

Genetic analyses of heading date of *Japonica* rice cultivars from Northeast China

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Abstract

Northeast regions of China (38–55°N latitude) play an important role in *Japonica* rice planting. Heading dates of 10 *Japonica* rice cultivars native to the Northeast of China were investigated and their sensitivities to photoperiod and temperature were analyzed. The results showed that these *Japonica* rice cultivars were insensitive to photoperiod but strongly sensitive to temperature, i.e. a high temperature can markedly shorten the heading date. Genetic analyses were conducted on these 10 cultivars using a set of heading date tester lines. All these *Japonica* cultivars carried a dominant early heading gene *Ef-1*, and most of these cultivars carried the photoperiod insensitivity allele *e₁*, and two types of alleles were presented at the *Se-1* locus, including recessive photoperiod insensitivity gene *Se-1^r* and dominant strong photoperiod-sensitivity (PS) gene *Se-1^s*. The PS of these cultivars carrying *E₁* or *Se-1^s* can be repressed or weakened by *Ef-1* and the recessive allele *hd2* they carried. These results provided a reasonable explanation to the adaptability of *Japonica* rice to the high latitude environment of the Northeast China, and could be useful for breeding new cultivars well adapted to the high latitude regions and expanding the rice cultivation range.

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Keywords: Genetic analyses; Heading date; *Japonica* rice (*Oryza sativa* L.); Northeast China; Photoperiod-sensitivity; Temperature-sensitivity

1. Introduction

Heading date (HD) is one of the most important traits for the adaptation of rice to different cultivation areas and cropping seasons, which can be divided into basic vegetative phase (BVP) and photoperiod-sensitivity phase (PSP). It is essentially determined by three factors, i.e. duration of the basic vegetative growth (BVG), photoperiod-sensitivity (PS) and temperature-sensitivity (TS). Several major genes for HD have been identified in rice: *Ef-1*, as a major gene controlling the duration of BVG, is located on chromosome 10, and can accelerate floral initiation under both short and long days, and also partially counteract the effects of PS gene under long days (Tsai, 1986; Kinoshita, 1995; Sato et al., 1988; Nishida et al., 2002; Xu et al., 2006); other genes

including *E₁*, *E₂*, *E₃*, *Se-1*, *Se-2*, *Se-3(t)*, *Se-4*, *Se-5*, *Se-6*, *Se-7* and *Se-9(t)*, are found to be responsible for PS (Kinoshita, 1995; Maheswaran et al., 1995; Ohshima et al., 1993; Okumoto et al., 1992; Okumoto and Tanisaka, 1997; Yokoo and Okuno, 1993; Shen et al., 1994). Among these genes, *E₁* and *Se-1* are known as major and strong PS genes and have proven to be the most ubiquitous alleles controlling HD (Ichitani et al., 1997, 1998b; Okumoto et al., 1996). In addition, the recessive inhibitor *i-Se-1* confers early heading even under long days due to complete inhibition of *Se-1* (Ohshima et al., 1993; Ohshima and Kikuchi, 1994; Luo et al., 2002). Otherwise, a great progress has been made in the mapping and cloning of quantitative trait locus (QTL) for heading date in rice recently. A number of QTLs for HD have been identified using different populations (Yano et al., 1997, 2001; Lin et al., 1998; Li et al., 1995; Maheswaran et al., 2000), and *Hd1*, *Hd3a*, *Hd6* and *Ehd1* have been map-based cloned (Yano et al., 2000; Takahashi et al., 2001; Kojima et al., 2002; Doi et al., 2004).

The Northeast regions (38–55°N latitude) play an important role in the *Japonica* rice planting of China, which is also one of

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the northern-limit rice cultivation regions in the world, having a short and cool summer with a long natural day-length. In such environment, rice cultivars from other regions exhibit a slow growth rate and HD is strongly delayed, and only extremely early heading varieties are able to adapt to such growth conditions. However, the systemic researches of the HD among cultivars in Northeast of China are deficient, and little is known of the genetic basis of HD.

In the present study, the PS, TS of HD and HD genotype of *Japonica* rice cultivars from the Northeast of China were investigated. The results will be helpful in elucidating the genetic mechanism of rice varieties adaptive to this environment, breeding new cultivars well adapted to the high latitude regions and expanding the rice cultivation range.

2. Materials and methods

2.1. Plant materials

We employed the genetic stocks as follows: (1) heading date near-isogenic lines, including EG0, EG1, ER, LR, T65m and T65E^bm (Yamagata et al., 1986; Ichitani et al., 1997, 1998a,b; Inoue et al., 1998), two heading date QTL near-isogenic lines of Nipponbare, NIL(*Hd1*) and NIL(*Hd2*) (the *Hd* genes were introgressed from the cultivar Kasalath) (Yamamoto et al., 1998; Lin et al., 2000) were used as tester lines; (2) tested cultivars, including Hejiang19, Kongyu131, Wuyoudao1, Kenjiangdao10, Heijiao951, Kenjiangdao6, Dongnong416, Songjing3, Jijing80 and Shennong129 which came from the Northeast of China; (3) the F₁ and F₂ populations derived from the crosses between tested cultivars and near-isogenic lines.

2.2. Photoperiod-sensitivity analysis

The 10 tested cultivars from the Northeast of China were grown under artificial short-day (SD, 9 hL(light)/15 hD(dark)) and natural long-day (LD) conditions on the farm at Tuqiao town in Nanjing (32°N), in 2006. The photoperiod of LD conditions from May to August were ranged from 13.2 hL/10.8 hD to 14.2 hL/9.8 hD. The temperatures of SD and LD conditions were almost same, the mean value were shown in Fig. 1. PS was analyzed according to the difference of HD under these SD and LD conditions. The seeds were sown on 20 May

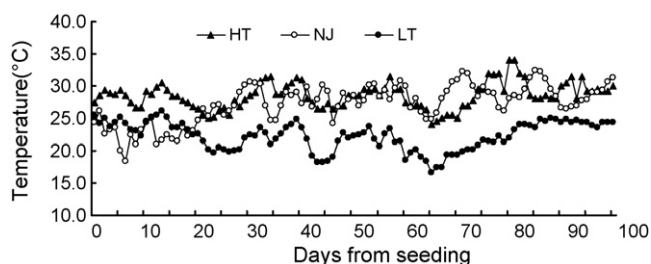


Fig. 1. The daily mean temperatures from seeding to heading in greenhouse (HT), natural low-temperature (LT) condition in the winter at Lingshui county, Hainan province (from 25 November of 2006 to March of 2007) and natural high temperature in the summer at Nanjing (NJ) (from 20 May to the end August of 2006) of China.

and ten seedlings of each cultivar were transplanted in SD and LD condition with spacing of 13.3 cm × 26.7 cm on 15 June. Crop management followed commercial rice production.

2.3. Temperature-sensitivity analysis

The 10 tested cultivars were grown in greenhouse (high-temperature, HT), or under natural low-temperature (LT) condition in winter at Lingshui county, Hainan province (18°29'N) in China. The mean temperatures in greenhouse (HT) and under natural low-temperature condition (LT) were shown in Fig. 1. The photoperiod of HT and LT conditions from November of 2006 to March of 2007 in Lingshui were the same, which ranged from 11.0 hL/13.0 hD to 11.9 hL/12.1 hD. The TS of tested cultivars was analyzed according to difference of HD under HT and LT condition. In 2006, the seeds were sown on 25 November and ten seedlings of each cultivar were transplanted in HT and LT condition with spacing of 13.3 cm × 26.7 cm on 15 December. Crop management followed commercial rice production.

2.4. Genotypes analysis of heading date

A set of F₁ and F₂ populations derived from the crosses between tester lines [(EG0, EG1, ER, LR, T65m, T65E^bm, Nipponbare, NIL(*Hd1*) and NIL(*Hd2*)] and 10 tested cultivars were used to analyze the genotypes for major HD gene of these tested cultivars from the Northeast regions. Parents and corresponding F₁ and F₂ were grown on the farm in the Institute of Food Crops of Jiangsu Academy of Agricultural Sciences in Nanjing (32°N), in 2006. Sowing and transplanting were made on 17 May and on 16 June, respectively. Ten plants of parents and their respective F₁, along with about 200 plants of F₂ were transplanted with spacing of 13.3 cm × 26.7 cm. Crop management followed commercial rice production.

HD was recorded for each plant when the first developing panicle emerged about 1 cm beyond the leaf sheath of the flag leaf, and monitored every 2d. For the parents and F₁ hybrids, the mean days to heading of individuals were taken as HD.

3. Results

3.1. The *Japonica* cultivars from Northeast China were insensitive to photoperiod

The HD of the 10 cultivars from Northeast China under SD (9 hL/15 hD) and LD (about 14 hL/10 hD) conditions are shown in Fig. 2. The HD of these cultivars did not show significant difference whether under SD or LD conditions except for that of the cultivar Songjing3, suggesting that most of *Japonica* cultivars from Northeast China were insensitive to photoperiod.

3.2. The *Japonica* cultivars from Northeast China were sensitive to temperature

The HD of 10 cultivars from Northeast China under HT and LT conditions are shown in Fig. 3. The HD of these cultivars

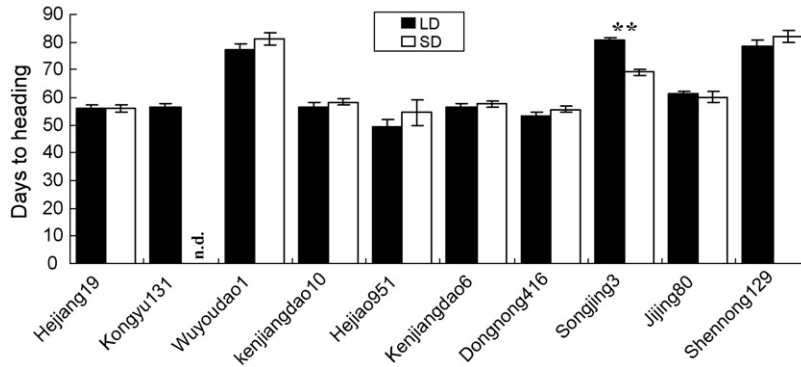


Fig. 2. The heading date of the 10 cultivars from the Northeast regions of China under natural long-day (LD) and artificial short-day (SD) condition. **Heading date in SD significantly shorter than in LD (*t*-test *P*-value <0.01); n.d.: not determined. Values are expressed as means ± S.D., *n* = 10.

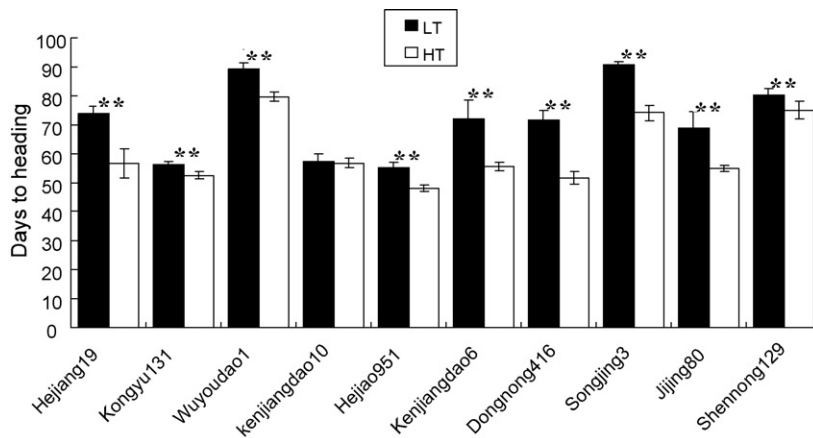


Fig. 3. The heading date of the 10 cultivars from the Northeast regions of China under natural low-temperature (LT) and greenhouse high-temperature (HT) condition. **Heading date in HT significantly shorter than in LT (*t*-test *P*-value <0.01); n.d.: not determined. Values are expressed as means ± S.D., *n* = 10.

were significantly different under these two conditions except for that of the cultivar Kenjiangdao10, suggesting that most of *Japonica* cultivars from Northeast of China were sensitive to temperature, and HD could be shorten markedly in the high-temperature condition. Otherwise, compared the results from Figs. 2 and 3, we can found the HD of the most *Japonica* cultivars in the summer of Nanjing where has long-day and high temperature were close to that in the greenhouse condition but significantly shorter than that in the natural low-temperature condition in the winter of Lingshui county, Hainan province where has short-day. Since these cultivars were insensitive to photoperiod, these result also demonstrated that the HD of these cultivars were sensitive to temperature.

3.3. The genotypes for major HD genes of the Japonica cultivars from Northeast China

3.3.1. Allelic relationships at the *E1* locus

The near-isogenic lines EG0 and EG1 both carried a PS allele *Se-1ⁿ* at the *Se-1* locus and a dominant early heading gene *Ef-1*, differing only at the *E1* locus. That is, the genotype of EG0 at the *E1* loci was *e1e1*, and EG1 was *E1E1* (Ichitani et al., 1997, 1998a,b; Nishida et al., 2001) (Table 1). The PS allele *E1* was dominant over the *e1* (Okumoto et al., 1992, 1996). The HD of EG1 was 19.2d longer than EG0 in Nanjing. The HD of the F1

plants from the crosses between EG1 and Hejiang19, Kongyu131, Wuyoudao1, Kenjiangdao10, Hejiao951, Kenjiangdao6, Dongnong416 and Jijing80 were 18.3, 18.8, 18.3, 17.1, 14.4, 15.3, 22.0 and 16.0d longer than those from the crosses between EG0 and these cultivars, respectively, but the F1 hybrids between EG1 and Songjing3 exhibited similar HD to F1 hybrids between EG0 and Songjing3 (Fig. 4A), suggesting that the cultivars Hejiang19, Kongyu131, Wuyoudao1, Kenjiangdao10, Hejiao951, Kenjiangdao6, Dongnong416 and

Table 1
Genotypes and heading date in Nanjing natural long-day condition of heading date major genes tester lines

Test lines	Locus				Heading date
	<i>E1</i>	<i>Se-1</i>	<i>Ef-1</i>	<i>Hd2</i>	
EG0	<i>e1e1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>		71.2 ± 0.6
EG1	<i>E1E1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>		90.4 ± 0.7
ER	<i>E1E1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>		80.7 ± 1.3
LR	<i>E1E1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>		102.7 ± 1.0
T65E ^{bm}	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>		75.6 ± 1.6
T65m	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>ef-1ef-1</i>		96.9 ± 1.7
Nipponbare	<i>E1E1</i>	<i>Se-1ⁿSe-1ⁿ</i>		<i>Hd2Hd2</i>	86.9 ± 1.0
NIL(<i>Hd1</i>)	<i>E1E1</i>	<i>Se-1^eSe-1^e</i>		<i>Hd2Hd2</i>	77.4 ± 1.0
NIL(<i>Hd2</i>)	<i>E1E1</i>	<i>Se-1ⁿSe-1ⁿ</i>		<i>hd2hd2</i>	79.9 ± 1.5

Values are expressed as means ± S.D., *n* = 10.

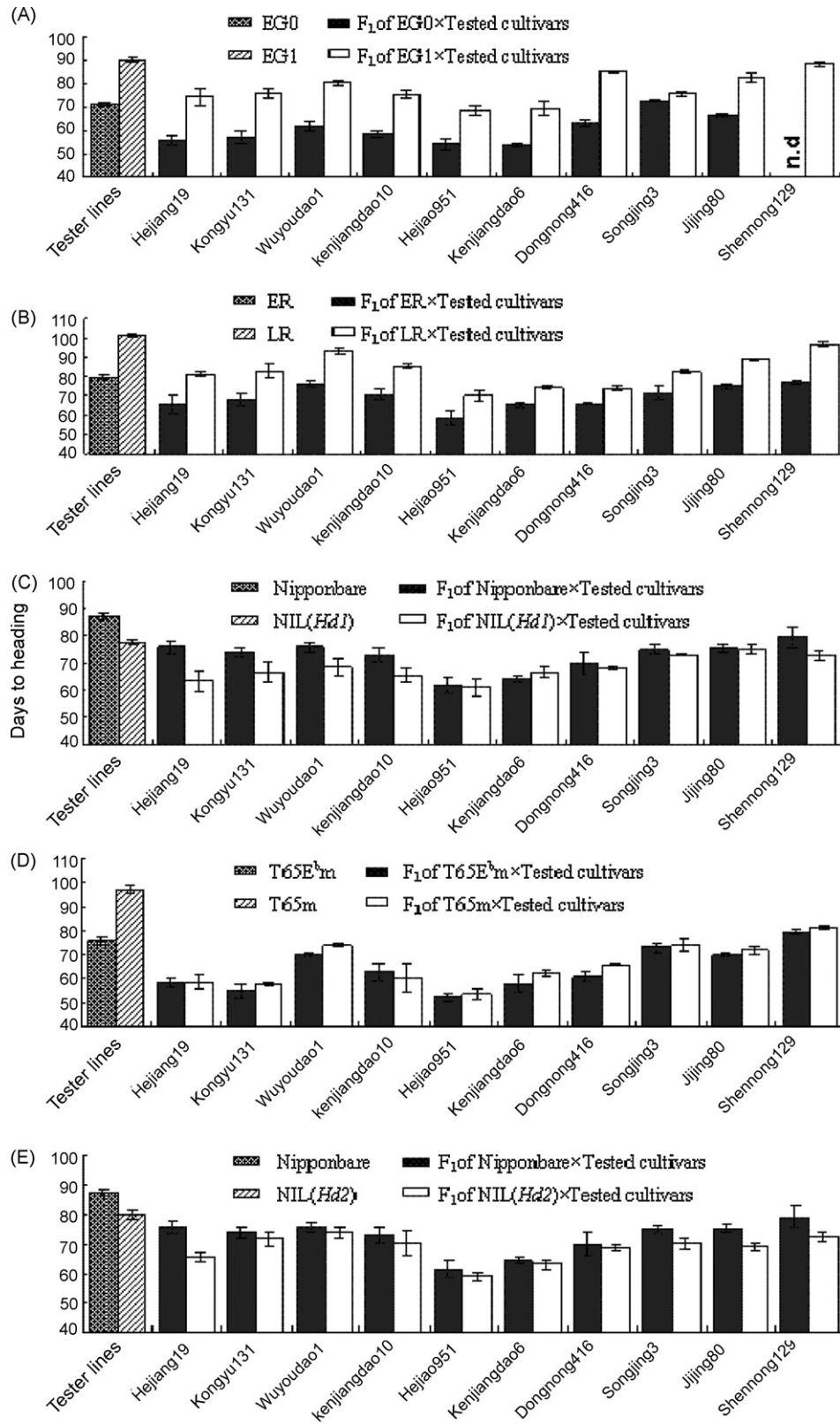


Fig. 4. Heading date of test lines and F₁ hybrids of test lines crossed with tested cultivars. (A) Heading date of EG0, EG1 and F₁ hybrids of EG0, EG1 crossed with tested cultivars. (B) Heading date of ER, LR and F₁ hybrids of ER, LR crossed with tested cultivars. (C) Heading date of Nipponbare, NIL(*Hd1*) and F₁ hybrids of Nipponbare, NIL(*Hd1*) crossed with tested cultivars. (D) Heading date of T65E^bm, T65m and F₁ hybrids of T65E^bm, T65m crossed with tested cultivars. (E) Heading date of Nipponbare, NIL(*Hd2*) and F₁ hybrids of Nipponbare, NIL(*Hd2*) crossed with tested cultivars. n.d.: not determined. Values are expressed as means ± S.D., n = 10.

Table 2
The genotypes of heading date of the 10 cultivars from the Northeast regions of China

Lines	Locus			
	<i>E1</i>	<i>Se-1</i>	<i>Ef-1</i>	<i>Hd2</i>
Kongyu131	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Wuyoudao1	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Kenjiangdao10	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Hejiao951	<i>e1e1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Kenjiangdao6	<i>e1e1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Dongnong416	<i>e1e1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>	<i>Hd2Hd2</i>
Hejiang19	<i>e1e1</i>	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>	<i>hd2hd2</i>
Shennong129	–	<i>Se-1^eSe-1^e</i>	<i>Ef-1Ef-1</i>	<i>hd2hd2</i>
Jijing80	<i>e1e1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>	<i>hd2hd2</i>
Songjing3	<i>E1E1</i>	<i>Se-1ⁿSe-1ⁿ</i>	<i>Ef-1Ef-1</i>	<i>hd2hd2</i>

Jijing80 all carried a recessive photoperiod insensitivity allele *e1*. Songjing3 was likely to possess the dominant PS allele *E1* (Table 2).

3.3.2. Allelic relationships at the *Se-1* locus

The difference of the near-isogenic lines ER and LR was at the *Se-1* locus. LR harbored the PS allele *Se-1ⁿ*, but ER carried the photoperiod insensitivity allele *Se-1^e*; Similarly, Nipponbare harbored the PS allele *Se-1ⁿ*, but the near-isogenic line NIL(*Hd1*) has been constructed by introgression of *hd1* (*Se-1^e*) from the *indica* variety Kasalath in the Nipponbare genetic background (Yano et al., 1997, 2000; Lin et al., 2000; Yamamoto et al., 1998) (Table 1). *Se-1ⁿ* and *Se-1^e* were dominant over *Se-1^e*, and the PS of *Se-1ⁿ* was stronger than that of *Se-1^e* (Yokoo and Kikuchi, 1977). ER and NIL(*Hd1*) headed 22.0 and 9.5d earlier than LR and Nipponbare in Nanjing, respectively. The F₁ hybrids of ER and NIL(*Hd1*) crossed with Hejiang19, Kongyu131, Wuyoudao1, Kenjiangdao10, Shennong129 also headed about 22.0 and 9.5d earlier than those of LR and Nipponbare crossed with them (Fig. 4B and C), suggesting the cultivars Hejiang19, Kongyu131, Wuyoudao1, Kenjiangdao10 and Shennong129 carried the recessive photoperiod insensitivity allele *Se-1^e* at the *Se-1* locus (Table 2). The heading date of the F₁ hybrids between LR and Hejiao951, Kenjiangdao6, Dongnong416, Songjing3 and Jijing80 were significantly longer than the F₁ hybrids of ER crossed with them (Fig. 4B), while the F₁ hybrids of Nipponbare crossed with them exhibited almost the same HD as NIL(*Hd1*) crossed with them (Fig. 4C), suggesting Hejiao951, Kenjiangdao6, Dongnong416, Songjing3 and Jijing80 carried the PS allele *Se-1ⁿ* whose PS was slightly weaker than *Se-1ⁿ* at the *Se-1* locus (Table 2).

3.3.3. Allelic relationships at the *Ef-1* locus

The tester line T65E^bm headed 21.3d earlier than T65m, differing in the *Ef-1* locus (Table 1), while the HD of the F₁ hybrids between T65E^bm and all of the 10 *Japonica* rice cultivars were not significantly different compared with that of T65m and them (Fig. 4D). The result showed that the 10 *Japonica* rice cultivars all carried the dominant early heading allele *Ef-1* at the *Ef-1* locus (Table 2).

3.3.4. Allelic relationships at the *Hd2* locus

The near-isogenic line NIL(*Hd2*) carries *hd2* from Kasalath in the Nipponbare genetic background (Yano et al., 1997; Lin et al., 2000), and headed earlier than Nipponbare under long days, but later than Nipponbare under short days. This implied that *hd2* could inhibit the effect of *Hd1* (*Se-1*) (Luo et al., 2003; Xu et al., 2005). NIL(*Hd2*) headed 7.0d earlier than Nipponbare in Nanjing. The F₁ hybrids of NIL(*Hd2*) crossed with Hejiang19, Songjing3, Jijing80 and Shennong129 also headed about 7.0d earlier than those of Nipponbare crossed with them (Fig. 4E), suggesting the cultivars Hejiang19, Songjing3, Jijing80 and Shennong129 carried the *hd2*. While the HD of the F₁ hybrids of NIL(*Hd2*) crossed with Kongyu131, Wuyoudao1, Kenjingdao10, Hejiao951, Kenjiangdao6 and Dongnong416 were not significantly different compared with those of Nipponbare crossed with them (Fig. 4E), suggesting the cultivars Kongyu131, Wuyoudao1, Kenjingdao10, Hejiao951, Kenjiangdao6 and Dongnong416 all carried *Hd2*.

3.3.5. Segregation of HD in F₂ populations from crosses 'tester lines × tested cultivars'

In order to further confirm the result of genotyping, the frequency distributions of HD in the F₂ populations derived from crosses between tester lines and tested cultivars are shown in Fig. 5. The HD of F₂ population from the cross EG0 × Dongnong416 showed a narrower range of distribution than that from 'EG1 × Dongnong416' (Fig. 5A and B). This demonstrated that Dongnong416 carried *e1*, like EG0 at the *E1* locus. Similarly, the F₂ population from the cross 'T65E^bm × Dongnong416' showed a narrower distribution range of HD than that of 'T65m × Dongnong416' (Fig. 5F and G), which also indicated that Dongnong416 carried *Ef-1*, like T65E^bm. The HD of F₂ population from the cross 'ER × Dongnong416' showed a similar range of distribution to that from 'LR × Dongnong416' (Fig. 5H and I), while compared with the F₂ population from the cross 'NIL(*Hd1*) × Dongnong416', the HD of the F₂ population from the cross 'Nipponbare × Dongnong416' was concentrative (Fig. 5C and D), suggesting that Dongnong416 carried *Se-1ⁿ*. Most of the plants in the F₂ population from the cross 'NIL(*Hd2*) × Dongnong416' had moderate HD (Fig. 5E), while the HD of most plants in the F₂ population from the cross 'Nipponbare × Dongnong416' fasten on biggish value, suggesting that NIL(*Hd2*) carried the recessive allele *hd2* which inhibited the expression of *E1* or *Se-1* and confirmed that Dongnong416 carries *Hd2*. The frequency distributions of HD in the F₂ populations derived from the crossed between tester lines and other tested cultivars also further demonstrated the genotypes of other cultivars from the Northeast China (data not shown).

4. Discussion

Rice can grow under various climatic conditions by long-period introduction and domestication, although it is a short-day plant. HD is critical for adaptation to specific cultivation conditions and cropping season, which can be divided into

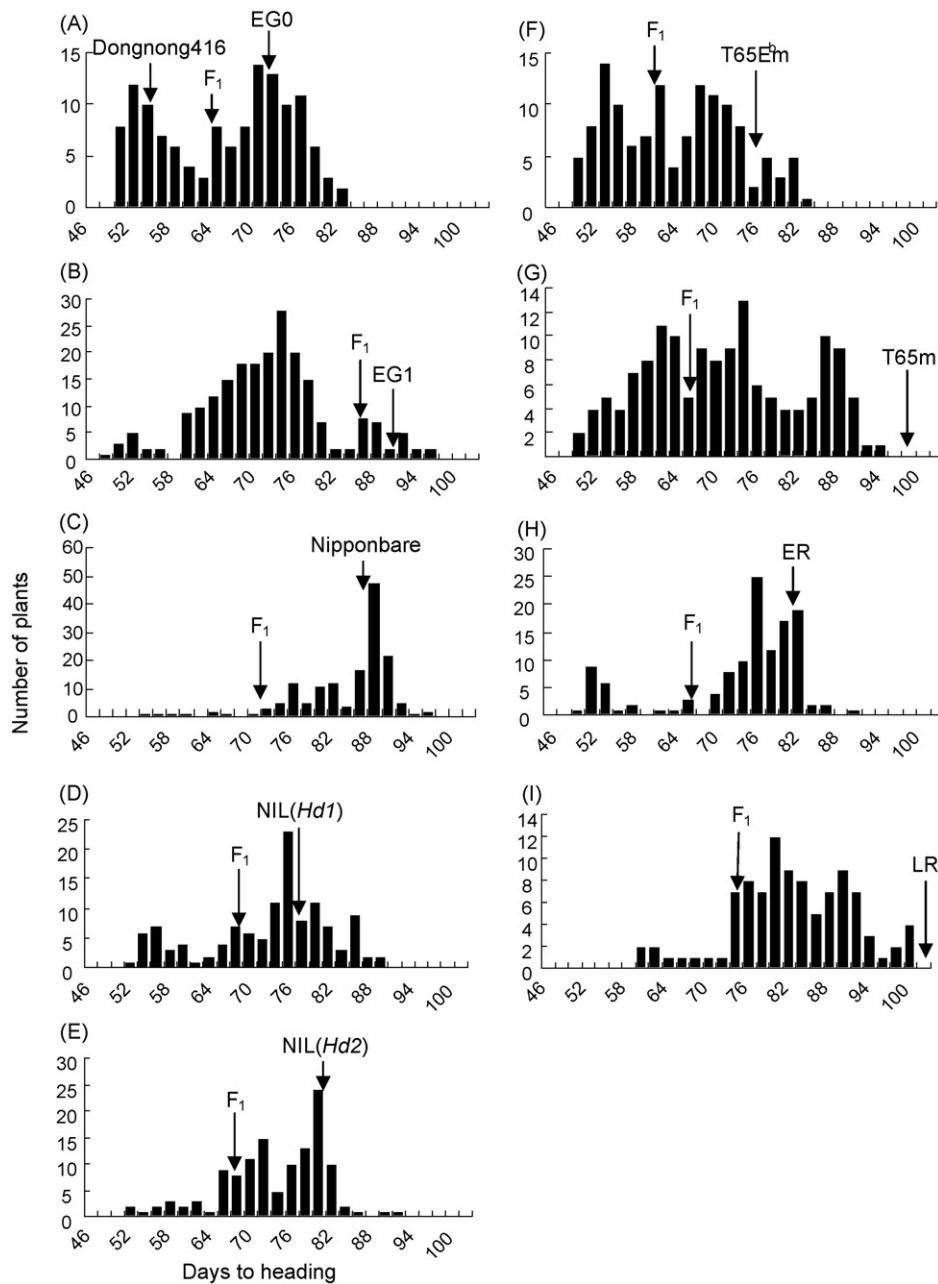


Fig. 5. Frequency distribution of days to heading of F_2 population derived from the crosses between heading time tester lines EG0, EG1, ER, LR, T65E^bm, T65m, Nipponbare, NIL(*Hd1*), NIL(*Hd2*) and Dongnong416. (A) F_2 of EG0 × Dongnong416; (B) F_2 of EG1 × Dongnong416; (C) F_2 of Nipponbare × Dongnong416; (D) F_2 of NIL(*Hd1*) × Dongnong416; (E) F_2 of NIL(*Hd2*) × Dongnong416; (F) F_2 of T65E^bm × Dongnong416; (G) F_2 of T65m × Dongnong416; (H) F_2 of ER × Dongnong416; (I) F_2 of LR × Dongnong416.

basic vegetative phase and photoperiod-sensitivity phase. The length of the BVP is decided by the temperatures, but the PSP is decided by the photoperiod during the growing period (Chang et al., 1969). The genotype of major HD genes have specific rule in different environments. The areas including Northeast China, far Eastern Russia, Europe and Hokkaido of Japan represent the northern limit of rice cultivation, where are characterized by low temperatures and long natural day-length during the growing period, and only extremely early heading varieties are able to adapt to these growth conditions.

The previous study shown that the *Se-1* was an important locus influencing the adaptability of Japanese rice cultivation.

The photoperiod-insensitive allele *Se-1^e* mainly distributes in the rice cultivation of the high latitude regions (41–45°N), Southeast regions (36–41°N) and other lower latitude regions (21–30°N). The photoperiod-sensitive allele *Se-1ⁿ* mainly distributes in the rice cultivation of the southwest regions of Japan (31–36°N) (Okumoto et al., 1992, 1996; Ichitani et al., 1997, 1998a). The cultivars of Hokkaido have been subjected to substantial characterization for HD, including several genetic studies. It is known that a photoperiod-insensitive allele *e₁* at the *E₁* locus is essential for the success of these cultivars (Okumoto et al., 1996). An extremely early heading cultivar from the former Soviet Union, USSR5 was analyzed the genetic

basis for its early heading. The results showed that the early heading of USSR5 was controlled by the presence of photoperiod-insensitive alleles e_1 and $Se-1^e$, and the dominant earliness gene $Ef-1$ (Jiang et al., 2007). Recently, HD genotype of middle *indica* cultivars are planted in the middle to lower regions of the Yangtze River of China were investigated, the result suggested that most middle *indica* cultivars carried the recessive allele $hd2$, which could inhibit the expression of E_1 or $Se-1$ they carried (Xu et al., 2007).

In this paper, the HD genotypes of 10 *Japonica* rice cultivars which were typical and widely cultivated in Northeast China were analyzed. The results showed that dominant early heading gene $Ef-1$ could induce short BVP essentially in these cultivars, most of which carried recessive e_1 at E_1 locus, and two types of alleles were present at the $Se-1$ locus, including recessive photoperiod insensitivity gene $Se-1^e$ and dominant strong PS gene $Se-1^n$. The PS of these cultivars carrying the PS genes E_1 or $Se-1^n$ can be repressed or weakened by $Ef-1$ and recessive allele $hd2$ they carried, resulting in weak or no PS in these cultivars which accordingly exhibited short BVP and short growth duration. Otherwise, the experiment of photoperiod-sensitivity analysis through SD and LD treatment also confirmed that the *Japonica* rice cultivars of Northeast China were weak or photoperiod insensitive and have short PSP. The analysis of temperature-sensitivity under HT and LT treatments confirmed that these cultivars were sensitive to temperature, and the BVP and HD could be shorten markedly when these cultivars were transplanted in the high-temperature condition. These results give a reasonable explanation why the growth period of the *Japonica* rice cultivars of Northeast China is shorten markedly in the lower latitude area in summer, and indicated that the germplasms from different northern-limits of rice cultivation shared the same HD characterization after long-term domestication.

Recently, a great progress has been made in the studies of quantitative trait locus mapping and cloning for HD in rice. A series of QTLs have been identified in different populations (Yano et al., 1997, 2001; Lin et al., 1998; Li et al., 1995; Maheswaran et al., 2000). A photoperiod-sensitivity QTL on chromosome 7, $qDTH-7$, differentiates the varieties in the northernmost limit of rice cultivation into two genetic bases—Europe and Hokkaido (Fujino and Sekiguchi, 2005). Using a F_2 populations derived from USSR5 and N22 (a widely compatible Indian cultivar), five QTLs for HD were detected on chromosomes 1, 2, 7, 9 and 10, respectively, by our previous study (Jiang et al., 2007). All USSR5 alleles at these loci decreased HD except for $qHd-9$. The result showed that USSR5 carried the nonfunctional allele at $qHd-7$, a locus that might be identical to E_1 based on its chromosomal location. This result is similar to those described by both Okumoto et al. (1996) and Fujino and Sekiguchi (2005). Thus, the insensitive allele e_1 is essential where low sensitivity is required for adaptation to high latitudes. Similar considerations based on chromosomal locations suggest that the QTL detected on chromosome 10 is identical to the dominant early heading allele $Ef-1$ (Tsai, 1986; Kinoshita, 1995; Sato et al., 1988).

Therefore, the *Japonica* rice cultivars from the Northeast regions of China have short basic vegetative phase, weak or no photoperiod sensitivity and the heading date is strongly sensitive to high temperature, which is similar to the cultivars in the Hokkaido of Japan and far Eastern Russia with early maturity and weak photosensitivity (Ichitani et al., 1997; Jiang et al., 2007). This indicated that the rice varieties are gradually insensitive to day-length and have no demands for growth temperature by long-period natural selection and artificial domestication, then it can adapt to the high latitude regions that are characterized by the low temperatures and long natural day-length during the growth period. This provides the important practical and theoretical basis for the rice breeding of new cultivars well adapted to the high latitude regions and expanding the rice cultivation range.

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