. Laurie
Crop Genetics Department, John Innes Centre, Norwich Research Park, Colney, Norwich NR4 7UH, UK

Z. H. He
CIMMYT China Office, C/O CAAS, Zhongguancun South Street, Beijing 100081, China

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Introduction

The adaptation of common wheat (*Triticum aestivum* L.) cultivars to diverse environmental conditions is greatly influenced by flowering time (Whitechurch and Slafer 2002), which is mainly determined by three groups of genes: vernalization response genes (*Vrn* genes), photoperiod response genes (*Ppd* genes) and

developmental rate genes (earliness per se, *Eps* genes) (Snape et al. 2001). The first two groups of genes are environment-dependent, whereas the third is largely environment-independent. Photoperiod response in wheat is described as sensitive when timely flowering occurs only in long days, and insensitive when flowering occurs in either long- or short-day environments. Photoperiod response is closely associated with adaptability and grain yield in European and Canadian wheat cultivars (Martinic 1975; Hunt 1979; Worland et al. 1994, 1998a, b). In Asia, Mediterranean and North African regions, most landraces are sensitive to photoperiod, whereas all improved cultivars with high yield potential are insensitive (Ortiz Ferrara et al. 1998). These results imply that the introduction of photoperiod insensitivity into improved wheat cultivars in these regions enhanced their adaptation to a broader range of environments than landraces with sensitivity to photoperiod.

Photoperiod response in wheat is mainly controlled by the genes *Ppd-D1* (previously designated *Ppd1*), *Ppd-B1* (*Ppd2*) and *Ppd-A1* (*Ppd3*) located on the short arms of chromosomes 2D, 2B and 2A, respectively (Welsh et al. 1973; Law et al. 1978). The dominant alleles *Ppd-D1a*, *Ppd-B1a* and *Ppd-A1a* confer photoperiod insensitivity, whereas the recessive alleles *Ppd-D1b*, *Ppd-B1b* and *Ppd-A1b* confer photoperiod sensitivity (Pugsley 1966; Dyck et al. 2004). The *Ppd-D1a* allele for photoperiod insensitivity is generally considered the most potent, followed by *Ppd-B1a* and *Ppd-A1a* (Scarath and Law 1984). However, recent work by Tanio and Kato (2007) showed that *Ppd-B1a* could be as strong as *Ppd-D1a*.

Significant progress was recently achieved in molecular characterization of photoperiod response gene *Ppd-D1* in wheat. Beales et al. (2007) isolated homologues of barley *Ppd-H1* from a 'Chinese Spring' wheat BAC library, exploiting the collinear relationship between wheat gene *Ppd-D1* and barley gene *Ppd-H1* (Dunford et al. 2000; Turner et al. 2005). Sequence alignments from wheat cultivars with known *Ppd-D1* alleles revealed a 2,089-bp deletion upstream of the coding region in wheat cultivars with the allele *Ppd-D1a*. Subsequently, gene-specific primer sets were developed based on the sequence deletion enabling detection of allelic variants at the locus. A 414-bp fragment was amplified for the *Ppd-D1b* allele using primer pairs Ppd-D1_F and Ppd-D1_R1, whereas a 288-bp fragment

was detected for the allele *Ppd-D1a* using primer pairs Ppd-D1_F and Ppd-D1_R2 (Beales et al. 2007).

China is the largest wheat producer and consumer in the world. The wheat-growing area was divided into 10 major agro-ecological zones based on differences in wheat types, growing seasons, presence of major biotic and abiotic stresses, and responses to temperature and photoperiod in different regions (Fig. 1) (He et al. 2001; Zhuang 2003; Zhang et al. 2008). Chinese wheat is unique in several aspects. China is a secondary centre of origin for wheat, and more than 20,000 landraces are stored in the national gene bank. Cultivars are early maturing to fit the multi-cropping system, and unique products are produced and consumed. Autumn-sown winter and facultative cultivars are the most common types and are grown in the Northern China Autumn-sown Winter and Facultative Wheat Region, including the North China Plain Winter Wheat Zone (Zone I, around 4% of the total wheat area) and the Yellow and Huai Rivers Valley Facultative Wheat Zone (Zone II, 60%). Autumn-sown spring wheat is grown in the Southern China Autumn-sown Spring Wheat Region, comprising the Middle and Lower Yangtze Valley Autumn-Sown Spring Wheat Zone (Zone III, 13%), the Southwestern Autumn-Sown Spring Wheat Zone (Zone IV, 10%), and Southern Autumn-Sown Spring Wheat Zone (Zone V, <1%). Spring-sown spring wheat (7%) is grown in Spring-sown Spring Wheat Region, including the Northeastern Spring Wheat Zone (Zone VI), the Northern Spring Wheat Zone (Zone VII), and the Northwestern Spring Wheat Zone (Zone VIII). Spring-sown spring wheat and autumn-sown winter wheat regions, comprising about 6% of the area, include the Qinghai-Tibetan Plateau Spring-Winter Wheat Zone (Zone IX) and Xinjiang Winter-Spring Wheat Zone (Zone X). There are significant differences in the length of the growth cycle, temperature and photoperiod among the different regions (Jin 1983, 1997; Zhuang 2003). The growth habits and genotypes at the *Vrn-A1*, *Vrn-B1*, *Vrn-D1* and *Vrn-B3* vernalization loci in Chinese wheat cultivars were documented in a previous study (Zhang et al. 2008). It was found that some cultivars from different wheat zones carried the same vernalization genotypes, but could not be introduced from one zone to another due to inappropriate maturity. For example, some spring wheat cultivars with the semi-dominant *Vrn-D1* allele planted over a large

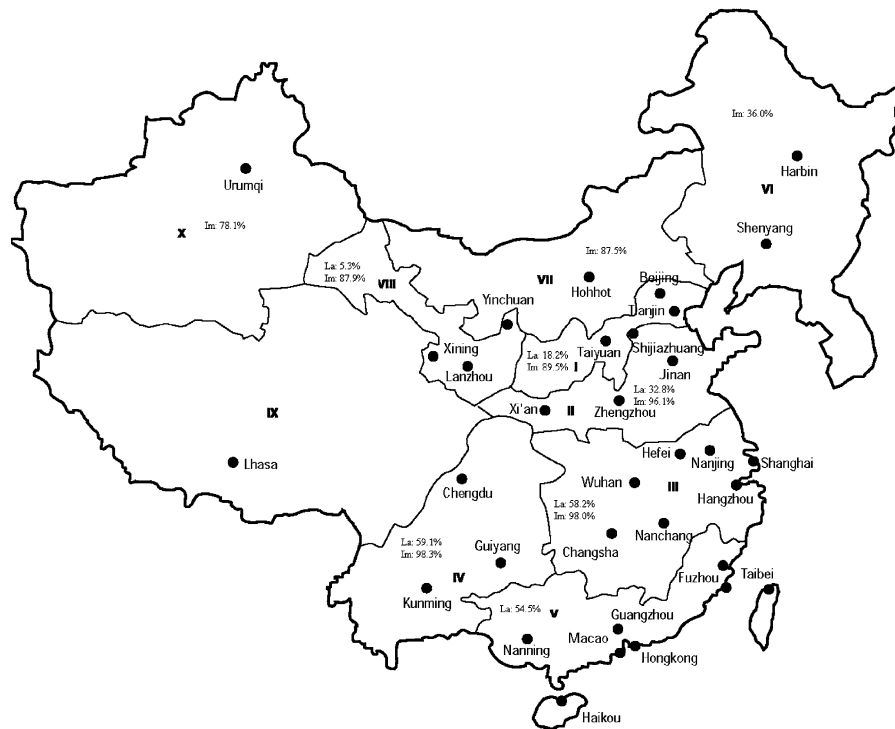


Fig. 1 Distribution of the photoperiod insensitive *Ppd-D1a* allele in landraces and improved cultivars from various wheat zones of China. I = Northern Winter Wheat Zone, II = Yellow and Huai Rivers Valleys Facultative Wheat Zone, III = Middle and Lower Yangtze Valleys Autumn-Sown Spring Wheat Zone, IV = Southwestern Autumn-Sown Spring

Wheat Zone, V = Southern Autumn-Sown Spring Wheat Zone, VI = Northeastern Spring Wheat Zone, VII = Northern Spring Wheat Zone, VIII = Northwestern Spring Wheat Zone, IX = Qinghai-Tibetan Plateau Spring-Winter Wheat Zone, X = Xinjiang Winter and Spring Wheat Zone. La and Im indicate landraces and improved cultivars, respectively

area in Zone II were too late or too early in maturity when grown in Zone III (Jin 1983, 1997; Dong and Zheng 2000; Zhuang 2003). Therefore, characterization of photoperiod response genes in Chinese wheat cultivars is crucial to fully understanding their adaptability to regional environments, and for providing important information for wheat breeding programs elsewhere using Chinese wheat germplasm.

Materials and methods

Plant materials

A total of 926 Chinese wheat cultivars collected from nine major zones were used for characterization of photoperiod genotypes at the *Ppd-D1* locus using allele-specific primers. They included 438 landraces, 475 improved cultivars and 13 introduced cultivars that had significant impacts on Chinese wheat

production and breeding after the 1940s. The number of entries from each production zone was dependent on the wheat area and the number of cultivars developed by local breeding programs (Table 1, Fig. 1). All accessions are available from the National Key Facility for Crop Genetic Resources and Improvement, Institute of Crop Science, CAAS, China.

DNA extraction and molecular marker analysis

Genomic DNA was extracted from seeds following the procedure of Gale et al. (2001). PCR primers were synthesized by Beijing Augct Biological Technology Co. Ltd. (<http://www.augct.com>) based on the report of Beales et al. (2007).

Allelic variants at the *Ppd-D1* locus were detected using three gene-specific primers in a multiplex PCR assay, in which the primer pair Ppd-D1_F (5'-ACG CCTCCCACTACTAG-3') and Ppd-D1_R1 (5'-TG TTGGTTCAAACAGAGAGC-3') produced a 414-bp

Table 1 Distribution of photoperiod insensitive allele *Ppd-D1a* in landraces and improved cultivars from various wheat zones

Zone ^a	No. of cultivars tested			No. of cultivars with <i>Ppd-D1a</i>			<i>Ppd-D1a</i> Frequency (%)		
	Landrace	Improved cultivar	Subtotal	Landrace	Improved cultivar	Subtotal	Landrace	Improved cultivar	Subtotal
I	77	57	134	14	51	65	18.2	89.5	48.5
II	134	206	340	44	198	242	32.8	96.1	71.2
III	134	51	185	78	50	128	58.2	98.0	69.2
IV	22	60	82	13	59	72	59.1	98.3	87.8
V	33	na	33	18	na	18	54.5	na	54.5
VI	na ^b	25	25	na	9	9	na	36.0	36.0
VII	na	24	24	na	21	21	na	87.5	87.5
VIII	38	33	71	2	29	31	5.3	87.9	43.7
X	na	32	32	na	25	25	na	78.1	78.1
Total	438	488	926	169	442	611	38.6	90.6	66.0

^a Zone I = Northern China Plain Winter Wheat Zone, Zone II = Yellow and Huai Rivers Valleys Facultative Wheat Zone, Zone III = Middle and Lower Yangtze Valleys Autumn-Sown Spring Wheat Zone, Zone IV = Southwestern Autumn-Sown Spring Wheat Zone, Zone V = Southern Autumn-Sown Spring Wheat Zone, Zone VI = Northeastern Spring Wheat Zone, Zone VII = Northern Spring Wheat Zone, Zone VIII = Northwestern Spring Wheat Zone, Zone X = Xinjiang Winter-Spring Wheat Zone

^b na = not available

fragment in genotypes with the photoperiod sensitive allele *Ppd-D1b*, whereas primer pair Ppd-D1_F and Ppd-D1_R2 (5'-CACTGGTGGTAGCTGAGATT-3') yielded a 288-bp fragment in those with photoperiod insensitive allele *Ppd-D1a*. PCR was performed in a Peltier PTC 200 thermal cycler (Waltham, MA), with a 20- μ l volume containing 1 \times PCR buffer with 1.5 mM of MgCl₂, 200 μ M of each of dNTPs, 5 pmol of the primer Ppd-D1_F and 2.5 pmol each of Ppd-D1_R1 and Ppd-D1_R2, 1 unit of *Taq* DNA polymerase (Takara Biotechnology Co. Ltd. Dalian, China) and 30–60 ng of template DNA. Thermocycling conditions were an initial denaturation at 94°C for 2 min, followed by 40 cycles of 30 s at 94°C, 30 s at 52°C, 1 min at 72°C, and a final extension step at 72°C for 5 min. Amplified PCR fragments were separated on a 1.2% agarose gel at 200 V for 30 min, stained with ethidium bromide, and visualized using UV light.

Results

Distribution of the *Ppd-D1a* allele in various wheat zones

Of 926 cultivars, 315 amplified a 414-bp PCR fragment, indicating the presence of the *Ppd-D1b* allele, and 611 genotypes gave a 288-bp fragment, indicative of the photoperiod-insensitive *Ppd-D1a*

allele (Fig. 2). The overall frequency of the dominant *Ppd-D1a* allele in Chinese wheats was 66.0%, but frequencies varied across regions (Table 1, Fig. 1). For example, the highest frequency was found in the Southwestern Autumn-sown Spring Wheat Zone (Zone IV, 87.8%) and the Northern Spring Wheat Zone (Zone VII, 87.5%), and the lowest was in the Northeastern Spring Wheat Zone (Zone VI, 36.0%). Among the four autumn-sown wheat zones where both landraces and improved cultivars were tested in this study, the frequency of *Ppd-D1a* in the Northern China Plain (Zone I) was much lower than that in the middle (Zone II) and southern parts (Zones III and IV).

Comparisons of *Ppd-D1* genotypes in landraces and improved cultivars among different regions

The frequency of the *Ppd-D1a* in 263 improved cultivars released in Zones I and II (94.7%) was three fold that among 211 landraces (27.5%). The frequency of *Ppd-D1a* also increased markedly from landraces (58.3%) to improved cultivars (98.2%) in Zones III and IV. For Zones VI, VII and VIII, the frequency of *Ppd-D1a* in improved cultivars was 71.9%. Generally, the frequency of the *Ppd-D1a* in landraces (38.6%) was much lower than in improved cultivars (90.6%), a consequence of the introduction

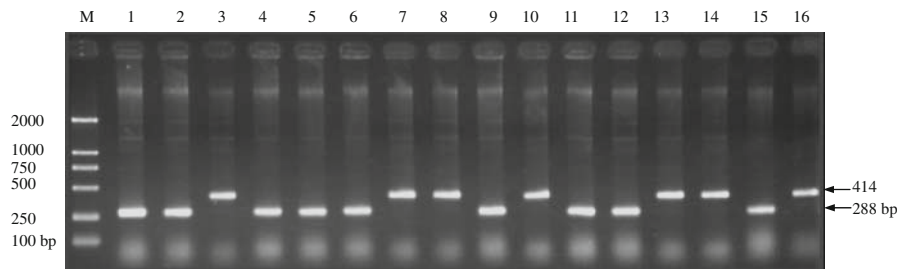


Fig. 2 Amplification products of multiplex PCR assays using primers Ppd-D1_F, Ppd-D1_R1 and Ppd-D1_R2 to detect recessive photoperiod sensitive (*Ppd-D1b*, 414-bp product) and dominant photoperiod insensitive (*Ppd-D1a*, 288-bp product) alleles at the *Ppd-D1* locus. M-DNA marker 2000, 1 Opata 85,

2 Akakomugi, 3 Chinese Spring, 4 Youzimai, 5 Mazhamai, 6 Neixiang 5, 7 Biyumai (Quality), 8 Gansu 96 (CI12203), 9 Boai 7023, 10 Villa Glori, 11 Mianyang 15, 12 Fan 6, 13 Xinkehan 9, 14 Xuzhou 438, 15 Yangmai 5, 16 Neixiang 36

of *Ppd-D1a* to improve cultivar adaptation to various environments.

Among landraces in the autumn-sown wheat zones, the frequencies of *Ppd-D1a* in Zones I to V were 18.2, 32.8, 58.2, 59.1, and 54.5%, respectively. The frequency of *Ppd-D1a* was comparably lower (5.3%) in landraces from Zone VIII, a spring-sown spring wheat area. This indicated that the presence of *Ppd-D1a* in landraces gradually increased from north to south in the five autumn-sown wheat zones (I, II, III, IV and V).

Among improved cultivars, those in Zones II, III, and IV located in the middle and southern parts of China had high frequencies of *Ppd-D1a*, ranging from 96.1 to 98.3%, followed by Zones I (89.5%), VII (87.5%), VIII (87.9%), and X (78.1%), and the lowest frequency was observed in Zone VI (36.0%). This again showed the increasing frequency of *Ppd-D1a* in improved cultivars from north to south.

In Zone I, six improved cultivars, Dongfanghong 3, Yuandong 8585, Longdong 1, Qingxuan 1, Triumph, and Early Premium, had *Ppd-D1b*. Dongfanghong 3 released in 1968 and Yuandong 8585 developed in the 1980s were both late maturing cultivars from Beijing. Longdong 1 and Qingxuan 1 were developed and grown in the winter wheat area of Gansu province at an altitude of 1,300–1,600 m, where one crop per year is practiced under rained conditions and late maturity is preferred for achieving high yields, thus photoperiod sensitivity is preferred. Triumph and Early Premium were introduced from Kansas State University in the 1940s and it would be expected that they carried photoperiod sensitivity alleles, especially before the green revolution. Thus, all currently improved cultivars with early maturity in

Zone I carry the *Ppd-D1a* where early maturity is needed to avoid sprouting damage and to allow optimal sowing of maize after wheat.

In Zone II, improved cultivars with the *Ppd-D1b* allele included Ji 5099 (high quality, average yield, late maturity), Shijiazhuang 407 (selected from Triumph/Yanda 1817 in 1956), Neixiang 36 (reselection of landrace Baihoumai in the 1960s), Qida 195 (reselection of a landrace), Xuzhou 438 (reselection of a landrace), Zhongliang 5, Zhongliang 11 and Quality (an Australian introduction). Zhongliang 5 and Zhongliang 11 were released in the winter area of Gansu province in the 1960s. Thus, seven of them except for Shijiazhuang 407 are expected to carry *Ppd-D1b* allele. However, further investigation is needed to understand the early maturity of Shijiazhuang 407. Therefore, all current cultivars with early maturity in this zone carry the *Ppd-D1a* allele.

In Zones III and IV, all 109 improved cultivars with early maturity carried the *Ppd-D1a*, and only two improved cultivars (Villa Glori and Orofen) with late maturity had the *Ppd-D1b* (Jin 1983; Zhuang 2003). Villa Glori introduced from Italy in 1936, and Orofen introduced from Chile, were leading cultivars before the 1970s. Again, all current cultivars with early maturity carry the *Ppd-D1a* allele.

Zone VI is a high latitude environment, thus cultivars are expected to have a certain level of photoperiod sensitivity (He et al. 2001). Nine improved cultivars, Kefeng 4, Longmai 12, Longmai 19, Longmai 26, Longmai 30, Longfumai 3, Longfumai 4, Longfumai 12, and Longfumai 14, had the *Ppd-D1a*. Kefeng 4 was developed by Keshan Wheat Research Institute in Keshan of Heilongjiang province at latitude of 48°03' in 1977. Other eight

improved cultivars were developed by the Heilongjiang Academy of Agricultural Sciences in Harbin at latitude 45°41'. It is generally believed that cultivars from Harbin have less degree of photoperiod sensitivity and relative narrow adaptation in Heilongjiang in comparison with cultivars developed from Keshan (He et al. 2001). Thus, it was surprised that Kefeng 4 developed from Keshan does not have the *Ppd-D1b* allele, but it may carry other genes that affect flowering time. This needs further study.

In Zone VII, only three improved cultivars (Banong 1, Mengmai 22 and Dabaipi) had the *Ppd-D1b*. Banong 1 and Dabaipi with late maturity were released before the 1970s. Mengmai 22 with mid to late maturity was developed in 1993, but was grown only in the area close to Heilongjiang (Zone VI), and therefore was expected to carry the *Ppd-D1b*.

In Zone VIII, improved cultivars, Hongnong 1, Jiunong 2, Longmai 5 and CI 12203, had the *Ppd-D1b*. Hongnong 1, Jiunong 2 and Longmai 5 were released before 1960, and further investigation is needed to understand their adaptation since all three have mid maturity. CI 12203, introduced to Gansu (Zone VIII) from the USA in 1944, was named Gansu 96 in China, and was expected to carry the *Ppd-D1b* allele.

In Zone X, seven improved cultivars identified with *Ppd-D1b* included Kashize 5, Kuidong 4, Kuihua 1, Xindong 16, Xindong 17, Xindong 18 and Xindong 23. All were developed and grown in Xinjiang, and were expected to have photoperiod sensitivity.

Origin of *Ppd-D1a* in improved Chinese wheat cultivars

Four hundred and forty two improved cultivars with *Ppd-D1a* were identified in this study. Pedigree analysis showed that *Ppd-D1a* in Chinese improved cultivars was mainly derived from three primary sources: the Japanese landrace Akagomughi and Chinese landraces Mazhamai and Youzimai (Fig. 2).

Italian cultivars Mentana, Abbondanza and Funo with the *Ppd-D1a* allele were introduced into China in the 1930s and 1956, respectively. They played a crucial role in wheat production and breeding in Zones III, IV, and VIII, and 87, 110 and 98 cultivars, respectively, were developed in China using one of them as a parent (Jin 1983, 1997). These Italian introductions were derived from crosses involving Akagomughi (Worland 1999). Their derivatives, Boai

7023, Yangmai 1, Sumai 3, Mianyang 4, Emai 6, Hongtu, Doudou 1, Ganmai 8 and Longchun 8, became leading cultivars and important breeding parents (Zhuang 2003).

More than 17 leading cultivars, such as Beijing 10, Shandongfu 63, Jinan 9 and Yannong 15, with *Ppd-D1a* were developed from the Henan landrace Youzimai (Zhuang 2003). Youzimai, a leading cultivar in the 1950s, with good yield, early maturity and broad adaptation, was widely distributed in the northern part of Zone II. More than 88 cultivars including Beijing 8, Taishan 1, Jinan 2, Bima 1 and Bima 4 were derived from the Shaanxi landrace Mazhamai, another broadly adapted high yielding genotype (Jin 1983, 1997; Zhuang 2003).

Discussion

Selection for earlier flowering and photoperiod insensitivity has been an important step in improving the adaptation of wheat in many environments. Wheat germplasm from the International Maize and Wheat Improvement Centre (CIMMYT) is characterized with photoperiod insensitivity and broad adaptation. It was developed through shuttle breeding between two contrasting Mexican environments, and subsequently widely used in developing countries (Trethowan et al. 2007). A total of 257 wheat cultivars and advanced lines from CIMMYT were assayed using the same primers as in the present study, and 234 (91.1%) carried *Ppd-D1a*. The remaining 8.9%, consciously developed for high latitude environments in central Asia and northeastern China, carried *Ppd-D1b* (unpublished data). Major objectives in Chinese wheat breeding programs since 1949 have been high yield potential, broad adaptation, and early flowering and maturity to fit multi-cropping systems. Clearly the photoperiod insensitive allele *Ppd-D1a* was the target of that strategy for most areas except for spring wheat in northeastern China and winter wheat in Gansu and Xinjiang. This accounts for the significant increase in the frequency of the photoperiod insensitive *Ppd-D1a* allele.

In both the autumn-sown and spring-sown wheat regions, the frequency of *Ppd-D1a* decreased from the south where insensitivity was obligatory for early maturity to north where insensitivity is increasingly

less essential due to the gradual increase of photoperiod length in the wheat growing regions (Zhuang 2003). Compared with spring-sown regions, a higher frequency *Ppd-D1a* was found in autumn-sown regions, where the shorter photoperiod length during the wheat growing stage was present (Fig. 1). The cultivars with the strongest dominant allele removing the need for vernalization (*Vrn-A1*) combined with other dominant vernalization gene(s), in Zone VI, a spring wheat zone, are commonly considered the most sensitive to photoperiod response, and this was supported by the lowest frequency of *Ppd-D1a* among the improved cultivars released in the region (Zhuang 2003; Zhang et al. 2008). Conversely in the autumn-sown Zones I, II, III and IV, it is important for wheat cultivars to flower and mature as early as possible in order to avoid the regular hot and desiccating summer conditions (He et al. 2001). Combining *Ppd-D1a* with a single moderate dominant vernalization allele (*Vrn-D1*) in cultivars in Zones II, III and IV allows adjustment of the growth cycle to achieve higher yields, whereas *Ppd-D1a* in combination with winter genotypes in Zone I permits avoidance of vegetative-stage frost damage as well as allowing a long grain-filling period before the onset of humid and hot summer conditions (Zhuang 2003; Zhang et al. 2008).

In addition to *Ppd-D1*, other genes such as *Ppd-A1*, *Ppd-B1* and earliness per se may also have important roles in cultivar adaptation. However, allele-specific markers are currently not available for these loci (Beales et al. 2007). Further investigation is therefore needed to understand the distribution and importance flowering time genes in relation to the adaptation and productivity of wheat in China. For example, our previous study showed that nine early heading cultivars (Jimai 36, Taishan 1, Lumai 23, Laizhou 953, Weimai 8, Yumai 66, Yumai 70, Xuzhou 14 and Emai 6) carried recessive alleles at all four vernalization loci as determined by allele-specific assays, but all reached ear emergence in 76–108 days (Zhang et al. 2008). In the present study, these nine cultivars were showed to carry *Ppd-D1a* which, alone, should not cause such early flowering. These cultivars are therefore likely to carry novel alleles at one or more additional *Vrn* loci that remove the need for vernalization or additional photoperiod insensitive alleles at *Ppd-A1* and (or) *Ppd-B1* loci. The existing diagnostic assays are

valuable in pin-pointing the needs of future research in understanding the genetics of adaptation.

The reduced height gene *Rht8* located on chromosome 2D, derived from Japanese landrace Akakomugi, was introduced into Chinese wheat improved cultivars. The *Rht8* gene was found to take a dominant position with frequencies of 46.8% in 220 wheat genotypes from autumn-sown wheat regions, has less effect on reduced height than *Rht-B1b* and *Rht-D1b* (Zhang et al. 2006). It was reported that *Rht8* in close linkage with the photoperiod insensitivity gene (*Ppd-D1a*) reduced plant height by around 10% without significant negative effects on yield (Börner et al. 1993; Worland et al. 1998a, b). The *Ppd-D1a* allele for day length insensitivity together with the less reducing height *Rht8* allele has proved highly effective in providing Chinese wheats with adaptation to specific environments, especially after the green revolution.

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