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ORIGINAL PAPER

Dynamic and comparative QTL analysis for plant height in different developmental stages of *Brassica napus* L.

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Abstract

Key message **This report describes a dynamic QTL analysis for plant height at various stages using a large doubled haploid population and performs a QTL comparison between different populations in *Brassica napus*.**

Abstract Plant height (PH) not only plays an important role in determining plant architecture, but is also an important character related to yield. The process of determining PH occurs through a series of steps; however, no studies have focused on developmental behavior factors affecting PH in *Brassica napus*. In the present study, KN DH, a large doubled haploid population containing 348 lines was used for a dynamic quantitative trait locus (QTL) analysis for PH in six experiments. In all, 20 QTLs were identified at maturity, whereas 50 QTLs were detected by conditional mapping method and the same number was identified by unconditional mapping strategies. Interestingly, five unconditional QTLs *ucPH.A2-2*, *ucPH.A3-2*, *ucPH.C5-1*, *ucPH.C6-2* and *ucPH.C6-3* were identified that were consistent over the all growth stages of one or two particular experiments, and one conditional QTL *cPH.A2-3* was expressed throughout the entire growth process in one experiment. A total of 70 QTLs were obtained after combining QTLs identified at maturity, by conditional and unconditional mapping strategies, in which 25 showed opposite genetic effects in different periods/stages and experiments. A consensus map containing 1357 markers was constructed to compare QTLs identified in the KN population with five previously mapped populations. Alignment of the QTLs detected in different populations onto the consensus map showed that 27 were repeatedly detected in different genetic backgrounds. These findings will enhance our understanding of the genetic control of PH regulation in *B. napus*, and will be useful for rapeseed genetic manipulation through molecular marker-assisted selection.

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Introduction

Rapeseed (*Brassica napus*, AACC, $2n = 38$) is one of the world's most important oilseed crops, and plant height (PH) is a crucial trait related to crop production (Li et al. 2007). PH is a typical quantitative trait under complex genetic control and influenced by environmental conditions (Chen et al. 2007; Quijada et al. 2006; Udall et al.

2006). PH shows a close association with lodging in *B. napus* (Quijada et al. 2006; Udall et al. 2006), which can significantly decrease seed yield, final dry weight and harvest index (Islam and Evans 1994); however, lodging can be decreased to some degree by reducing PH. In addition, PH can also be used as a model trait suitable for developmental biology research. Thus, dissecting the genetic bases of PH is very important to geneticists and plant breeders.

Quantitative trial locus (QTL) mapping is a preliminary step and an effective approach to dissect the genetic mechanisms of complex quantitative traits (Mauricio 2001). Considering the importance of PH, some efforts have been made to identify the QTLs for PH using various segregating mapping populations in *B. napus*. Of these, 3–15 QTLs were detected in single population, with individual QTL accounting for 2.7–28.6 % of the phenotypic variation (PV) (Butruille et al. 1999; Zhao et al. 2005; Quijada et al. 2006; Udall et al. 2006; Li et al. 2007; Chen et al. 2007; Mei et al. 2009). More recently, Shi et al. (2009) detected 87 QTLs for PH using DH and reconstructed F_2 populations, and a total of 44 consensus QTLs were obtained after combining these QTLs with overlapping confidence intervals (CIs). Basunanda et al. (2010) and Würschum et al. (2012) identified 21 and five QTLs for PH in *B. napus*, respectively. Ding et al. (2012) performed QTL mapping in recombinant inbred lines across two phosphorus treatments and nine QTLs for PH were detected. In the above-mentioned studies, considerable numbers of QTLs for PH were distributed across 18 linkage groups except on C8 in *B. napus*. However, most of the previous studies have focused on final PH without considering developmental behavior. According to the theory of developmental genetics, genes are expressed selectively at different growth stages following a certain sequence of time and place (Xu and Shen 1991). The formation of PH in *B. napus* occurs through a series of steps regulated by genes with obvious dynamic characteristics during different developmental stages. Thus, these previous studies could not fully reflect the genetic effects expressed during different developmental stages and the genetic basis of PH has remained ambiguous. It is necessary, therefore, to understand the gene action due to distinct gene expression in specific growing periods for quantitative trait manipulation (Xu 1997). Zhu (1995) introduced a methodology for conditional genetic analysis to identify QTLs expressed at different time points across plant development. Since then, many agronomic traits have been investigated for gene expression patterns based on the conditional QTL mapping method, such as protein content and protein index, blast resistance, grain filling, fat content and fat index, tiller number and PH in rice (Li et al. 2008; Takai et al. 2005; Wang et al. 2008; Yan et al. 1998; Yang et al. 2006; Zheng et al. 2011); pod number in the main stem, seed weight, linolenic acid content and PH in soybean (Han et al. 2011; Sun et al. 2006; Teng et al. 2009); and PH in wheat (Wang et al. 2010; Wu et al. 2010) and maize (Yan et al. 2003). At the same time, much more information could be provided by conditional and unconditional QTL mapping methods using phenotypic data collected at different developmental stages compared to only at the final stage (Wang et al. 2010). Nevertheless, to our knowledge, very few studies have considered dynamic QTLs of PH at particular stages of the whole life cycle in rapeseed.

In the present study, a DH population containing 348 lines was used to investigate the dynamic QTLs for developmental behavior of PH in *B. napus* in six experiments. The objectives were to: (1) identify QTLs affecting PH development using both unconditional and conditional mapping approaches; and (2) compare the QTLs for PH with those detected in other populations, and provide useful information to further understanding of the genetic control of PH in *B. napus*.

Materials and methods

Plant materials

The DH population containing 348 lines, derived from a cross between 'KenC-8' and 'N53-2' (named the KN DH population), was previously used for developing a linkage map (KN map) (Wang et al. 2013). The KN map was constructed with 403 molecular markers: 275 SSRs (simple sequence repeats), 117 SRAPs (sequence-related amplified polymorphisms), 10 STSs (sequence tagged sites) and one IFLP (intron fragment length polymorphism). The length of the 19 linkage groups was in the range of 42.9–154.2 cM, with a total length of 1783.9 cM and an average marker interval of 4.4 cM according to the Kosambi function (Wang et al. 2013).

Field trials and PH measurements

The KN DH population together with the two parents was evaluated at three different locations. The materials were planted in a winter rapeseed area, Dali of Shaanxi Province (coded DL), in northwest China for 3 years (September–May of 2010–2011, 2011–2012 and 2012–2013); in a spring rapeseed area, Sunan of Gansu Province (coded GS), in northwest China for 2 years (April–September of 2011 and 2012); and a semi-winter rapeseed area, Wuhan of Hubei Province (coded WH), in central China for 1 year (October 2012–May 2013). Year–location combinations were treated as experiments, for example, 10DL means that the experiment was carried out in 2010 at DL. Details of the climatic conditions during the growing season for each

of the six experiments are described in Online Resource 1. Seeds were sown during the last 5 days of September in DL and the middle 10 days of April in GS each year, and on 7th October in WH. The field experiments were in a randomized complete block design with three replications in DL and two replications in GS and WH. The experimental unit was a two-row plot with 12 plants per row and 40 cm between the rows (Wang et al. 2013), and field management followed normal agricultural practice.

Five representational plants in the middle of each plot were selected to measure PH during plant development. PH was measured from the surface of the soil to the tip of each plant, and measured at eight successive times in 10DL, 11DL, 12DL and 12WH experiments, and six and seven times in 11GS and 12GS during the whole rapeseed growth period, designated as T_1–T_F (Online Resource 2), respectively. The measurement was conducted every 5 days during T_1–T_7 stages in DL and WH, and T_1–T_5 in 11GS and T_1–T_6 in 12GS. At maturity, PH was designated as T_F. All lengths were determined in centimeters. The average of PH in each DH line across two or three replicates was used as raw data in the analysis.

Data analysis and QTL detection

Basic statistical analysis was implemented using SPSS 18.0 software (SPSS Inc., Chicago, IL, USA). The SEA-G3DH with the mixed major gene and polygene inheritance model was used to analyze the PH in KN population (Gai et al. 2003; Cao et al. 2013). SEA-G3DH includes 39 different models. We first use AIC [Akaike's Information Criterion (Akaike 1977)] to select the best fitting models, and 1–4 models with the least AIC were recognized as candidate genetic models. Then, the likelihood ratio test was used to test whether these models show significant difference according to Wang and Gai (2001). Genetic parameter was estimated using the best fitting model with the default settings in the software.

Unconditional phenotypic values were the data measured at different stages, and conditional phenotypic value of $T(t) - T(t-1)$ indicates the time interval of plant growth from stage $t-1$ to t, and the data collection methods were according to Zhu (1995). The WinQTL Cartographer 2.5 with composite interval mapping (CIM) model was used to determine the unconditional QTLs with additive effect for PH (Wang et al. 2012; Zhu 1995). Conditional QTLs were determined by the combination of the CIM and conditional data collection methods. The effects during the period from seeding to T_1 stage were recognized as the T_1 unconditional genetic effects. Significance levels for the LOD scores were first determined by 1000-permutation test based on a 5 % experiment-wise error rate. Based on the fact that most of the QTLs detected in the present study were co-localized with others, to avoid missing these QTLs with small genetic effects but repeatedly appeared in multiple environments, a lower LOD score corresponding to approximately $P = 0.15$ with LOD of 2.5 was used to identify unconditional and conditional QTLs, and these QTLs were termed 'identified QTLs'. QTL CIs were determined by 2-LOD intervals surrounding the QTL peak. QTLs that mapped to the same region with overlapping CIs were assumed to be the same (Arcade et al. 2004). BioMercator 2.1 software was used to integrate these identified QTLs into consensus QTLs using the meta-analysis method (Arcade et al. 2004; Goffinet and Gerber 2000), which has been successfully used in *B. napus* (Feng et al. 2012; Shi et al. 2009; Wang et al. 2013; Zhao et al. 2012). If an identified QTL had no overlapping CI with others, it was also regarded as a consensus QTL.

The consensus QTL nomenclature followed the description of McCouch et al. (1997) with minor modifications. A designation '*tfPH*', '*unPH*' or '*cPH*' followed with the linkage group (A1–A10 and C1–C9) was used to name the QTLs detected at the final time, by unconditional or conditional QTL mapping methods, respectively, while '*qPH*' was used to name the consensus QTLs integrated from the three types of QTLs mentioned above. If two or more consensus QTLs were identified in a linkage group, a hyphen '-' with a serial number of the QTL was added. For example, QTL *qPH.A2-2* indicates the second consensus QTL for PH on A2 linkage group.

Construction of the consensus map and QTL comparison for PH between different populations

To compare QTLs for PH detected in different populations, QTLs in previous studies were projected onto the KN genetic map using the map projection package in the BioMercator 2.1 software (Arcade et al. 2004; Goffinet and Gerber 2000). These included one F_2 population SE (Li et al. 2007); three DH populations: TN (Shi et al. 2009), BE (Ding et al. 2012) and QN (Chen et al. 2007); and one fixed IF_2 from QN population (named QN-IF_2) (Chen et al. 2007). As the TN and BE maps shared numerous common markers (represented by the same name) with the KN map on the corresponding linkage groups, a consensus map was constructed by projecting markers from the two maps onto the KN map based on these common markers. If there were no more than two common loci between TN/BE and KN maps, a third intermediate map was used to achieve projection as described by Jiang et al. (2014).

A 'two-round' strategy of QTL projection was adopted according to the description of Wang et al. (2013). In the first round, identified QTLs in different populations were collected and integrated into consensus QTLs using BioMercator 2.1. In the second round, these consensus QTLs were projected onto the KN or consensus map.

Direct projection of QTLs from an individual population onto the KN map was adopted when there were sufficient loci in common. Otherwise, QTLs were projected onto the consensus map. In addition, candidate genes responsible for PH in TN and BE populations were also projected onto the consensus map based on the common markers, and then these genes were used to identify homologous genes in *B. rapa* (Wang et al. 2011), *B. oleracea* (Liu et al. 2014) and *B. napus* (Chalhoub et al. 2014) using BLAST analysis.

Results

Phenotypic variation and genetic analysis for PH

The phenotypic values of PH for the KN population and its parents in different measuring stages in six experiments are presented in Table 1. In DL location, the male parent KenC-8 was higher than the female parent N53-2 during T_1–T_5 stages. However, N53-2 grew higher than KenC-8 during T_6–T_F (Table 1; Fig. 1). In GS, KenC-8 was significantly higher than N53-2 for all stages except the final stage T_F. At stage T_F, the PH of N53-2 was higher than KenC-8 (Table 1; Fig. 1). The main reason was that N53-2 was a winter-type cultivar and could not finish vernalization in the spring rapeseed area of GS, and so could not enter into reproductive growth and remained in vegetative growth until harvest.

There was high phenotypic variation and transgressive segregation in the KN population, with some lines taller than the tall parent or shorter than the short parent at all stages in all experiments (Table 1). For example, at the T_F stage in the 11DL experiment, the minimum PH of the population was 98.5 and the maximum 199.0 cm, with average of 154.8 cm, while the male and female parents were 151.7 and 165.3 cm, respectively. These indicated that PH was quantitatively inherited traits controlled by multiple genes. Most values of skewness and kurtosis for the distributions of PH in the KN population were <1.0 in absolute values (Table 1), suggesting that the segregation pattern of PH in diverse experiments appeared to fit a normal distribution model and the data were suitable for QTL analysis.

Pair plots were plotted for analyzing the linear relationship between the PH at different growth stages (Online Resource 3). From the results, it can be initially concluded that there was a strong positive linear relationship between the PH at adjacent growing periods. However, PH at maturity was not significantly correlated with PH at T_1-T_3 stages in six experiments. In spring environment (11GS and 12GS), there was a weak or no linear relationship between PH at maturity and all other stages. The correlation between flowering time (FT) and PH was also analyzed in five experiments (Online Resource 4). Except for in 11DL, FT was highly negatively correlated with PH at all developmental stages except for the last two in other four experiments (10DL, 12DL, 12GS and 12WH). Especially in the first six stages in 12GS, the Pearson correlation coefficients level ranged from –0.90 to –0.74.

The mixed major gene and polygene inheritance model was used to analyze the two parents and KN population for PH under each experiment. The results showed that the best fitness genetic models for PH in different developmental stages were different, and a total of eight best fitting models were selected out among the 39 models (Online Resource 5). The genetic model 4MG–AI, which was four major genes additive and epistasis inheritance model, was widely suitable for PH at 14 different stages. The heritability of major genes was ranged from 34.63 to 97.66 %, indicating that PH in *B. napus* was determined by the combination of major genes and poly-genes, mainly by the major genes. The selection in early generation may be effective in *B. napus* breeding.

QTL analysis for PH at the mature stage in the KN population

As most previous studies for PH in *B. napus* were only based on the phenotypic value at the mature stage, QTLs for PH at maturity were also analyzed for comparison with results of other studies.

A total of 31 identified QTLs distributed across 10 chromosomes were detected in six experiments, with additive effects in the range of −5.12 to 7.12 and the contributory percentage of single QTLs of 3.23–11.01 % (Table 2). Among these QTLs, 19 identified QTLs with overlapping CIs were further integrated into eight consensus QTLs, and the average CI of single QTL was reduced from 9.1 to 5.0 cM. Only one QTL (*tfPH.A3-1*) was consistently detected in four experiments and explained 3.69–11.01 % of PV; another QTL (*tfPH.A3-3*) was stably expressed in three experiments, and explained 6.04–8.76 % of PV, indicating that these two QTLs were the main-effect QTLs in the KN DH population. No QTL was repeatedly detected in more than four experiments, whereas six QTLs were detected in two different experiments, including a spring macro-environment special QTL (*tfPH.A2-3*) only expressed at GS, four winter macro-environment special QTLs (*tfPH.C6-1*, *tfPH.C6-2*, *tfPH.C9-3* and *tfPH.C9-4*) only repeatedly detected at DL, and one QTL (*tfPH.C9-1*) expressed at both DL and WH. The other 12 non-overlapping QTLs were also regarded as consensus QTLs. In total, there were 20 consensus QTLs for PH based on the phenotypic value at the mature stage in the present study (Table 2; Fig. 2).

Table 1 Phenotypic values of plant height (cm) for the KN population and its parents in eight different growth stages evaluated in six experiments

Experiments	Stages	Parents		DH lines				
		KenC-8	N53-2	Min.	Max.	Mean ± SD	Skewness	Kurtosis
10DL	T_1	20.3 ± 2.28	12.7 ± 0.58	4.0	27.0	13.8 ± 3.30	0.08	1.21
	T_2	53.7 ± 6.03	37.0 ± 1.01	10.0	60.7	36.6 ± 8.90	−0.50	0.66
	T_3	68.0 ± 8.35	54.3 ± 4.51	12.0	79.0	51.6 ± 11.55	−1.08	1.64
	T_4	103.0 ± 6.29	87.7 ± 4.93	17.0	107.3	81.6 ± 13.47	−1.72	1.42
	T_5	134.3 ± 8.19	131.3 ± 9.07	37.0	144.3	114.2 ± 14.27	−1.72	1.95
	T_6	145.0 ± 9.22	157.0 ± 2.65	69.3	164.3	132.0 ± 14.95	−1.22	2.28
	T_7	147.3 ± 10.58	163.7 ± 7.23	81.0	171.3	141.6 ± 14.71	−1.02	1.75
	T_F	155.7 ± 6.03	166.0 ± 5.58	94.3	182.0	145.2 ± 14.60	−0.82	1.19
11DL	T_1	26.3 ± 2.08	15.0 ± 3.0	7.0	45.7	20.8 ± 5.33	0.29	1.34
	T_2	51.7 ± 2.02	32.3 ± 4.16	10.3	68.3	38.0 ± 9.40	0.03	0.35
	T_3	93.3 ± 2.89	66.7 ± 6.43	19.0	103.5	74.3 ± 13.29	−0.69	1.00
	T_4	119.7 ± 6.11	105.7 ± 2.52	52.3	148.7	112.3 ± 13.25	−1.18	2.78
	T_5	132.7 ± 11.02	126.0 ± 11.14	79.7	167.7	130.2 ± 13.89	−0.91	1.95
	T_6	142.7 ± 11.78	153.3 ± 11.67	90.3	186.7	144.9 ± 14.41	−0.67	1.57
	T_7	145.0 ± 9.85	160.0 ± 10.44	95.7	193.0	152.6 ± 15.02	−0.42	0.59
	T_F	151.7 ± 5.86	165.3 ± 6.24	98.5	199.0	154.8 ± 15.14	−0.46	1.03
12DL	T_1	44.3 ± 3.79	23.0 ± 3.61	8.0	53.3	27.6 ± 7.81	0.25	0.69
	T_2	69.0 ± 6.08	51.7 ± 5.77	13.7	81.3	47.4 ± 11.65	−0.23	0.27
	T_3	91.0 ± 4.0	77.3 ± 3.51	30.0	111.0	76.7 ± 13.42	−0.82	1.06
	T_4	111.3 ± 5.29	105.0 ± 1.73	56.0	137.7	99.2 ± 12.82	−0.64	1.18
	T_5	126.7 ± 1.15	119.3 ± 3.21	62.3	161.3	113.6 ± 13.87	−0.61	1.52
	T_6	134.3 ± 6.93	139.3 ± 6.81	67.3	171.0	121.5 ± 14.19	−0.36	0.97
	T_7	138.0 ± 4.64	150.0 ± 1.15	76.7	175.7	130.8 ± 14.22	−0.56	0.85
	T_F	145.7 ± 4.35	156.7 ± 6.24	87.3	180.3	133.9 ± 14.67	−0.44	0.45
11GS	T_1	57.5 ± 8.50	25.0 ± 3.0	10.0	121.5	50.5 ± 24.29	0.62	−0.15
	T_2	79.0 ± 6.05	33.0 ± 2.03	17.0	147.0	74.2 ± 31.45	0.34	−0.84
	T_3	109.0 ± 11.50	42.5 ± 2.50	26.0	169.0	101.4 ± 37.49	−0.15	−1.22
	T_4	147.5 ± 2.52	60.5 ± 4.50	38.0	181.0	125.5 ± 36.69	−0.60	−0.92
	T_5	176.0 ± 6.0	80.0 ± 3.0	52.5	193.0	151.4 ± 32.67	−1.27	0.58
	T_F	190.0 ± 2.53	201.5 ± 13.45	141.0	276.5	190.1 ± 19.23	0.57	2.85
12GS	T_1	36.0 ± 6.03	19.5 ± 2.52	10.0	115.5	36.2 ± 19.41	1.18	1.36
	T_2	62.5 ± 4.51	30.0 ± 4.04	14.0	134.0	61.0 ± 28.45	0.50	−0.56
	T_3	99.0 ± 3.06	43.5 ± 9.54	16.5	160.0	86.8 ± 34.85	0.14	−1.04
	T_4	145.0 ± 3.21	59.5 ± 7.50	17.5	177.5	115.9 ± 36.97	−0.36	−1.04
	T_5	180.5 ± 4.59	78.5 ± 2.52	47.5	189.0	140.6 ± 33.96	−0.73	−0.68
	T_6	193.0 ± 7.50	120.0 ± 11.58	69.5	203.5	157.8 ± 32.07	−0.79	−0.53
	T_F	208.5 ± 4.51	228.0 ± 10.40	123.0	261.0	200.2 ± 23.31	−0.38	1.26
12WH	T_1	53.0 ± 3.05	34.0 ± 4.58	10.0	73.0	31.6 ± 12.13	0.63	−0.07
	T_2	114.5 ± 6.03	77.5 ± 6.65	16.5	120.0	73.4 ± 20.50	−0.15	−0.35
	T_3	129.0 ± 5.13	112.0 ± 4.58	34.5	142.0	99.5 ± 19.02	−0.37	0.18
	T_4	140.5 ± 4.04	134.5 ± 2.65	55.5	156.5	117.4 ± 17.24	−0.53	0.79
	T_5	152.0 ± 3.79	154.5 ± 2.08	80.5	176.0	134.7 ± 16.84	−0.28	0.24
	T_6	157.5 ± 2.89	168.0 ± 3.61	89.5	180.5	142.5 ± 16.03	0.01	−0.22
	T_7	158.0 ± 4.52	175.0 ± 4.72	104.0	185.0	149.7 ± 15.21	−0.36	−0.03
	T_F	165.0 ± 3.08	178.5 ± 5.96	115.0	191.5	158.1 ± 14.11	−0.06	0.11

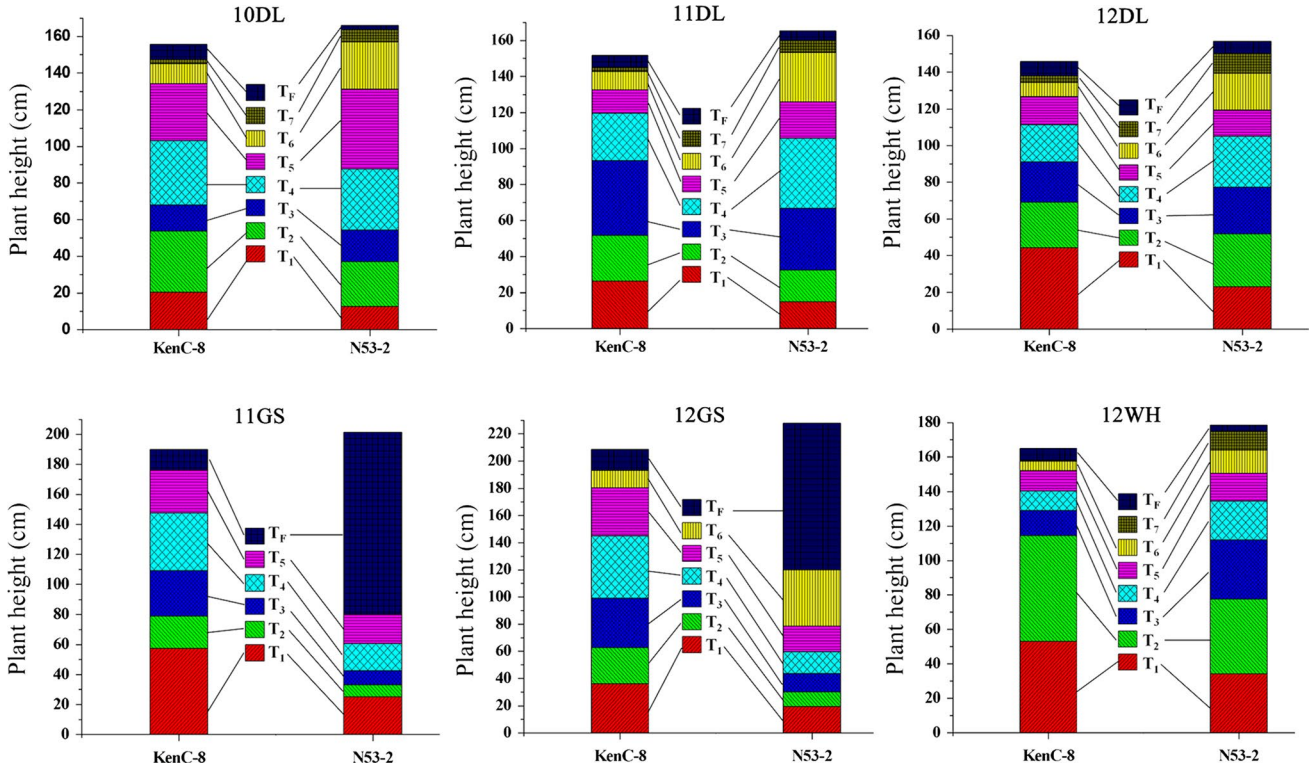

Fig. 1 Distribution of plant height in the two parents of KN DH population. The units of *y* axis are the phenotypic values of PH for the KenC8 and N53-2 in multiple developmental stages/periods of the life cycle in six experiments. PH in different stages/periods was discriminated with *different color boxes* (T_1 *red*, T_2 *green*, T_3 *blue*, T_4 *cyan*, T_5 *magenta*, T_6 *yellow*, T_7 *dark yellow*, T_F *navy*) (color figure online)

Unconditional QTL mapping for PH in the developing stages of the KN population

Except for the data collected at the final stage in the KN population, the phenotypic values at five (in 11GS), six (12GS) and seven (10DL, 11DL, 12DL and 12WH) developmental stages were used to identify unconditional QTLs for PH in different experiments, respectively (Online Resource 2).

Up to 231 identified QTLs distributed throughout 15 chromosomes (excluding A5, A8, C7 and C8) were identified, individually explaining 2.18–27.32 % of PV, with additive effects in the range of −19.60 to 6.85 (Table 3; Online Resource 6). There were 217 identified QTLs with overlapping CIs and these were integrated into 36 consensus QTLs. The other 14 non-overlapping consensus QTLs were also considered as consensus QTLs. In total, 50 unconditional consensus QTLs were obtained in the KN DH population (Table 3; Fig. 2). Of these QTLs, 11 consensus QTLs distributed on chromosomes A2, A3, A7, A9, A10 and C5 were only expressed at GS, while 13 consensus QTLs located on A3, A6, C2, C6 and C9 were only identified at DL (Table 3). For example, QTL *ucPH.A3-2* located on A3, with the closely linked marker CB10036 of 2.16 cM, was only expressed at T_1–T_5 stages in 11GS and T_2 in 12GS experiments, while *ucPH.A3-10*, with the closely linked marker BnGMS291 of 0.43 cM, was only expressed at T_6–T_7 stage in 11DL and T_7 in 10DL experiments (Online Resource 6). In addition, two QTLs (*ucPH.A10-5* and *ucPH.A10-6*) on A10 chromosome with linked markers of 1.01 and 4.81 cM, respectively, were repeatedly detected at all three locations but with significantly different additive effects in the different experiments. Interestingly, five unconditional QTLs (*ucPH.A2-2*, *ucPH.A3-2*, *ucPH.C5-1*, *ucPH.C6-2* and *ucPH.C6-3*) were expressed steadily in all stages of one or two particular experiments. For example, QTL *ucPH.A2-2*, which showed an initially increased effect and then decreased in absolute value and closely linked with marker BnGMS135, was consistently detected at all developmental stages in 11GS and 12GS experiments (Fig. 3). Thus, a total of 50 QTLs showed effects on PH at different stages according to unconditional QTL analysis, but only 20 were identified at the harvest stage, suggesting that some QTLs were detected at particular stages but not at the last stage.

Conditional QTL mapping in the KN population

The measured stages were divided into three growing stages according to the life cycle of rapeseed: stem

Table 2 QTLs for plant height detected at the mature stage in six experiments

Consensus QTLs				Identified QTLs						Env.[e]
QTL[a]	Peak	Marker[b]	CI	Chr.[c]	LOD	Peak	CI[d]	Additive	R^2 (%)	
tfPH.A1-1	0	niab032 (0)	0.0–6.8	A1	3.02	0	0.0–6.8	2.92	3.74	12DL
tfPH.A2-1	37.6	B060E11-1b (37.56)	34.3–39.9	A2	3.21	37.6	34.3–39.9	2.99	3.88	11DL
tfPH.A2-2	48.5	B070J05b (44.49)	39.9–58.5	A2	2.55	48.5	39.9–58.5	2.95	3.76	11DL
tfPH.A2-3	64.4	BnGMS135 (64.05)	58.9–69.9	A2	7.51	64.1	59.4–71.2	5.9	9.26	11GS
				A2	3.95	66.1	53.3–82.2	5.76	5.8	12GS
tfPH.A3-1	135.5	S002B15-1b (136.86)	132.3–138.8	A3	5.67	132.6	122.5–141.3	7.12	9.08	12GS
				A3	6.64	134.6	127.7–139.4	4.76	9.69	11DL
				A3	2.83	136.6	123.2–139.4	2.82	3.69	10DL
				A3	8.71	136.6	128.8–138.9	6.51	11.01	11GS
tfPH.A3-2	140.1	BnGMS291 (140.12)	139.4–141.8	A3	5.33	140.1	139.4–141.8	4.03	6.74	11DL
tfPH.A3-3	147.2	e7m8-158 (145.7)	146.1–148.4	A3	4.46	142.6	141.8–147.7	5.87	6.04	12GS
				A3	6.95	145.7	143.0–147.7	5.95	8.76	11GS
				A3	5.22	147.7	145.7–148.3	4.19	7.21	11DL
tfPH.A7-1	9	Ra2G10b (10.55)	0.0–14.6	A7	3.86	9	0.0–14.6	4.26	4.69	11GS
tfPH.A7-2	24.6	BnGMS151 (14.63)	14.6–41.1	A7	3.74	24.6	14.6–41.1	5.2	6.83	11GS
tfPH.C1-1	68.7	BnGMS301 (68.71)	52.5–73.7	C1	2.62	68.7	52.5–73.7	−2.81	3.36	12DL
tfPH.C2-1	27.7	e18m6-298 (19.72)	8.0–40.5	C2	2.71	27.7	8.0–40.5	−4.31	4.48	11GS
tfPH.C3-1	74.8	e10m25-383 (74.74)	60.6–86.0	C3	2.8	74.8	60.6–86.0	−2.78	3.56	10DL
tfPH.C3-2	113.8	MR049 (113.89)	107.2–129.2	C3	3.69	113.8	107.2–129.2	4.23	4.36	11GS
tfPH.C4-1	0	SA5 (0)	0.0–1.3	C4	4.12	0	0.0–1.3	−3.45	5.32	12DL
tfPH.C6-1	67.2	e18m15-394 (67.22)	66.2–68.2	C6	2.55	67.2	65.8–68.6	2.92	3.24	10DL
				C6	2.66	67.2	65.9–68.6	3.02	3.23	11DL
tfPH.C6-2	77.1	CNU053 (77.08)	72.3–81.9	C6	3.34	77.1	71.4–85.1	3.31	4.36	10DL
				C6	3.33	77.1	71.4–85.1	3.31	4.14	11DL
tfPH.C9-1	0	ZAAS326 (0)	0.0–1.0	C9	7.45	0	0.0–1.0	−5.12	9.87	12DL
				C9	2.58	0	0.0–7.2	−3.34	3.69	12WH
tfPH.C9-2	3.6	e21m12-313 (3.64)	1.0–5.5	C9	6.1	3.6	1.0–5.5	−4.6	7.46	11DL
tfPH.C9-3	8.4	e11m13-497 (8.4)	7.3–9.5	C9	5.55	8.4	7.6–10.7	−-4.36	7.29	10DL
				C9	5.06	8.4	7.2–10.4	−4.37	6.79	12DL
tfPH.C9-4	14.9	e19m2-425 (14.89)	12.4–17.4	C9	6.95	14.9	13.7–20.4	−4.79	9.03	10DL
				C9	4.89	14.9	11.4–18.8	−4.06	6.03	11DL

DL Dali, *GS* Gansu, *WH* Wuhan, *10*, *11*, *12* denote the year of 2010, 2011 and 2011, respectively

[a] Consensus QTLs detected at the mature stage in different experiments

[b] The closest marker and the marker position in the KN map

[c] Chromosome

[d] The 2-LOD confidence interval of QTLs

[e] The experiment in which QTLs were detected

elongation (I: $T_2 - T_1$ and $T_3 - T_2$), flowering (II: $T_4 - T_3$, $T_5 - T_4$ and $T_6 - T_5$) and green-ripe stages (III: $T_7 - T_6$ and $T_F - T_7$ in 10DL, 11DL, 12DL and 12WH; $T_F - T_5$ in 11GS and $T_F - T_6$ in 12GS). A total of 116 conditional identified QTLs were detected in six experiments (Online Resource 7) and explained 2.71–23.99 % of the PV with additive effects ranging from −5.90 to 19.97 (Table 4). At stage I, there were 46 identified QTLs detected in all six experiments, and five (11GS, 12DL and 12WH) to 13 (12GS) identified QTLs were obtained in single experiment (Online Resource 7). At stage II, six (12GS) to nine (10DL and 11DL) identified QTLs were detected in single experiment, except that only two QTLs were expressed in 11GS, and a total of 42 QTLs were obtained. Up to 88 identified QTLs were detected at the first two stages (I, II), consistent with the rapid growth of plants during these stages. During stage III, only one QTL was expressed in 10DL and no QTL was found in 11DL, 12DL and 12WH

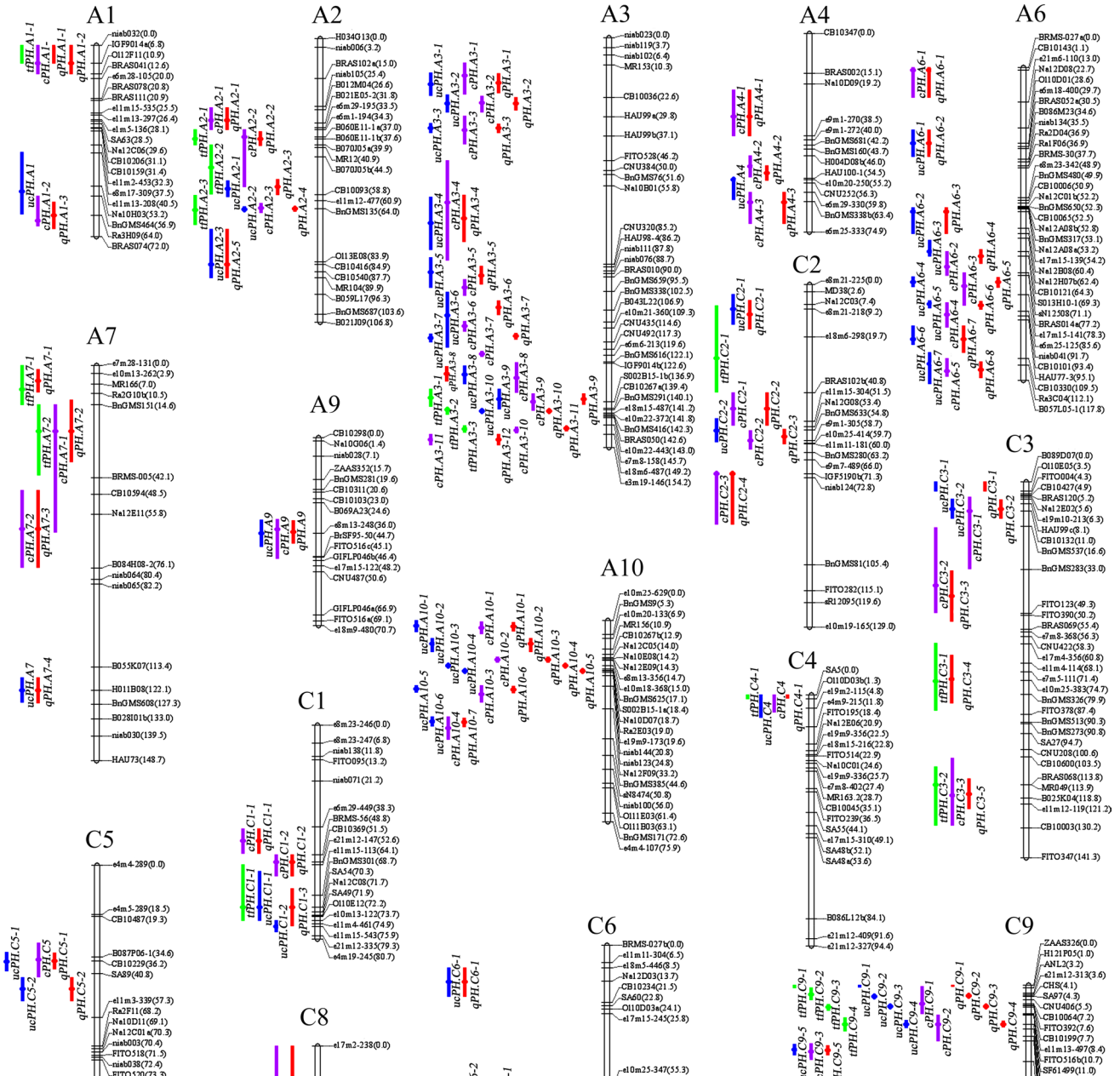

Fig. 2 The locations of QTLs associated with plant height in the KN map. The linkage groups are represented by *vertical bars*. The loci names are listed on the *right* of the linkage groups, and the positions are shown in the following *brackets*, given in centimorgan (cM). The consensus QTLs for PH detected by different mapping strategies are indicated by *bars* with various backgrounds on the left of each linkage group. (*Green bars* QTLs were detected at the mature stage, *blue bars* unconditional QTLs, *purple bars* conditional QTLs, *red bars* QTLs were integrated from the above three types of QTLs) (color figure online)

at T_F-T_7 stage. However, 10 and eight QTLs were identified in 11GS and 12GS throughout stage III, with mean additive effects of 10.44 and 11.30, respectively. These suggested that the alleles from female parent N53-2 greatly increased PH during the last periods in both 11GS and 12GS.

Table 3 Unconditional consensus QTLs for plant height in the KN DH population

Con QTLs[a]	Chr.	Peak	LOD	Add.	R^2 (%)	CI	Stages[a]
ucPH.A1	A1	55.2	2.67	2.72	3.58	40.3–63.6	12DL.T5
ucPH.A2-1	A2	56.5	11.31–12.89	−14.03 to −7.67	15.47–18.80	53.6–59.4	*12GS.T6/12GS.T1*
ucPH.A2-2	A2	64.1	2.98–24.92	−19.55 to 2.55	3.47–27.32	63.1–65.1	10DL.T4//11GS.T5/11GS.T4/11GS.T3/11GS.T2/11GS.T1//12GS.T6/12GS.T5/12GS.T4/12GS.T3/12GS.T2/12GS.T1
ucPH.A2-3	A2	84.9	3.56	0.69	4.23	71.6–89.9	10DL.T1
ucPH.A3-1	A3	17.5	2.79–6.63	−10.16 to −3.67	3.41–7.25	13.2–21.9	*12GS.T6/12GS.T5/12GS.T4/12GS.T3/12GS.T1*
ucPH.A3-2	A3	24.8	5.05–8.58	−10.85 to −6.67	5.64–9.58	21.6–28.0	*11GS.T5/11GS.T4/11GS.T3/11GS.T2/11GS.T1//12GS.T2*
ucPH.A3-3	A3	34.0	5.01–7.06	−10.17 to −6.38	4.89–6.67	32.2–35.8	*11GS.T3/11GS.T1//12GS.T3/12GS.T2*
ucPH.A3-4	A3	69.8	2.67–3.48	−2.21 to −1.37	5.3–6.37	59.9–79.7	**11DL.T2/11DL.T1**
ucPH.A3-5	A3	88.3	2.99–3.50	−1.10 to −0.62	3.35–4.16	82.7–93.9	**10DL.T1//11DL.T1**
ucPH.A3-6	A3	104.5	3.87	−7.06	4.79	95.7–116.6	12GS.T6
ucPH.A3-7	A3	113.0	2.72–4.04	−7.20 to −3.48	3.01–3.77	111.5–114.6	*11GS.T4/11GS.T3//12GS.T5/12GS.T4/12GS.T3/12GS.T2/12GS.T1*
ucPH.A3-8	A3	126.8	3.64–5.45	−9.12 to −6.45	4.61–6.14	123.4–130.3	*11GS.T4/11GS.T3//12GS.T5/12GS.T4/12GS.T3/12GS.T2*
ucPH.A3-9	A3	136.1	2.56–5.56	2.60 to 4.27	2.99–7.93	132.4–139.9	10DL.T6‖11DL.T7‖12WH.T7/12WH.T6
ucPH.A3-10	A3	140.6	4.04–6.37	3.38 to 3.99	5.06–7.14	139.8–141.3	**10DL.T7//11DL.T7/11DL.T6**
ucPH.A4	A4	55.2	3.48	2.13	4.02	54.5–62.5	10DL.T2
ucPH.A6-1	A6	28.6	2.88–3.13	−2.71 to −2.49	3.51–3.67	23.6–33.6	**12DL.T7/12DL.T4**
ucPH.A6-2	A6	54.2	2.88	−2.09	3.09	52.8–62.4	12DL.T2
ucPH.A6-3	A6	69.3	3.56	−0.70	4.38	65.0–71.1	10DL.T1
ucPH.A6-4	A6	80.7	2.79–6.20	−4.38 to −0.98	3.86–8.59	78.7–82.6	10DL.T3/10DL.T2/10DL.T1//11DL.T2/11DL.T1//12DL.T1//12WH.T4/12WH.T2/12WH.T1
ucPH.A6-5	A6	89.1	3.05–5.81	−2.44 to −0.93	4.10–7.74	87.7–90.6	**10DL.T3/10DL.T2/10DL.T1//11DL.T2/11DL.T1**
ucPH.A6-6	A6	102.2	4.17–5.37	−2.35 to −1.51	6.16–7.87	97.3–104.2	**11DL.T2/11DL.T1**
ucPH.A6-7	A6	111.6	2.51–3.45	−6.73 to −2.27	2.84–4.12	107.2–118.9	11DL.T3//11GS.T5
ucPH.A7	A7	122.1	2.58–2.60	3.29 to 3.93	2.54–2.76	117.4–126.8	*11GS.T1//12GS.T1*
ucPH.A9	A9	35.9	2.50–2.90	5.59 to 6.01	2.18–3.48	31.0–41.0	*11GS.T3/11GS.T2//12GS.T3*
ucPH.A10-1	A10	2.0	3.48–4.66	−8.37 to −7.57	4.13–5.66	0.0–4.3	*11GS.T5‖12GS.T6/12GS.T5*
ucPH.A10-2	A10	8.9	3.18	−7.62	4.04	6.9–11.8	11GS.T5
ucPH.A10-3	A10	17.0	2.82–4.75	−9.98 to −3.12	2.80–4.73	16.4–17.7	11GS.T3/11GS.T2/11GS.T1//12DL.T2//12GS.T4/12GS.T3//12WH.T1
ucPH.A10-4	A10	19.0	4.80	−9.93	4.49	18.4–19.6	11GS.T4
ucPH.A10-5	A10	25.8	2.84–7.59	−11.42 to −1.22	4.29–10.19	24.6–27.0	10DL.T2/10DL.T1//11GS.T4/11GS.T3/11GS.T2/11GS.T1//12DL.T3/12DL.T2//12GS.T4/12GS.T3/12GS.T2//12WH.T6/12WH.T4/12WH.T3/12WH.T2/12WH.T1
ucPH.A10-6	A10	38.1	3.30–7.73	−9.52 to −1.35	4.53–11.23	36.3–39.8	10DL.T5/10DL.T4/10DL.T3/10DL.T1/12DL.T1//11DL.T4/11DL.T3/11DL.T2/11DL.T1//12GS.T3/12GS.T2/12GS.T1//12WH.T5
ucPH.C1-1	C1	68.7	2.80	−2.89	3.32	55.0–73.7	11DL.T7
ucPH.C1-2	C1	75.9	2.65	−2.51	3.11	73.7–77.9	11DL.T5
ucPH.C2-1	C2	9.3	2.64–2.85	−5.68 to −2.63	2.72–3.11	3.7–14.9	11DL.T6//12GS.T6/12GS.T5
ucPH.C2-2	C2	54.9	3.27–3.78	1.22 to 2.77	3.60–4.39	50.6–59.2	**11DL.T3/11DL.T2/11DL.T1**
ucPH.C3-1	C3	0.0	2.75	1.49	3.28	0.0–3.5	12DL.T1
ucPH.C3-2	C3	10.1	2.56–4.02	−3.34 to 5.13	3.24–4.80	6.4–13.7	10DL.T5//11DL.T7//12DL.T2/12DL.T1//12WH.T4
ucPH.C4	C4	0.0	3.03	−2.85	3.44	0.0–8.3	11DL.T7
ucPH.C5-1	C5	36.3	2.60–5.90	−8.68 to −4.02	2.68–5.49	32.8–39.8	10DL.T5‖11GS.T5/11GS.T4/11GS.T3/11GS.T2/11GS.T1‖12GS.T6/12GS.T5/12GS.T4

Table 3 continued

Con QTLs[a]	Chr.	Peak	LOD	Add.	R^2 (%)	CI	Stages[a]
ucPH.C5-2	C5	46.6	2.93–3.62	−7.87 to −7.14	4.01–4.79	42.3–51.0	*11GS.T3//12GS.T5/12GS.T4/12GS.T3*
ucPH.C6-1	C6	13.8	3.61	−3.10	4.01	8.5–19.4	11DL.T6
ucPH.C6-2	C6	58.8	2.62–11.51	1.43 to 6.07	3.68–15.40	58.1–59.6	**10DL.T3/10DL.T2//11DL.T7/11DL.T6/11DL.T5/11DL.T4/11DL.T3/11DL.T2/11DL.T1//12DL.T3**
ucPH.C6-3	C6	67.3	3.06–14.71	1.08 to 6.85	4.24–17.72	67.1–67.5	10DL.T7/10DL.T6/10DL.T5/10DL.T4/10DL.T3/10DL.T2/10DL.T1//11DL.T7/11DL.T6/11DL.T5/11DL.T4/11DL.T3/11DL.T2/11DL.T1//12DL.T5/12DL.T4/12DL.T3/12DL.T2//12WH.T4/12WH.T3/12WH.T2/12WH.T1
ucPH.C6-4	C6	72.8	2.52–12.94	1.61 to 6.42	3.47–17.93	71.8–73.7	10DL.T7/10DL.T6/10DL.T5//11DL.T7/11DL.T6/11DL.T4/11DL.T3/11DL.T1//12DL.T4/12DL.T3/12DL.T2/12DL.T1//12WH.T5/12WH.T4/12WH.T3/12WH.T2
ucPH.C6-5	C6	79.8	4.60–8.58	3.87 to 5.08	6.60–11.80	77.3–82.2	**12DL.T6/12DL.T5**
ucPH.C9-1	C9	0.0	3.15–7.38	−4.78 to −3.17	4.34–9.40	0.0–0.9	12DL.T7//12WH.T7/12WH.T6
ucPH.C9-2	C9	4.3	3.18–7.21	−4.95 to −3.13	4.07–8.83	3.6–4.7	**11DL.T7//12DL.T6/12DL.T5**
ucPH.C9-3	C9	8.0	4.68–7.21	−4.41 to −3.53	5.62–8.38	7.3–8.8	**10DL.T7/10DL.T6//11DL.T6/11DL.T5/11DL.T4/11DL.T3**
ucPH.C9-4	C9	14.7	4.31–6.92	−4.82 to −3.27	5.43–8.74	13.4–16.0	**10DL.T7/10DL.T6/10DL.T5/10DL.T4//11DL.T7/11DL.T6/11DL.T5//12DL.T6/12DL.T5/12DL.T4**
ucPH.C9-5	C9	24.4	3.43–4.40	−3.56 to −2.54	4.41–5.76	22.4–26.4	**12DL.T6/12DL.T5/12DL.T4/12DL.T3/12DL.T2**
ucPH.C9-6	C9	48.3	4.88	4.58	5.92	41.4–50.3	12GS.T1

[a] Stages with bold indicated that the QTL was only expressed at DL location, while stages with italics indicated that the QTL was only expressed at GS location

The 116 conditional identified QTLs were integrated into 50 consensus QTLs, including 23 consensus QTLs integrated from 89 identified QTLs with overlapping CIs and 27 non-overlapping identified QTLs (Online Resource 7). A striking finding was that the same QTLs had opposite additive effects in different experiments, such as QTLs *cPH.A3-2*, *cPH.A3-5*, *cPH.A3-8*, *cPH.A6-4*, *cPH.A7-1* and *cPH.A10-3* (Online Resource 7). In addition, 11 QTLs had opposite additive effects at different periods even in the same experiment, including *cPH.A3-1*, *cPH.A2-3*, *cPH.A3-3*, *cPH.A3-6*, *cPH.A3-7*, *cPH.A10-1*, *cPH.A10-4*, *cPH.C5*, *cPH.C6-1*, *cPH.C6-2* and *cPH.C6-3* (Online Resource 7). For example, QTL *cPH.A2-3* had a negative additive effect during stage I in both 11GS and 12GS, but had a positive additive effect during stages II and III (Fig. 3). These findings implied that some QTLs showed different expression patterns in different experiments, or even in the same experiment but during different developmental periods. None of these QTLs associated with PH were expressed throughout the entire growth process, except that one QTL (*cPH.A2-3*) was detected during all five developmental periods in 11GS. These phenomena were consistent with the theory of developmental genetics that genes are expressed selectively at different developmental periods.

Integration of QTLs detected by unconditional and conditional QTL analyses

To understand the difference in QTL detection in different developmental growing periods and experiments, all QTLs detected at the mature stage, by unconditional and conditional QTL methods, were further integrated into consensus QTLs using a meta-analysis method. In total, 16 chromosomes (excluding A5, A8 and C7) in the KN population were shown to harbor loci affecting PH, and 378 identified QTLs with additive effects in the range of −19.55 to 19.97 were detected, individually accounting for 2.18–27.32 % of PV (Online Resource 8).

Of the 378 QTLs, 360 identified QTLs with overlapping CIs were integrated into 52 consensus QTLs, and the remaining 18 identified QTLs were only detected during one period/stage (Online Resource 8). Altogether, 70 consensus QTLs were obtained, and 19, 13 and 38 QTLs were detected by only unconditional, only conditional and both unconditional and conditional QTL methods, respectively (Fig. 2; Online Resource 8). Except for one QTL *qPH.A1-1* (also referred to as *tfPH.A1-1*), the remaining 19 QTLs detected at the mature stage were all co-localized with other QTLs detected by unconditional and/or conditional QTL methods. An important finding was that 33 QTLs

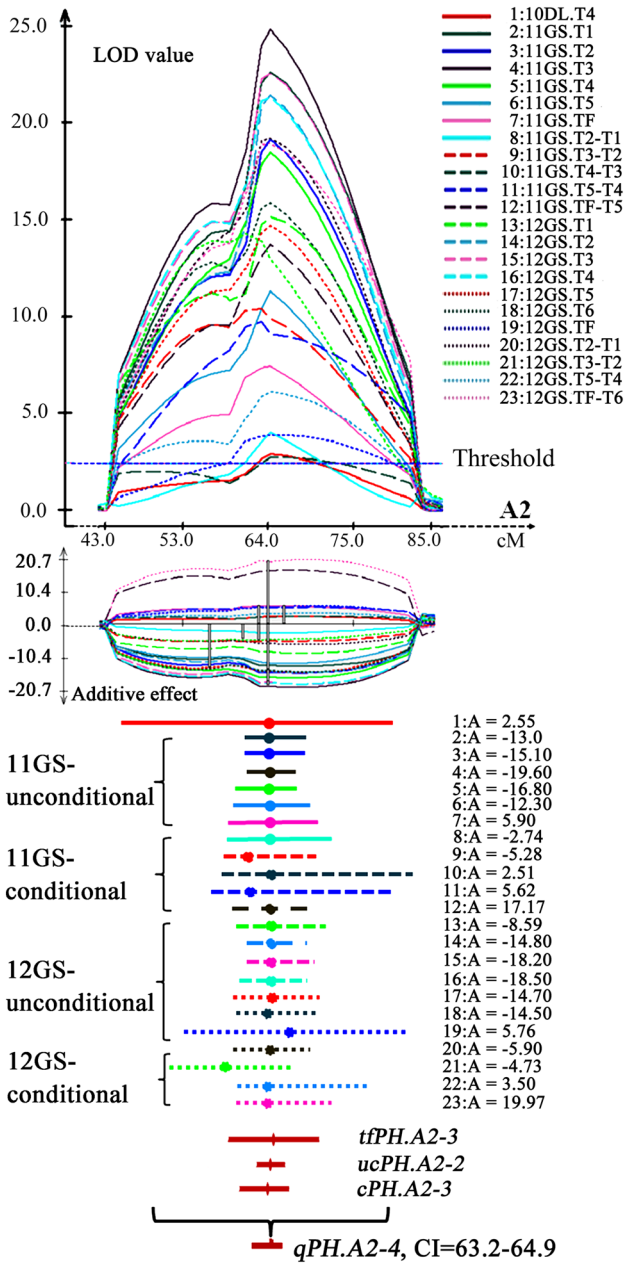

Fig. 3 Demonstration of QTLs with opposite genetic effects in the different periods/stages. Original QTLs identified in the different periods/stages of different experiments are shown by *curves* above the line of linkage group, and their additive effect are shown by *curves* of the *same color* below the line of the linkage group. The CIs of QTLs are shown by the same type of lines with original QTL curves and the sizes of additive effect are also listed on the *right* of the CIs. The *solid dull-red lines* are the CIs of the integrated QTLs by meta-analysis. *A* additive effect (color figure online)

were repeatedly detected over the whole growth season under different field conditions but not at the mature stage. For example, seven QTLs (*qPH.A3-7*, *qPH.A3-8*, *qPH.A6-5*, *qPH.A10-6*, *qPH.A10-7*, *qPH.C5-1* and *qPH.C6-2*) were repeatedly detected during >10 periods and stages but not at stage T_F (Online Resource 8), and these QTLs were also very important for PH during the growing stages. This result indicated that combining unconditional and conditional mapping methods could more precisely reveal the dynamic QTLs for this trait.

QTL comparison for PH between different populations

A total of 786 and 840 markers were mapped to the TN and BE maps, respectively (Ding et al. 2012; Shi et al. 2009). A consensus map with 1357 markers was constructed by projecting the markers from TN and BE maps onto the KN map based on the common markers (Online Resource 9). The consensus map covered 2203.0 cM with an average interval of 1.62 cM between adjacent markers. The length ranged from 57.0 (C7) to 283.7 cM (A7) for each individual chromosome, with average length of 115.9 cM.

There were 15, 12, 17, 87 and 9 identified QTLs for PH detected in QN, QN-IF$_2$, SE, TN and BE populations, respectively (Chen et al. 2007; Ding et al. 2012; Li et al. 2007; Shi et al. 2009). After integrating those QTLs with overlapped CIs in the same population, 9, 11, 15, 44 and 7 consensus QTLs were, respectively, obtained in the five populations (Online Resource 10). Subsequently, these consensus QTLs were projected onto the consensus map using BioMercator 2.1 software (Fig. 4; Online Resource 9). As a result, 33 consensus QTLs on the TN genetic map were projected onto the consensus map, accounting for 75.0 % (33/44) of the total consensus QTLs. Similarly, four, six, seven and nine QTLs on BE, QN, QN-IF$_2$ and SE populations were projected onto the corresponding linkage groups of the consensus map, respectively (Online Resource 10), accounting for 57.1 (4/7), 66.7 (6/9), 63.6 (7/11) and 60.0 % (9/15) of the total consensus QTLs on the individual map.

Comparing the projected QTLs from other populations onto the consensus map with the QTLs detected in the KN population (including unconditional and conditional QTLs) showed that 27 QTL intervals were stably detected in different populations (Fig. 4). These included six and four intervals located on A3 and A7, respectively; three each on A6, C3 and C6; two each on A1, A2 and A10; and one each on A9 and C4. An interesting finding was that only six QTLs detected at the mature stage of the KN population were co-localized with other populations, including with four QTLs in TN (A2, A3 and A7) and two in QN (C3 and C6) populations. However, a large number of QTLs detected by unconditional/conditional mapping methods were co-localized with QTLs from previous studies. For example, there were three QTLs located on chromosome A3 identified at maturity, and two were co-localized with QTLs in the TN population but none with other populations (Fig. 4). Nevertheless, QTLs from BE (*BE-qPH.A3*),

Table 4 Conditional consensus QTLs for plant height in the KN DH population

Con QTLs	Chr.	Peak	LOD	Add.	R^2 (%)	CI	Stages
cPH.A1-1	A1	6.8	4.47	−2.76	6.35	0.0–10.9	12GS.T3-T2
cPH.A1-2	A1	66.0	3.91	2.99	5.93	56.9–68.0	12GS.T4-T3
cPH.A2-1	A2	30.6	2.90	1.35	4.03	25.9–34.3	11DL.T3-T2
cPH.A2-2	A2	37.0	4.19	1.53	5.16	34.3–55.8	11DL.T3-T2
cPH.A2-3	A2	63.7	2.79–19.29	−5.90 to 19.97	4.13–23.99	61.9–65.5	11GS.TF-T5/11GS.T5-T4/11GS.T4-T3/11GS.T3-T2/11GS.T2-T1//12GS.TF-T6/12GS.T5-T4/12GS.T3-T2/12GS.T2-T1
cPH.A3-1	A3	14.3	4.46–5.23	−3.37 to 9.99	5.24–8.16	9.6–21.2	11GS.TF-T5/11GS.T2-T1
cPH.A3-2	A3	24.5	2.58–4.59	−2.82 to 1.35	3.94–5.32	22.0–27.9	12GS.T2-T1//12DL.T4-T3
cPH.A3-3	A3	34.8	3.66–4.80	−2.91 to 8.86	3.96–5.37	29.7–40.0	12GS.TF-T6/12GS.T2-T1
cPH.A3-4	A3	61.9	2.68	1.70	5.08	46.2–83.8	11DL.T4-T3
cPH.A3-5	A3	94.0	2.52–3.51	−2.09 to 1.35	2.97–4.73	91.0–96.9	10DL.T4-T3//12DL.T2-T1//12GS.T2-T1
cPH.A3-6	A3	108.6	2.71–6.29	−2.31 to 11.01	3.67–7.46	106.8–110.4	12WH.T5-T4//11DL.T5-T4//12GS.TF-T6/12GS.T2-T1
cPH.A3-7	A3	119.0	3.75–9.16	−3.04 to 14.13	4.73–10.98	117.9–120.0	12WH.T5-T4//11GS.TF-T5/11GS.T3-T2//12GS.TF-T6
cPH.A3-8	A3	127.9	2.73–2.77	−2.07 to 1.17	2.95–3.94	122.4–133.5	12GS.T2-T1//12WH.T5-T4
cPH.A3-9	A3	137.1	3.03–3.96	1.21 to 1.71	3.92–6.21	134.0–140.3	10DL.T6-T5/10DL.T5-T4//11DL.T6-T5/11DL.T4-T3//12DL.T5-T4
cPH.A3-10	A3	147.7	2.70–5.91	1.19 to 11.49	4.18–6.8	146.5–148.9	11DL.T6-T5/11DL.T4-T3//11GS.TF-T5//12DL.T5-T4
cPH.A3-11	A3	151.3	3.18	1.54	5.35	149.3–153.3	10DL.T5-T4
cPH.A4-1	A4	31.3	2.98	−1.79	7.07	21.4–38.5	12GS.T6-T5
cPH.A4-2	A4	50.0	2.79	−1.43	4.84	46.0–54.0	12GS.T6-T5
cPH.A4-3	A4	63.5	2.52	2.42	3.60	59.8-71.5	12GS.T4-T3
cPH.A6-1	A6	1.1	2.93	1.07	4.19	0.0–11.2	11DL.T5-T4
cPH.A6-2	A6	75.1	2.50	1.18	3.68	69.3–78.3	11DL.T7-T6
cPH.A6-3	A6	82.3	5.21	1.73	7.81	77.3–89.4	10DL.T6-T5
cPH.A6-4	A6	93.1	2.76–3.22	−1.08 to 7.05	2.71–4.49	88.5–97.7	11DL.T2-T1//11GS.TF-T5
cPH.A6-5	A6	114.2	3.22	7.98	3.33	109.5–116.2	11GS.TF-T5
cPH.A7-1	A7	3.9	2.65–2.81	1.13 to −2.03	2.80–3.89	0.0–9.1	12DL.T5-T4//12GS.T2-T1
cPH.A7-2	A7	24.6	2.68	−2.54	4.20	14.6–62.6	12GS.T2-T1
cPH.A7-3	A7	61.4	2.56–3.30	1.30 to 1.42	3.96–5.24	46.8–76.0	10DL.T6-T5//12DL.T7-T6
cPH.A9	A9	34.6	2.95	2.24	3.42	30.8–45.6	12GS.T2-T1
cPH.A10-1	A10	2.8	2.7–3.73	−2.28 to 9.47	3.03–3.96	0.6–5.1	11GS.TF-T5//12GS.TF-T6/12GS.T2-T1
cPH.A10-2	A10	14.9	2.63–4.15	1.59 to 10.36	3.77–4.10	13.9–15.9	11GS.TF-T5//12DL.T4-T3//12GS.TF-T6
cPH.A10-3	A10	27.7	2.84–6.19	−2.32 to 10.45	3.07–8.47	24.6–30.8	10DL.T2-T1//11GS.TF-T5//12GS.TF-T6
cPH.A10-4	A10	40.5	2.85–4.11	−3.19 to 1.61	4.39–6.75	36.3–44.7	11DL.T7-T6//12WH.T6-T5/12WH.T2-T1
cPH.C1-1	C1	43.7	2.92–3.98	−1.68 to −1.30	5.78–5.90	39.0–48.3	10DL.T7-T6//12DL.T6-T5
cPH.C1-2	C1	51.5	2.91	−1.65	4.50	48.8–56.8	12DL.T6-T5
cPH.C2-1	C2	46.8	6.04	−2.16	10.51	40.8–53.0	10DL.T4-T3
cPH.C2-2	C2	58.7	3.86	−1.53	5.30	54.9–62.0	10DL.T4-T3
cPH.C2-3	C2	71.3	4.31	−1.97	5.93	71.1–90.2	11DL.T4-T3
cPH.C3-1	C3	11.0	2.62	1.91	3.44	5.6–32.6	12WH.T2-T1
cPH.C3-2	C3	39.0	3.01	−1.19	5.21	17.2–49.1	11DL.T5-T4
cPH.C3-3	C3	117.9	3.45	1.34	4.58	103.9–129.2	10DL.T6-T5
cPH.C4	C4	0.0	3.74	−1.32	5.26	0.0–6.3	12DL.T5-T4
cPH.C5	C5	35.7	2.67–5.17	−2.66 to 9.98	2.72–5.36	29.4–42.1	11GS.TF-T5/11GS.T3-T2//12GS.TF-T6/12GS.T3-T2
cPH.C6-1	C6	57.6	3.99–12.20	−1.53 to 3.35	6.09–17.40	56.2–58.9	10DL.T7-T6/10DL.T3-T2/10DL.T2-T1//11DL.T3-T2/11DL.T2-T1//12DL.T2-T1//12WH.T6-T5/12WH.T2-T1

Table 4 continued

Con QTLs	Chr.	Peak	LOD	Add.	R^2 (%)	CI	Stages
cPH.C6-2	C6	63.2	2.89–13.49	−2.18 to 3.02	4.31–17.86	61.9–64.4	10DL.TF-T7/10DL.T7-T6/10DL.T3-T2/10DL.T2-T1//11DL.T7-T6/11DL.T3-T2//12DL.T2-T1//12WH.T6-T5/12WH.T4-T3/12WH.T3-T2
cPH.C6-3	C6	66.8	2.53–7.76	−1.47 to 3.71	4.35–10.59	66.3–67.4	10DL.T7-T6/10DL.T3-T2//11DL.T7-T6/11DL.T3-T2/11DL.T2-T1//12WH.T4-T3/12WH.T2-T1
cPH.C6-4	C6	83.1	5.05	3.07	9.50	81.2–85.1	12DL.T3-T2
cPH.C8	C8	21.8	2.58	−1.27	3.65	0.0–45.1	12GS.T6-T5
cPH.C9-1	C9	7.2	6.02	−1.97	7.45	0.5–10.7	11DL.T3-T2
cPH.C9-2	C9	14.9	3.08	−1.27	3.54	11.4–21.1	10DL.T2-T1
cPH.C9-3	C9	25.1	2.53–2.70	−1.27 to −1.18	3.29–3.73	22.2–28.0	10DL.T2-T1//12DL.T2-T1

QN (*QN-qPH.A3*), QN-IF_2 (*QN.IF_2-qPH.A3*) and TN (*TN-qPH.A3-1*) populations were all aligned to the CI of QTL *cPH.A3-4* (conditional QTL) in the KN population, and QTLs *QN.IF_2-qPH.A3* and *TN-qPH.A3-1* also overlapped with QTL *ucPH.A3-4* (unconditional QTL) (Fig. 4; Online Resource 9). Among the 27 co-localized QTL intervals, 25 were QTLs in both KN and other maps, except for one each between SE and TN, TN and QN-IF_2 populations.

In addition, a total of 483 orthologs of 144 genes affecting PH in *Arabidopsis* were projected from TN and BE maps onto the consensus map and distributed across 17 chromosomes (excluding A4 and C7). After BLAST analysis, 118, 46 and 157 homologous genes in *B. rapa*, *B. oleracea* and *B. napus* matched the orthologous genes in *Arabidopsis*, respectively. There were 46 orthologous genes found underlying the 27 QTL intervals which were repeatedly detected in different populations (Online Resource 11), and 11, 4 and 16 homologous genes from *B. rapa*, *B. oleracea* and *B. napus* matched them, respectively. For example, the gene *AT2G44080* (homologous to *Bra000340* in *B. rapa* and *BnaA03g20650D* in *B. napus*) underlying the CI of conditional QTL *cPH.A3-4* on A3 chromosome in the KN population was also aligned to the CIs of *BE-qPH.A3* in BE and *QN-qPH-A3* in QN populations, respectively. Another example is gene *AT1G78440* (homologous to *Bol027481* in *B. oleracea* and *BnaC06g38910D* in *B. napus*) underlying the QTL interval, which was detected by conditional (*cPH.C6-3*) and unconditional (*ucPH.C6-3*) methods as well as at the mature stage (*tfPH.C6-1*) in the KN population, also detected in QN (*QN-qPH-C6-1*) and TN (*TN-qPH.C6-2*) populations. These genes, located on the CIs of QTLs that occurred steadily over different populations, might be candidate genes for PH in the future.

Discussion

The development of PH is time dependent and dynamic, but the QTL analysis of PH in *B. napus* was mainly focus on the QTLs identified at maturity in the previous studies (Butruille et al. 1999; Ding et al. 2012; Li et al. 2007; Quijada et al. 2006; Shi et al. 2009; Udall et al. 2006; Würschum et al. 2012; Zhao et al. 2005). However, the genetic control underlying the development of PH is still poorly understood in *B. napus*. This study adds additional information on QTL identification for PH at different growth stages by unconditional and conditional mapping methods.

Unconditional genetic effects are the net accumulation of sets of genes from the initial time of plant growth to the time point *t*. In contrast, conditional genetic effects at time *t* can reveal the net effects of gene expression from time $t-1$ to *t*, which is a temporal expression pattern of the related genes. In the present study, a total of 20 QTLs associated with PH were identified at maturity, while 50 QTLs were identified across different development stages other than maturity. It is clear that more than half of the QTLs identified by the unconditional QTL mapping method were not detected using the data only at maturity (Fig. 2; Online Resource 8), even though they had larger additive effects, were associated with higher LOD scores and accounted for a larger proportion of PV. For example, QTL *ucPH.A10-5* was stably expressed in 10DL, 11GS, 12DL, 12GS and 12WH experiments at 16 different growth stages but not at maturity. In addition, 50 conditional QTLs underlying PH at different developmental periods were identified based on the data from six experiments. Of them, only one conditional QTL *cPH.A2-3* was expressed throughout the entire growth process in the 11GS experiment, and was also co-localized with *ucPH.A2-2* (unconditional QTL) and *tfPH.A2-3* (detected at maturity) (Fig. 3), indicating that this QTL was more structurally important in the 11GS experiment. However, 27 conditional QTLs were only expressed at a specific period in certain situations, indicating that gene expression was selective during the developmental process, as also found by Wang et al. (2010) in wheat and Yan et al. (2003) in maize. Sets of genes were selectively expressed at different developmental stages in soybean according to microarray analysis (Vodkin et al. 2004).

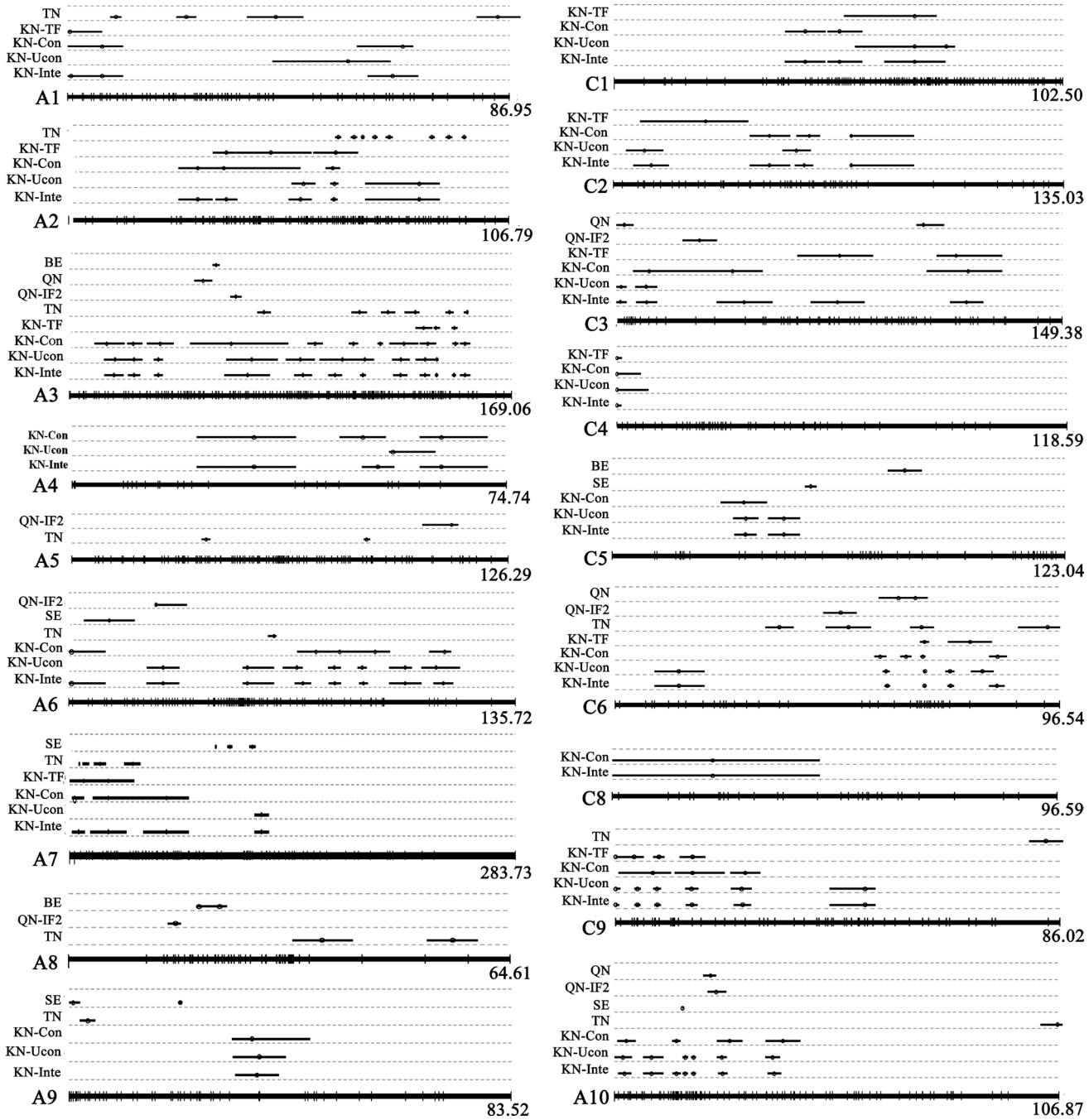

Fig. 4 Alignment of plant height QTLs identified in different populations to the consensus map. Whole linkage groups are shown with *black lines* labeled with molecular markers (*short vertical bars*) on the bottom, and full details of the consensus map are provided in Online Resource 5. The *Arabic numerals* listed on the *right side* show the length of linkage groups. The populations which harbored QTLs are listed on the left side of the linkage groups (*KN-TF*QTLs were identified at the mature stage in the KN population, *KN-Con* conditional QTLs in the KN population, *KN-Ucon* unconditional QTLs in the KN population, *KN-Inte* QTLs were integrated from the above three types of QTLs in the KN population). The *black lines* above the linkage groups show the QTL CIs and the *circles* indicate the peak position

Combining conditional and unconditional QTLs resulted in a total of 70 consensus QTLs, and 38 QTLs were detected by both unconditional and conditional QTL strategies (Fig. 2; Online Resource 8). In addition, 13 QTLs functioned for 1–3 specific periods, and were only detected by conditional mapping (Online Resource 8). It is possible that the genetic effects of these QTLs were too small to be identified by unconditional mapping. Notably,

52 consensus QTLs were repeatedly detected during the different periods/stages of the six experiments, whereas 25 had opposite genetic effects (Online Resource 8). For example, QTL *qPH.A2-4* was repeatedly detected 23 times, and showed opposite effects at different periods in 11GS and 12GS experiments (Fig. 3). A similar phenomenon was observed in the dynamic developmental behavior of PH and tillering in rice (Liu et al. 2010; Yan et al. 1998; Yang et al. 2006). This observation can be explained by genes exhibiting contrary genetic effects, or closely linked genes underlying a certain locus having opposite effects, being expressed selectively at different periods/stages.

In the present study, 20 consensus QTLs were identified at mature stage. Among them, QTL *tfPH.A2-3* was only repeatedly detected at GS with an average additive effect of 5.83, while *tfPH.A3-1* and *tfPH.A3-3* were stably expressed in 11GS and 12GS with average additive effects of 6.82 and 5.91, respectively (Table 2). These results showed that when alleles from the male parent KenC-8 existed in the three QTLs, the plants could decrease height by about 40 cm in GS. In addition, four winter macro-environment special QTLs (*tfPH.C6-1*, *tfPH.C6-2*, *tfPH.C9-3* and *tfPH.C9-4*) could only be repeatedly detected at DL in different years, and with average additive effects of 2.97, 3.31, −4.36 and −4.43, respectively. This means that when alleles of PH came from the male parent KenC-8 in *tfPH.C6-1* and *tfPH.C6-2*, and the female parent N53-2 in *tfPH.C9-3* and *tfPH.C9-4* synchronously, the PH could decrease by about 30 cm. These QTLs might be worthy of attention when doing marker-assisted selection (MAS) for developing varieties with special adaptability. Based on the breeding objective and differences in genetic background, pyramiding breeding by marker-assisted recurrent selection of the targeted QTL is an efficient and feasible approach for improving PH in *B. napus*. Among the 70 consensus QTLs detected at different periods/stages in six environments, more than half (41) were identified 1–3 times and had minor effects. Flint et al. (2005) pointed out that it might take 1500 years to clone all reported QTLs in the mouse genome at the current QTL cloning rate. Obviously, using such minor QTLs for MAS or cloning such QTLs via fine mapping is unlikely. However, these QTLs provide an important genetic resource for further research (Shi et al. 2009). Among the 20 consensus QTLs identified at maturity, 19 of them were all co-localized with other QTLs detected by unconditional and/or conditional QTL methods. We can predict these QTLs at early stages with no need for measurement of PH at maturity. Take QTL *qPH.C6-3* as example, it can be repeatedly detected at all of the seven growth stages as well as at maturity in 10DL (Online Resource 8). In T_3 stage, the QTL was detected with large LOD score (14.36) and PV (17.42 %), whereas with much smaller LOD score (2.55) and PV (2.92 %) at maturity. This means that T_3 stage might be a more reasonable sampling time for fine mapping and cloning of the QTL. Environments are manifestations of complex biotic, abiotic and agronomic factors, which can influence the expression and magnitude of QTLs (Raman et al. 2009). In 10DL and 11DL, the monthly mean temperature was much similar (Online Resource 1), and a similar number of 21 and 23 QTLs were identified during the whole growth stages by conditional mapping method, respectively. However, the monthly maximum temperature in 12DL was higher than in 10DL and 11DL during the $T_1 - T_7$ growing periods, resulting in flowering period was short and centralized, and only 14 conditional QTLs for PH were detected in 12DL. FT could have an impact on the QTL mapping results, one because of the problems with some plants not reaching maturity in the spring environment of GS, and two because of the strong negative correlation between FT and PH at all of developmental stages except for the last two in 10DL, 12DL, 12GS and 12WH (Online Resource 4). Additionally, most of the QTLs for PH were detected during the period of rapid growth stages. For example, 14 QTLs were identified during the period $T_1 - T_4$ in 11DL. Therefore, it was necessary to take effective measures to inhibit the early outgrow for gaining a suitable PH at maturity. The results indicate that conditional QTLs were expressed differently at different growth periods and can be used as a guideline for fertilization determination.

A consensus map is generally considered a powerful tool to survey the genetic diversity of loci/alleles underlying complex traits (Varshney et al. 2007; Wenzl et al. 2006), and can be successfully used to compare QTLs associated with oil content detected in different populations (Wang et al. 2013). In the present study, a consensus map was constructed to compare QTLs for PH identified in five other populations with the KN population. Using QTL projection, 58 consensus QTLs were successfully projected from the five individual maps onto 12 linkage groups of the consensus map, accounting for 67.4 % of the total QTLs (Fig. 4; Online Resource 10). In a previous study, Zhou et al. (2013) collected 1960 QTLs for yield and yield-related traits from published documents concerning *B. napus*, and then aligned 736 QTLs to an integrated QTL map, with an integration efficiency of 59.5 %.

Projecting the QTLs from individual maps onto the consensus map showed that 27 QTL intervals were repeatedly detected in different populations. It is noteworthy that three QTLs on chromosomes A2, A3 and C6 in the KN population were consistently detected by conditional and unconditional QTL approaches as well as at the final stage, were co-localized with QTLs detected in TN and QN populations, including *qPH.A2-4* co-localized with *TN-qPH.A2-1*, *qPH.A3-9* with *TN-qPH.A3-3*, and *qPH.C6-3* with *TN-qPH.C6-3* and *QN-qPH.C6-2*. These results demonstrated

that QTLs for PH located on A2, A3 and C6 appeared to be more consistent and could be detected in various gene pools. Compared with the results obtained by combining unconditional and conditional mapping, QTLs identified based on phenotypic values only at the final stage could not reveal the precise number and direction of action of the genes effecting PH in *B. napus*. Several other studies have mapped QTLs for PH, and numerous QTLs were found on 16 of the 19 chromosomes (excluding A4, A5 and C8) in *B. napus* (Basunanda et al. 2010; Mei et al. 2009; Quijada et al. 2006; Udall et al. 2006; Würschum et al. 2012). Unfortunately, these QTLs could not be exactly compared with those in the present study due to lack of common markers between different maps. In summary, QTLs for PH were observed in 18 linkage groups (excluding C8) in *B. napus* in previous studies. Interestingly, a QTL *qPH.C8-1* was identified on C8 by conditional mapping, although it was only weakly expressed during period $T_6 - T_5$ in the 12GS experiment. Our results demonstrated that combining conditional and unconditional mapping strategies might be a valid strategy for unraveling more important genetic information about developmental behavior factors of PH in *B. napus*, which will provide a theoretical basis for MAS.

Brassica napus has a common ancestor with *Arabidopsis*, and some similarities at the sequence level are expected because their progenitors diverged about 20 million years ago (Koch et al. 2000; Yang et al. 1999). Parkin et al. (2005) reported 21 blocks within the *Arabidopsis* genome in common with *B. napus* based on comparative analysis, and Schranz et al. (2006) proposed a set of 24 conserved chromosomal blocks in *B. napus*. Furthermore, the genome sequences of *B. rapa*, *B. oleracea* and *B. napus* have been released (Chalhoub et al. 2014; Liu et al. 2014; Wang et al. 2011), and so it is feasible to predict the orthologous genes for specific traits within the *Brassica* genome. So far, numerous important genes involved in different biological processes in *Arabidopsis* have been mapped to the target QTL intervals in *B. napus* by in silico mapping, such as QTLs for flowering time (Long et al. 2007; Raman et al. 2014), boron- and phosphorus-efficiency traits (Yang et al. 2010; Zhao et al. 2012), shoot mineral concentrations (Liu et al. 2009), seed yield and yield-related traits (Ding et al. 2012; Shi et al. 2009), seed fiber (Liu et al. 2013) and resistance to *L. maculans* (Raman et al. 2014). In the present study, 46 orthologous genes affecting PH in *Arabidopsis* were found underlying 27 QTL intervals which were stably detected in different populations. For example, *AT2G44080* and *AT1G78440* were located on the QTLs CIs that are stable in different populations (Online Resource 11). *AT2G44080* is an auxin-inducible gene and upregulated by brassinosteroid; it encodes *ARGOS-LIKE* (*ARL*) that regulates lateral organ growth mainly by influencing cell expansion (Feng et al. 2011; Hu et al. 2006). *AT1G78440* encodes a gibberellin 2-oxidase (GA_2-oxidase) that acts on C19 gibberellins (Thomas et al. 1999). Gibberellins (GAs) form a large family of endogenous hormones in plants, which have the most extensive physiological function and regulate various developmental processes, such as stem elongation, leaf expansion, trichome development and the transition from vegetative growth to flowering (Pimenta Lange and Lange 2006). GA_2-oxidase regulates GA metabolism, changes bioactive GA_1 and GA_4 into inactive GA_8 and GA_{34} and is thus capable of inactivating bioactive GAs (Rieu et al. 2008). These genes are speculated to be candidate genes for PH in *B. napus*.

Author contribution statement XW carried out the QTL analysis and wrote the manuscript. HW, YZ, JT, WZ, BL, LC and HC participated in the field experiment. HW, YL and LL made helpful suggestions to the manuscript. ML designed, led and coordinated the overall study.

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

Ethical standard The authors declare that the experiments comply with the current laws of the country in which they were performed.

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