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GENETIC SEGREGATION ANALYSIS OF A RAPESEED DWARF MUTANT

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Abstract

Dwarf resources in *Brassica napus* are very important for developing high-yield cultivars through dwarf-type and lodging-resistant breeding. However, few dwarf varieties have been available for this species. Here, we reported a new rapeseed dwarf mutant GRC1157, which exhibits obvious phenotypic variations on dwarf. Six generations (P_1, P_2, F_1, F_2, B_1, and B_2) were produced from a cross between dwarf mutant GRC1157 and an elite tall-type line XR16 to analyze genetic inheritances of plant height (PH), numbers of the 1st valid branch (VBN), main inflorescence length (MIL), pod numbers per main inflorescence (MPN), pod length (PL) and seed numbers per pod (PSN) using the mixed major gene plus polygene inheritance model. The genetic analysis shows different traits were controlled by different inheritance models: PH and PL by two pairs of additive-dominant-epistatic major genes plus additive-dominant-epistatic polygenes, MPN and PSN by two-pair additive-dominant-epistatic major genes plus additive-dominant polygenes, MIL by two-pair additive-dominant-epistatic major genes and VBN by one-pair additive-dominant major genes plus additive-dominant-epistatic polygenes. Furthermore, positive correlations between PH and some other traits were observed, suggesting that some traits may be co-regulated by several linkage or same loci/genes. In addition, high heritability (40.35–93.7%) were found for five traits (except VBN) in different segregating generations, indicating these traits were mainly affected by hereditary factors and suitable for early artificial selection. In sum, the dwarf mutant GRC1157 can serve as a valuable resource for rapeseed dwarf breeding and the genetic analysis in this study provided a foundation for further mapping and cloning dwarf genes in mutant GRC1157.

Keywords:*Brassica napus*; dwarf mutant; genetic analysis

Introduction

Rapeseed(*Brassica napus*) is one of themajor oil seed crops in the world. It has the second highest global market share of all oil-seeds and is used to produce edible oil, animal feed and biodiesel (Downey & Rakow, 1987). With the continued increasing of global population and their demand for edible oil, it has become essential to improve crop yield and quality through plant breeding. Plant height (PH) is an important trait for plant type and the reducing PH can improve lodging resistance and thus considerably increase crop yield and harvest index (Hedden, 2003). It has shown that lodging results in decreased rapeseed number of seeds per fruit and seed yield, fell by 17.5% and 16.2% respectively (Islam & Evans, 1994). In addition, any lodging also makes harvesting more difficult and increases the likelihood of losing grain during harvesting. The use of dwarf mutants in the breeding of dwarf wheat (*Triticum aestivum*) and rice (*Oryza sativa*) cultivars enabled impressive yield increases and contributed to the success of the 'Green Revolution' (Khush, 2001; Hedden, 2003). Therefore, exploring new rapeseed dwarf resource is crucial for breeding dwarf-type and lodging-resistant cultivars (Islam & Evans, 1994).

Dwarf mutants have been isolated in many species but relatively few dwarf resources are available for rapeseed. Some dwarf mutants in *B.napus* have been analyzed and different mode of inheritance were shown by genetic analysis. Shi *et al*. (1995) reported two *B. napus* dwarf mutants (*ds-1* and *ds-2*) induced by ethyl methanesulfonate, and further found that a pair of partially dominant genes determined the trait in *ds-1* (Huang *et al*., 2006; Liu *et al*., 2010). Li *et al*. (2013) discovered a dwarf mutant (*bndf-1*) from *B. napus* hybrid offspring and genetic analysis on F_1 and F_2 populations revealed that the dwarfism was controlled by an incomplete dominant gene. Dwarfism is also found to be controlled by a dominant single gene in mutant Aiyuan1 (Pu *et al*., 1995), a major dominant locus in mutant NJ7982 (Wang *et al*., 2016), a major gene with mainly additive effects in mutant NDF-1 (Li *et al*., 2010), an additive single gene in mutant *Bzh* (Foissit *et al*., 1995), a pair of recessive genes in mutant *bnaC.dwf*(Zeng *et al*., 2011), a pair of additive genes in mutant *nfd1* (Wang *et al*., 2004), a pair of additive-dominant major genes plus additive-dominant-epistatic polygenes in mutant 10D130 (Zhou *et al*., 2013). Moreover, Mei *et al*. (2006) demonstrated that dwarf trait could be controlled by at most three pairs of recessive genes and simultaneously influenced by maternal and cytoplasmic effects in mutant 99CDAM by genetic analysis. Information derived from above studies was valuable for isolation and mapping of dwarf genes as well as *Brassica* dwarf breeding.

In this study, we reported a new natural dwarf mutant GRC1157 which was selected from *B. napus* line2301

and exhibited significant dwarf phenotype. We used mutant GRC1157 as parental line to cross with an elite tall-type line XR16 to generate F_1 populations. Then, F_2, B1 ($F_1 \times P_1$) and B2 ($F_2 \times P_2$) populations were obtained further. We investigated the dwarf-related phenotype for these six generations (P_1, P_2, F_1, F_2, B_1 and B_2) and conducted genetic analysis using a mixed major gene plus polygene model. This study on heritability mode of dwarf mutant GRC1157 provided a foundation for further mapping and cloning dwarf genes, and this mutant also can serve as a valuable resource for rapeseed dwarf breeding.

Materials and Methods

Plant materials: XR16 (P_1) and GRC1157 (P_2) were used as parental lines which were bred inGuizhou Rapeseed Institute (Guiyang, Guizhou, China). XR16 is a S10 inbred line with a mean PH of ~200 cm whereas GRC1157 is a dwarf S9 inbred linewith a mean PH of ~90 cm. The parental lines were crossed to produce F_1 ($P_1 \times P_2$ and $P_2 \times P_1$) in the spring of 2013. The F_1 were used to generate F_2 seeds by self-crosses and B_1 ($F_1 \times P_1$) and B_2($F_1 \times P_2$) seeds by back-crosses in the spring of 2014. Seeds from populations of the six generations (P_1, P_2, F_1, F_2, B_1 and B_2) were sown in October of 2014. Field trials were conducted in Qinghe experimental base at Guizhou Rapeseed Institute. Seedlings were randomly transplanted at a row spacing of 50 cm and a plant spacing of 30 cm. Compound fertilizer (N: P: K = 1: 1: 1) was applied at a rate of 150 kg hm^{-1} as base fertilizer. Urea was applied at 75 kg hm^{-1} as dressing fertilizer. Other practices complied with conventional crop cultivation management.

Characterization of dwarf and yield related traits: Six dwarf and yield-related traits including plant height (PH, cm), numbers of the 1st valid branch (VBN), main inflorescence length (MIL, cm), pod numbers per main inflorescence (MPN), pod length (PL, cm) and seed numbers per pod (PSN) were investigated at the yellow ripening stage. The measurement methods foreach phenotype were described previously (Shi *et al*., 2011) and also as follows: PH was the height measured from the base of the stem to the tip of the main inflorescence. VBN represents the numbers of the1st valid branch arising from the main shoot. MIL was the length measured from the uppermost branch to the tip of the main inflorescence. MPN is the numbers of well-filled and normally developed pod on each main inflorescence. PL was the mean pod length of 15 pods sampled from the main inflorescence. PSN was the average numbers of well-filled seeds from 15 well-developed pods on the main inflorescence.

Data analysis: Genetic analysis of multi-generation traits was performedusing the mixed major gene plus polygene inheritance model as proposed by Gai *et al*. (2003), and Zhang and Gai (2000a, 2000b). Theparameters were estimated for each generation using the maximum likelihood method and the Iterated Expectation and Conditional Maximization (IECM) algorithm.The Akaike Information Criterion (AIC) value was used for selecting optimal model. In addition, a set of tests for goodness of fit including homogeneity tests (U_1^2, U_2^2 and U_3^2), Smimov tests ($_nW^2$) and Kolmogorov tests (D_n) was performed to determine the suitable model. Finally, the least square method was adopted to estimate genetic parameters (e.g., phenotypic value and variance of genes) based on the selected parameters and model. The software used for these analyses was provided by the National Center for Soybean Improvement, Nanjing Agricultural University (Nanjing, China).

Major-gene heritability: h^2_{mg} (%) = σ^2_{mg}/σ^2_p
Polygenic heritability: h^2_{pg} (%) = σ^2_{pg}/σ^2_p

The correlation analysis between PH and other traits were conducted using Excel 2003 (Microsoft Corp., Redmond, WA, USA).

Results

Phenotypic variation of dwarf mutant GRC1157: Phenotypic investigation and comparison between dwarf mutant GRC1157 and its derived *B. napus* line 2301 were performed during their entire growth period. The mutant GRC1157 showed low growth rate at the seedling stage and behaved obviousdifference between line 2301 at the bolting, flowering and adult stages. The difference was reflected on multiple investigated traits at the adult stages (Fig. 1A). Compared with ~170 cm of PH for line 2301,the PH of mutant GRC1157 was only ~90 cm. The mutant GRC1157 also showed obvious reductions in MIL, MPN, PL and PSN, but not in VBN trait (Fig. 1A). The homozygous dwarf mutant GRC1157 was reciprocally crossed with another *B. napus* elite and tall line XR16, andall F_1 plants displayed a phenotype similar to XR16 (Fig. 1B). These results indicated that dwarfism of mutant GRC1157 is a recessive trait, and cytoplasmic effect was notexisted. The F_2population showed trait segregation for PH and other related traits in a continuous distribution, suggesting the typicalquantitative inheritance. Moreover, multimodal distribution of phenotype was observed, indicative of the existence of major gene effects for dwarf and yield related traits in mutant GRC1157(data not shown).

Phenotypic values for dwarf and yield related traits in six generations: In the F_1 generation, three traits PH, VBN and MPN were all surpass those of the high-value parent, with strong positive heterosis. For MIL, PL and PSN, the mean valuesof the F_1 generation were between those of the two parents, with a tendency toward the high-value parent (Table 1).The coefficient of variation for each trait was remarkably higher in segregating populations (B_1, B_2 and F_2) compared with non-segregating populations (P_1, P_2 and F_1), indicating higher genetic polymorphism in the former. The individuals with extreme phenotype in six traits could be observed in segregating populations(B_1, B_2 or F_2), suggesting transgressive genetic inheritance (Table 1). In

addition, all six traits displayed continuous and multimodal distribution which indicated that these traits are quantitative and may be dominated by major genes.

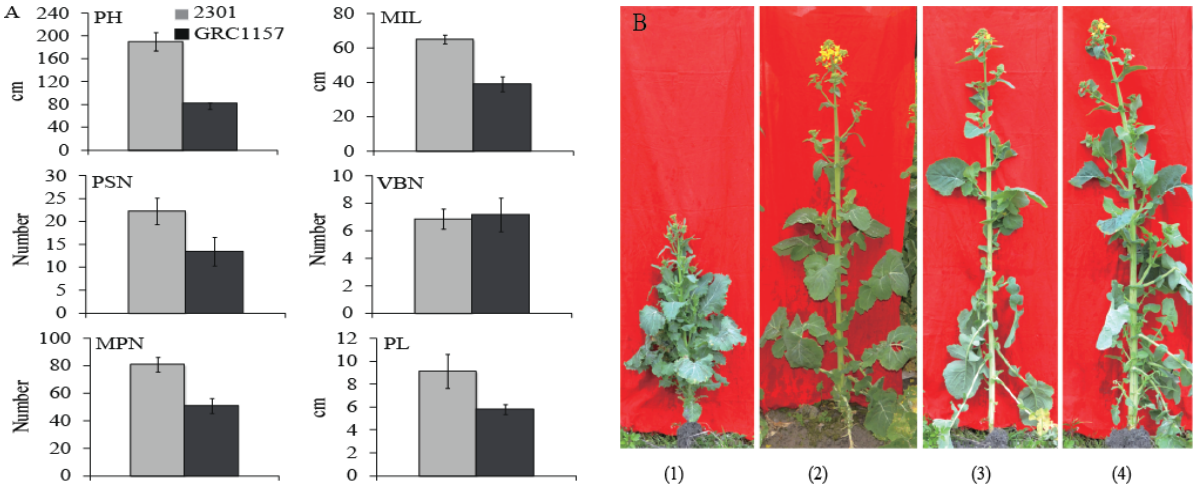

Fig. 1. Phenotypes analysis. (A) Phenotypes comparison between dwarf mutant GRC1157 and its derived *Brassica napus* line 2301 (wild type); (B) Four representative plants respectively corresponding to (1) the mutant GRC1157, (2) the F_1 hybrid derived fromGRC1157 and XR16, (3) the F_1 hybrid derived from XR16 and GRC1157 and (4) XR16.

Table 1. Phenotypic statistic values for plant type in six generations from a cross of GRC1157×XR16.

Trait	Generation	No. of plants	Max.	Min.	Range	Mean	SD	CV(%)
PH (cm)	P1	15	210.0	175.0	35.0	198.4	10.4	5.25
	F1	42	230.0	175.0	55.0	201.0	13.2	6.56
	P2	25	110.0	80.0	30.0	90.7	7.9	8.76
	B1	152	260.0	140.0	120.0	198.5	17.8	8.94
	B2	105	210.0	100.0	110.0	162.9	20.6	12.63
	F2	521	250.0	85.0	165.0	183.2	29.1	15.86
MIL(cm)	P1	15	96.0	56.0	40.0	76.1	11.5	15.08
	F1	32	95.0	50.0	45.0	71.7	10.3	14.43
	P2	25	54.0	30.0	24.0	42.2	5.6	13.24
	B1	152	120.0	45.0	75.0	78.2	12.5	15.94
	B2	105	95.0	25.0	70.0	61.1	13.5	22.09
	F2	502	120.0	13.0	107.0	66.2	19.1	28.84
MPN	P1	15	134.0	89.0	45.0	108.0	16.3	15.14
	F1	28	138.0	85.0	53.0	116.3	13.3	11.41
	P2	25	95.0	58.0	37.0	77.1	7.9	10.30
	B1	151	136.0	46.0	90.0	99.0	17.4	17.53
	B2	101	148.0	33.0	115.0	73.2	17.7	24.17
	F2	295	170.0	26.0	144.0	109.0	19.5	17.85
PL(cm)	P1	14	8.8	6.3	2.5	7.9	0.7	8.86
	F1	23	8.1	6.1	2.0	7.1	0.6	7.88
	P2	10	4.7	3.3	1.4	3.9	0.6	14.23
	B1	152	10.4	4.9	5.5	8.0	1.2	15.00
	B2	79	10.5	4.3	6.2	6.6	1.1	16.67
	F2	300	11.0	3.2	7.8	6.8	1.5	22.06
PSN	P1	14	22.5	11.0	11.5	17.7	3.5	19.77
	F1	16	20.3	11.0	9.3	15.3	2.6	16.99
	P2	10	10.3	6.0	4.3	7.9	1.4	18.24
	B1	153	28.5	4.3	24.2	18.0	4.6	25.56
	B2	79	21.5	4.7	16.8	11.9	3.3	27.73
	F2	300	26.7	1.0	25.7	11.5	5.2	45.22
VBN	P1	15	11.0	5.0	6.0	7.5	1.4	18.16
	F1	37	14.0	5.0	9.0	9.0	1.6	17.91
	P2	25	11.0	6.0	5.0	8.5	1.4	15.94
	B1	152	12.0	3.0	9.0	7.3	1.6	22.46
	B2	104	12.0	4.0	8.0	7.4	1.7	22.42
	F2	502	14.0	2.0	12.0	8.5	2.3	26.60

PH: plant height; VBN: numbers of the 1st valid branch; MIL: main inflorescence length; MPN: pod numbers per main inflorescence; PL: pod length and PSN: seed numbers per pod.

A suitable genetic model for dwarf and yield related traits: The phenotypicdata of six generations were used to carry outjoint analysisusing the mixed major gene plus polygene generic model. Maximum likelihood estimates (MLEs) and AIC values were calculated for 24 inheritance models using the maximum likelihood method and the IECM algorithm.These models belong to the following five types: one pair of major genes (model A), two pairs of major genes (model B), polygenes (model C), one pair of major genes plus polygenes (model D) and two pairs of major genes plus polygenes (model E). Three models with the smallest AIC value and relatively close values were selected as candidates.After testing goodness of fit (U_1^2, U_2^2, U_3^2, $_nW^2$ and D_n), those models with the smallest number of statistical quantities reaching significance and the smallest AIC values were selected (Table 2). By doing this, the optimal model were selected for different traits: the mixed two-pair additive-dominant-epistatic major genes plus additive-dominant-epistatic polygenes inheritance model for PH and PL, the mixed two-pair additive-dominant-epistatic major genes plus additive-dominant polygenes inheritance model for MPN and PSN,the mixed two-pair additive-dominant-epistatic major genes inheritance model for MIL and the mixed one-pair additive-dominant major genes plus additive-dominant-epistatic polygenes inheritance model for VBN.

The estimation ofgenetic parameters for dwarf and yield related traits: We estimated the first-order genetic parameters of six traits(PH, VBN, MIL, MPN, PL and PSN) according toabove optimal inheritance models (Table 3). Two pairs of major genes controlling PH, MPN and PL all exhibited positive addictive effects.The first pair of major genes controlling MIL had positive addictive effects whereas the second pair of major genes had negative addictive effects. Two pairs of major genes both had negative addictive effects for PSN and VBN, respectively. h_a/d_avalues of PH, MIL, PSN and VBN were 0.23, -0.01, -0.68 and 0.03. The additive effect was greater than the dominant effect, demonstrating partial dominance. Furthermore, MPN and PL had h_a/d_a values of -1.44 and -2.70 respectively, and the dominant effect was greater than the additive effect, demonstrating over-dominance.

The interactionbetween the additive effects of two pairs of major genes were -18.50, -2.06, -19.84, -0.25for PH, MIL, MPN and PL (all deviating toward GRC1157) and 3.11for PSN (deviating toward XR16). The interaction betweenthe dominant effectsfor PH, MIL and PSN were -4.33, -1.07 and -11.02, respectively (deviating toward GRC1157) and 51.73 and 2.26for MPN and PL, respectively(deviating toward XR16). Except for PL, the significant interactions between the additive and dominant effects of major genes for PH, MIL, MPN, and PSN were observed.

The estimation for second-order genetic parameters (Table 3) showed that the heritability of PH, MPN, PL, PSN and VBN in the B_1 population were 60.51%, 57.81%, 77.89%, 68.98% and 20.67%, respectively, and the major-gene heritability were 16.97%, 1.81%, 49.83%, 36.38% and 0.66%, respectively. The heritability of PH, MPN, PL, PSN and VBN in the B_2 population was 70.58%, 61.58%, 70.81%, 93.70% and 23.97%, respectively, with major-gene heritability of 46.93%, 61.58%, 54.23%, 93.70% and 0.98%, respectively. The heritability of PH, MPN, PL, PSN and VBN in the F_2 population were 85.24%, 67.33%, 84.24%, 84.29% and 59.19%, respectively, with major-gene heritability of 41.61%, 67.33%, 38.08%, 84.29% and 0.25%, respectively. In contrast, no polygenic effects were detected for MIL in three segregating populations B_1, B_2 and F_2, and the major-gene heritability for MIL was 40.35%, 49.15% and 74.61%, respectively.

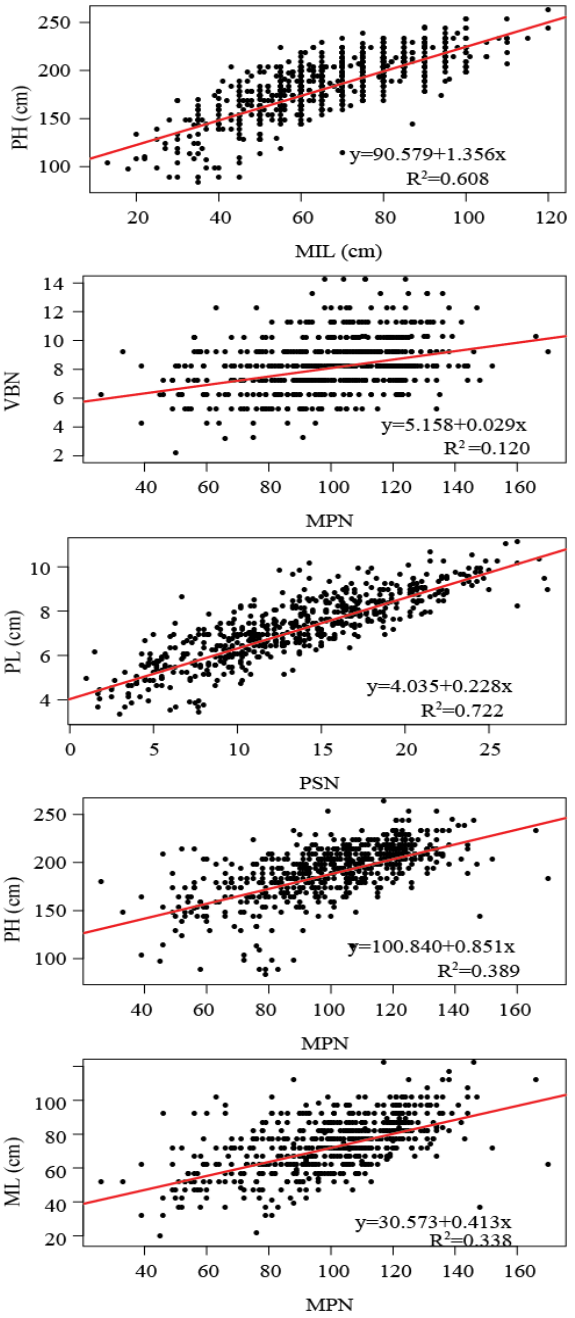

Fig. 2. Scattered distribution and trend line between plant height and related traits.

Correlation between PH and other related traits: Correlation analysis was performed for PH, VBN, MIL, MPN, PL and PSN in six generations. Significant positive correlations between MIL and PH (r = 0.780), MPN and PH (r = 0.624), MIL and MPN (r = 0.5), and PL and PSN (r = 0.849) were observed. Moreover, there was a relatively weak correlation between VBN and MPN (r = 0.346). Scattered distribution and trend line (Fig. 2) also revealed that MIL and MPN increased as PH became larger, and MPN increased along with MIL.

Table 2. Test for goodness-of-fit of selected genetic models.

Trai	Model	Implication of model	Max log likelihood value	AIC value	Test of goodness-of-fit
PH (cm)	E-1	MX2-ADI-AD	-3914.7	7859.3794	0/0/1/0/0
MIL (cm)	B-1	2MG-ADI	-3474.4586	6968.9171	0/0/0/0/0
MPN	E-1	MX2-ADI-AD	-2628.295	5286.5899	1/1/0/0/0
PL (cm)	E-0	MX2-ADI-ADI	-939.5102	1915.0205	0/0/0/0/0
PSN	E-1	MX2-ADI-AD	-1843.9619	3717.9237	0/0/0/1/0
VBN	D-0	MX1-AD-ADI	-1805.1673	3634.3346	0/0/0/2/0

Test of goodness-of-fit: five digitals denote numbers of significant statistic parameters of U_1^2, U_2^2, U_3^2,$_nW^2$,and D_n;MX: mixed major gene and polygene model. A: additive effect; D: dominance effect; I: interaction; PG: polygene model.

Table 3. Estimates of genetic parameters for plant traits in a cross of GRC1157×XR16.

Generation	Genetic parameter	PH(cm)	MIL (cm)	MPN	PL (cm)	PSN	VBN
	d_a	17.43	23.76	10.88	0.46	-2.63	-0.11
	d_b	17.43	-6.92	10.88	0.46	-2.63	
	h_a	3.96	-0.27	-15.69	-1.25	1.80	0.00
	h_b	-5.14	11.04	-32.89	-0.28	1.50	
	i	-18.50	-2.06	-19.84	-0.25	3.11	
	j_{ab}	-5.97	-7.13	13.74	0.42	3.26	
	j_{ba}	-15.08	12.25	-3.46	-0.55	-0.07	
	l	-4.33	-1.07	51.73	2.26	-11.02	
	[d]	17.89		-8.61		10.90	
	[h]	43.77		0.88		6.24	
	h_a/d_a	0.23	-0.01	-1.44	-2.70	-0.68	0.03
	h_b/d_b	-0.30	-1.60	-3.02	-0.60	-0.57	
B_1	σ^2_p	315.34	155.19	301.19	1.54	21.25	2.66
	σ^2_{mg}	53.50	62.62	5.45	0.77	9.14	0.02
	σ^2_{pg}	137.30		168.68	0.43	8.19	0.53
	h^2_{mg}(%)	16.97	40.35	1.81	49.83	36.38	0.66
	h^2_{pg}(%)	43.54		56.00	28.06	32.60	20.01
B_2	σ^2_p	423.21	182.06	313.02	1.17	11.13	2.77
	σ^2_{mg}	198.60	89.48	192.75	0.63	30.57	0.03
	σ^2_{pg}	100.08		0.00	0.19	0.00	0.64
	h^2_{mg} (%)	46.93	49.15	61.58	54.23	93.70	0.98
	h^2_{pg} (%)	23.65	0.00	0.00	16.58	0.00	22.99
F_2	σ^2_p	843.95	364.58	378.63	2.16	27.01	5.16
	σ^2_{mg}	351.19	272.01	254.91	0.82	22.77	0.01
	σ^2_{pg}	368.22		0.00	1.00	0.00	3.04
	h^2_{mg}(%)	41.61	74.61	67.33	38.08	84.29	0.25
	h^2_{pg}(%)	43.63		0.00	46.16	0.00	58.94

d_a: additive effect of the first major gene; h_a: dominant effect of the first major gene; d_b: additive effect of the second major gene; h_b: dominant effect of the second major gene; i: epistatic effect value between d_a and d_b; j_{ab}: epistatic effect value between d_a and h_b; j_{ba}: epistatic effect value between h_a and d_b; l: epistatic effect value between h_a and h_b; [d]: additive effect of polygene; [h]: dominant effect of polygene; σ^2_p: phenotypic variance; σ^2_{pg}: polygene variance; σ^2_{mg}: major gene variance; h^2_{mg}: heritability of major gene; $h2_{pg}$: heritability of polygene.

Discussion

Dwarf mutants have been utilized extensively in plant breeding to improve lodging resistance, and the introduction of dwarf cultivars was a major factor in the success of the "Green Revolution" in wheat and rice (Khush, 2001; Hedden, 2003). Their use has been associated with increased yields, higher fertility, early maturity, and high tillering capacity. The dwarf mutants were also useful for improving oilseed *B. napus* because many current cultivars are prone to lodging, which can lead to yield loss and difficulty harvesting. In this study, we reported a new *B. napus* dwarf mutant GRC1157 which show significant phenotype variationin dwarf-relatedtraits including PH, MIL, MPN, PL and PSN, but no obvious reduction on VBN and fertility. The PH distribution in F_1 population revealed that dwarfism of mutant GRC1157 is a recessive trait anddidn't affect by cytoplasmic effect. The multimodal distribution of traits in segregating populations indicated that the dwarf-related traitswere dominated by major gene effects and could be analyzed using the major gene plus polygene inheritance model.

Currently, quantitative trait locus (QTL) mapping studies showed that major QTL usually explained ~20% of the phenotypic variation of dwarf cultivars (Shi *et al*., 2009; Basunanda *et al*., 2010; Ding *et al*., 2012; Luo *et al*., 2015; Wang *et al*., 2015; Li *et al*., 2016; Jana *et al*., 2016; Shi *et al*., 2016). Only in few dwarf cultivars, the dwarfism were controlled by a pair or some major genes with large effect. The dominated genes may be recessive, completely dominant or partially dominant, andin some cases, dwarfism could becontrolled by three recessive genes or even more. In this study, we analyzed dwarf and yield related traits of a dwarf mutant GRC1157 using six generations (P_1, P_2, F_1, F_2, B_1, and B_2). The results revealed that PH, MIL, MPN, PL and PSN were possibly controlled by two pairs of major genes or polygenes. The major-gene heritability (h^2_{mg}) of PH was relatively low in the segregating generation B_1.However, this value increased in segregating generations B_2 and F_2, suggesting that the major genes for dwarfism were concentrated in mutant GRC1157, similar to the major gene inheritance observed for MPN. The major genes for MIL, PL, and PSN showed relatively high heritability in different segregating generations, indicating that equal genetic effects on MIL provided by two parents. The major gene for VBN exhibited substantially low genetic effects, indicating that this trait was mainly controlled by polygenes.

Correlation analysis between six traits revealed typical positive correlations between PH and MIL, PH and MPN, MIL and MPN, PL and PSN, VBN and MPN. This result suggested that the genes controlling the above traits were possibly partially same or highly-related. PH, MIL and MPN were responsible by two pairs of major genes. The first pair of major genes had addictive effects in the same direction and the second pair of major genes for PH and MPN had additive and dominant effects in the same direction. This result also supported that PH and other traits (MIL and MPN) may be controlled by several same or linkage loci/genes. In addition, regarding the two pairs of major genes for MIL and MPN, the first pair showed both additive and dominant effects in the same direction suggesting the same or linkage loci/genes controlled for both traits. In contrast, the major genes for PL and PSN exhibitedadditive and dominant effects in different directions, suggesting that these two traits may be under the control of different genes.

The level of heritability provided a guide for the timing of generation selection. The heritability of PH, MIL, MPN, PL and PSN was 40.35–93.7% in three segregating generations, indicating that PH and related traits were mainly affected by hereditary factors and were suitable for early selection. VBN showed substantially low heritability in segregating generations which is suitable for late selection. With regard to the composition and level of heritability, it is necessary to take some factors including major genes, polygenes and environmental factors into consideration when breeding.

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