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Genetic Analysis of Flowering Time in Pansies Using Mixed Major Gene Plus Polygene Inheritance Model

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Abstract. **The flowering time of pansy cultivars determines their ornamental application period and the profits of seedling growers. Revealing its genetic basis will be useful for breeding pansy cultivars with desired flowering times. In this study, three inbred pansy lines, DSRFY (D), XXL-YB (X), and EYO (E), with various blooming times were used to generate 12 genetic populations with two hybrid combinations (D × E and X × E). A mixed hereditary model of major and polygenic genes was used to uncover the genetic control of flowering time in pansies. The findings suggested that the flowering times of pansies are characterized by complex traits with continuous variations and normal distributions in the population and are controlled by multiple genes. The genetic basis of flowering time differed between the two hybrid combinations. The trait was governed by minor polygenes with additive-dominant-epistatic effects for D × E crossing combinations hybridized from two parents with a 10-day difference in flowering time, resulting in low heritability. The trait was regulated by two major genes and polygenes exerting additive-dominant-epistatic effects in the X × E hybridization from two parents with a 4-day difference in character, leading to high heritability. Our findings elucidate the genetic basis of pansy flowering time and provide a promising approach to detecting major genes or quantitative trait loci.**

The flowering time significantly affects plant sexual reproduction and adaptation (Hayama et al. 2003; Kuittinen et al. 1997; Lin et al. 2021). Desired flowering time for plants, particularly cross-pollinated plants, can provide the best opportunities for pollination by pollinators and, thus, produce more offspring. For instance, pansy blooms in early spring compete with many spring-flowering plants, such as roses and peonies, for pollinators (Veerman and van Zon 1965). Another advantage of an appropriate flowering time is the avoidance of abiotic and biotic stresses (Brightbill and Sung 2022; Cho et al. 2017). Heat-intolerant tulips and pansies bloom and set seeds in early spring before the hot summer arrives. Timely flowering can also bring more profits to seedling growers because it meets market needs (Kessler et al. 1999; Zhao et al. 2023). For pansy (*Viola* ×*wittrockiana*), one of the most popular bedding flowers for the cool seasons worldwide, cultivars that bloom early are in great demand because they can decorate the outdoor environment earlier than other flowers in spring and shorten the nursery period in hot summers when they are used for fall landscaping (Kessler et al. 1999; Niu et al. 2000; Warner and Erwin 2006). Additionally, a shorter seedling period implies lower costs and higher profits for commercial seedling producers. Therefore, genetic improvement of the flowering time of pansies has aroused the interest of plant breeders, and uncovering the genetic mechanisms underlying flowering time is crucial. However, no reports of the inheritance of the flowering time of pansies are available, leading to the breeding of early flowering cultivars of pansies, which is time-consuming and laborious.

Flowering times exhibit continuous variations in natural populations and are considered a complex trait (Abbas et al. 2022; Yano et al. 2001; Zhao et al. 2023). Traditional genetic biometric studies assume that complex traits are controlled by multiple independent genes with equal minor effects and generally estimate the overall effects of multiple genes. However, recent genome-wide association studies (GWAS) and studies using quantitative trait locus (QTL) mapping have revealed that the effects of multiple genes controlling complex traits are mostly unequal (Hori et al. 2016; Xu et al. 2016). Research of the model plant *Arabidopsis thaliana* showed that one major and six minor QTLs controlled flowering

Fig. 1. Three parental inbred lines adopted for the genetic population construction (photographs were obtained on the same day).

Table 1. Statistics of the flowering times of 12 generations of two hybridized combinations of pansy.

Hybridization combination	Generation	Min	Max	Median	*SD*	*CV* (%)	Skewness	Kurtosis
D × E	D	183	203	194	5.27	2.73	−0.20	−0.72
	E	174	188	184	4.26	2.33	−0.46	−0.95
	D × E_F_1	177	197	188	4.00	2.13	0.04	0.78
	D × E_F_2	173	204	191	4.86	2.55	−0.001	0.26
	D × E_D	180	203	193	4.94	2.57	−0.24	−0.59
	D × E_E	153	203	184	8.01	4.38	−1.16	3.38
X × E	X	177	200	188	4.83	2.56	0.08	0.86
	E	174	188	184	4.26	2.33	−0.46	−0.95
	X × E_F_1	173	192	186	5.22	2.82	−1.08	−0.97
	X × E_F_2	175	204	193	6.45	3.36	−0.32	−0.50
	X × E_X	168	203	187	6.98	3.72	−0.11	−0.37
	X × E_E	153	189	181	10.16	5.76	−1.09	0.03

SD = standard deviation; *CV* = coefficient of variation.

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time, and that the major QTL explained 53.4% of the total variance (Kuittinen et al. 1997). In addition to the additive effect, dominant effects between alleles and epistatic interactions between multiple genes controlling flowering time have been uncovered in many plants, including *A. thaliana* (Kuittinen et al. 1997), *Oryza sativa* (Yano et al. 2001), and *Chrysanthemum morifolium* (Song et al. 2020). Although QTL and GWAS are powerful tools that can reveal the genetic basis of complex traits, they are associated with molecular manipulation techniques, special equipment, and high research costs (Ehrenreich et al. 2009; Han et al. 2023).

A major gene plus polygene mixed inheritance analysis, developed by Gai and Wang (1998), can dissect the effects of major and minor genes and estimate the number of major genes and interaction effects between major genes solely from phenotypic data by combining a group of advanced statistical methods. These results will help formulate breeding strategies and QTL mapping. Therefore, this approach has been used for the inheritance analysis of some complex traits, such as the relative number of ray florets and flowering time of *C. morifolium* (Song et al. 2018; Wu et al. 2023), the main flower characteristics of *Plumbago auriculata* (Shen et al. 2020), tomato internode length (Sun et al. 2019) and the plant architecture of crape myrtle (Ye et al. 2017) and *V. cornuta* (Du et al. 2022).

Therefore, the objectives of this study were to reveal the inheritance architecture of pansy flowering time using a major gene plus polygene analysis based on phenotypic data and provide an understanding of whether there are differences in the genetic basis of the pansy flowering time with different genetic backgrounds. Our research elucidated the genetic basis of flowering time in pansies.

Materials and Methods

Plant material. Three pansy inbred lines, DSRFY (D), XXL (X), and EYO (E) (Fig. 1), with different blooming times, were adopted as crossing parents to produce the genetic populations. Specifically, plants from D and X were crossed with E as male parents in Spring 2021. The F_1 plants from the two hybridized combinations were self-pollinated to generate the F_2 generation and backcrossed with their parents to obtain the BC_1P_1 and BC_1P_2 populations in Spring 2022.

The seeds of six generations, i.e., F_1, F_2, BC_1P_1, BC_1P_2, and the two parents of each hybridized combination, were sown using 200-well trays with the seedling substance of peat: vermiculite (2:1). Seedlings with three to four true leaves were transplanted into pots (12 × 13 cm) filled with a peat:vermiculite:garden soil mixture (2:1:2). All plants were grown on the campus of the Henan Institute of Science and Technology, Xinxiang, Henan Province, China (lat. 113–115°E, long. 34–35°N). The growth environments of all the plant materials were consistent. Finally, 431 F_2 (D × E_F_2), 186 BC_1P_1 (D × E_D), 148 BC_1P_2 (D × E_E), 33 female parents (D), 33 male parents (E), and 33 F_1 (D × E_F_1) plants were obtained from the D × E hybridized combination. The same genetic populations were generated for X × E, resulting in 33 female parents (X), 33 male parents (E), 33 F_1 (X × E_F_1), 472 F_2 (X × E_F_2), 291 BC_1P_1 (X × E_X), and 328 BC_1P_2 (X × E_E).

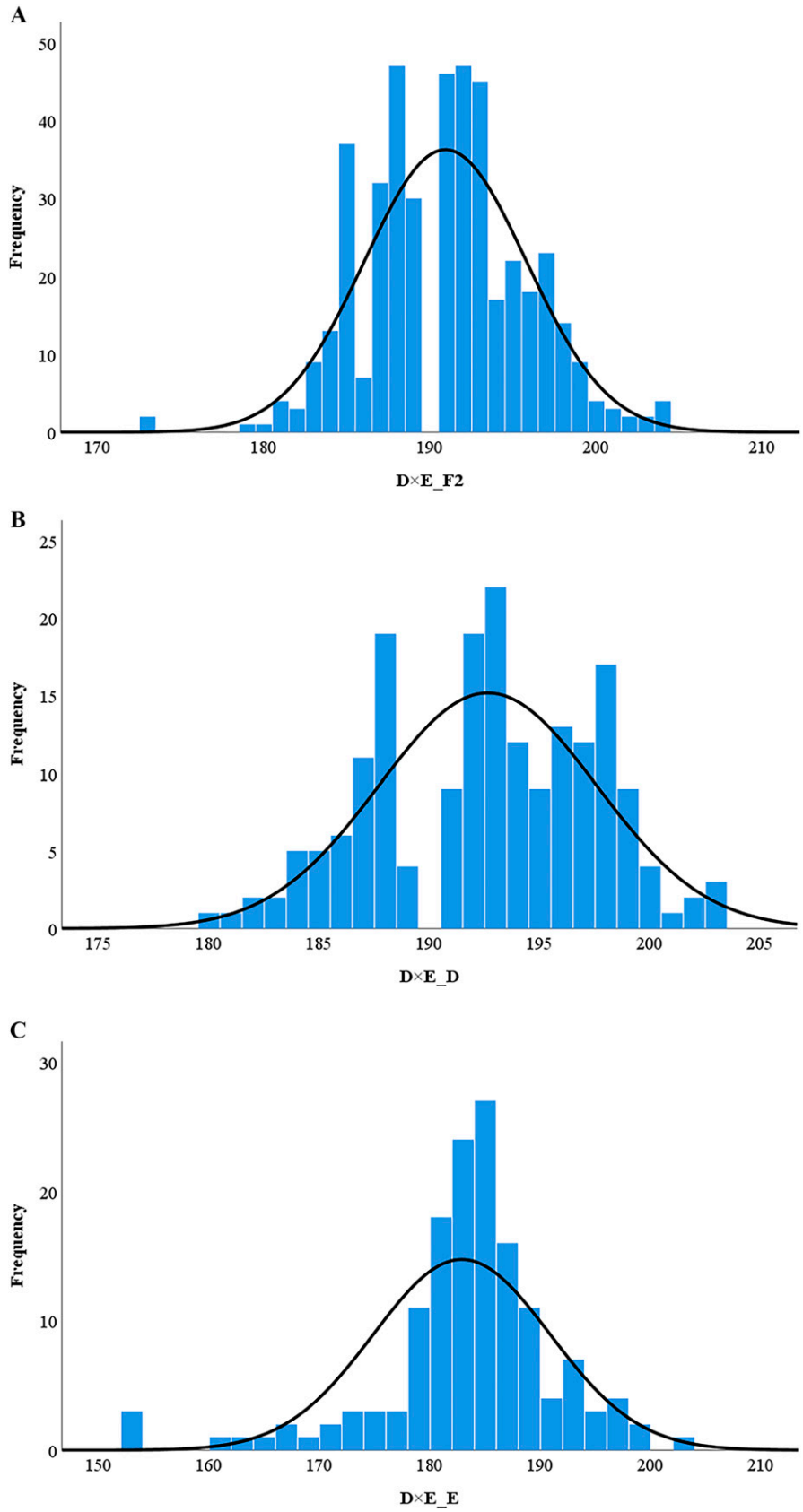

Fig. 2. Histogram of the frequency distribution of F_2, BC_1P_1, and BC_1P_2 in two hybridized combinations of pansy. (**A**) D × E_F_2. (**B**) D × E_D. (**C**) D × E_E. (**D**) X × E_F_2. (**E**) X × E_X. (**F**) X × E_E.

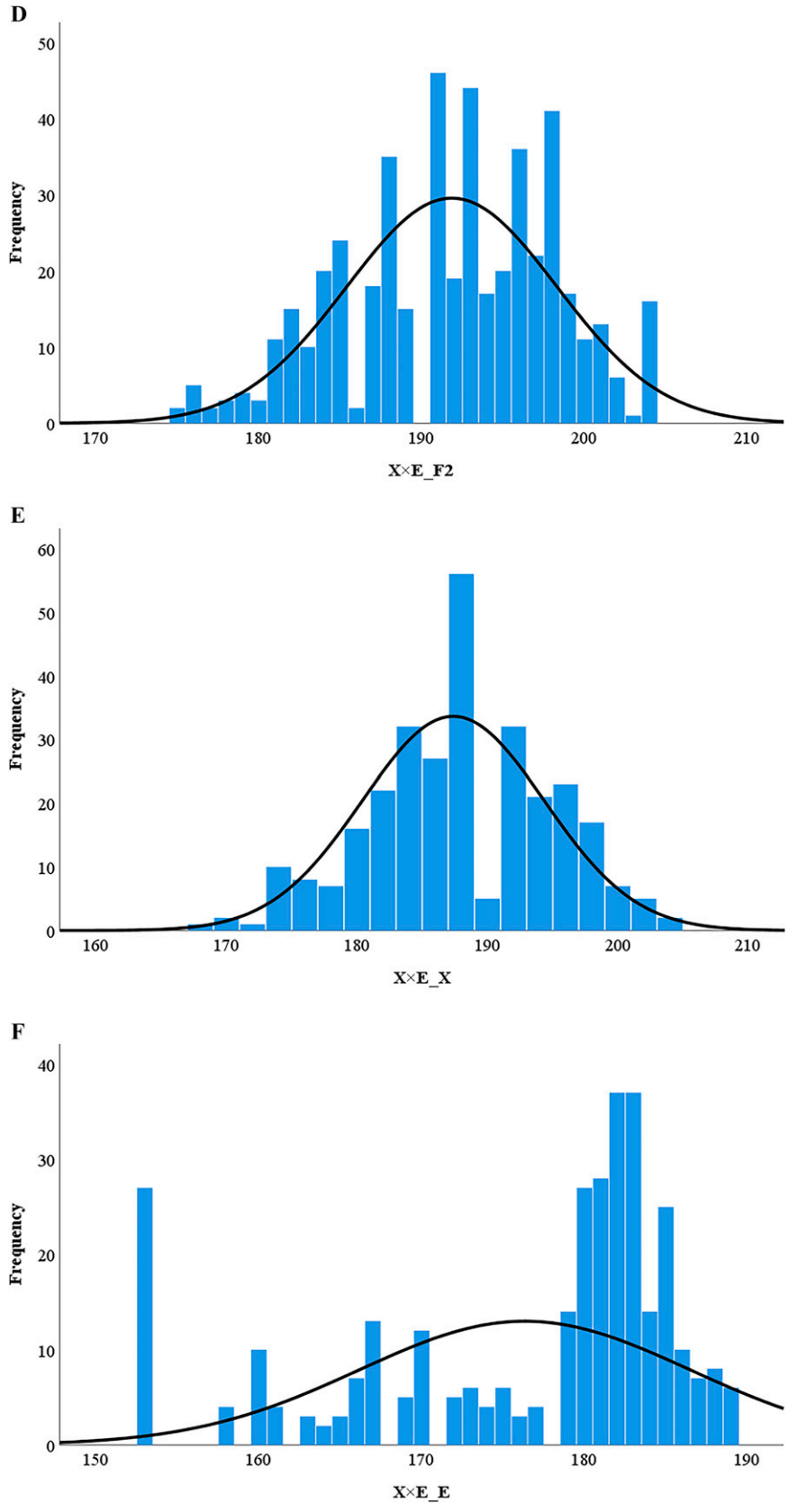

Fig. 2. *(Continued)*

Investigation of the flowering time. The flowering time of the 12 pansy populations was surveyed from 9:00 to 10:00 AM on each day from Feb 7 to 10 May 2023 (93 d). The number of days from seed sowing to first flower blooming was recorded as the flowering time of the individual plants. Flowering was confirmed when the flower had just unfolded and the stigma was exposed.

Statistical and genetic analyses. The medians, standard deviations (*SD*s), and coefficients of variation (*CV*s) were obtained using Excel 2023 (Microsoft, Redmond, WA, USA). The *CV* (%) was calculated according to the following formula:

$$CV\ (\%) = \text{standard deviation}/\text{mean value} \times 100$$

The histograms of the frequency distribution of segregated populations, skewness, and kurtosis were obtained using IBM SPSS Statistics 25 software. A genetic analysis was performed using a mixed major gene plus polygene inheritance model with six generations, namely P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2, according to Gai et al. (2003) and Corbesier et al. (2007). The analysis was performed using SEA software (Balcerowicz 2021). Specifically, three candidate genetic models for each hybridized combination were selected according to the principle of minimum Akaike's information criterion (AIC) values (Monniaux et al. 2017), for which the optimal model was determined based on the results of the suitability test of the candidate models. Finally, the genetic parameters of the optimal model were determined.

Results

Variation of pansy flowering time. An investigation of the pansy flowering time showed that the paternal inbred line (E) bloomed, on average, 10 and 4 d earlier than the two maternal inbred lines, i.e., D and X, respectively (Table 1). In the D × E hybridized combination, the flowering times of F_1, F_2, BC_1, and BC_2 were between those of the two parents; the flowering time of D × E_E approached that of the earlier-flowering recurrent parent E, whereas D × E_D tended toward the later-flowering recurrent parent D. The same occurred with the X × E hybridized combination, except that some plants of F_2 and X × E_E bloomed later than their later-flowering parent, X. The *CV*s of the segregated populations, including F_2 and BC_1, were greater than those of the parental inbred lines and the F_1 generations, except for the parental inbred line D. The variation within each population and the wide variation in segregated populations for this trait indicated that the flowering times of pansies are characterized by continuous variations in complex traits.

Frequency distribution of flowering time in the segregated pansy population. As indicated in Fig. 2, the flowering times of the F_2, BC_1P_1, and BC_1P_2 populations in both the D × E and X × E hybridized combinations displayed continuous variations and normal distributions, thus exhibiting complex traits. The absolute values of skewness and kurtosis of these segregated populations in flowering time were no more than 1 and 3, respectively (Table 1), indicating that the flowering time of pansy conformed to a normal distribution. This fitted the genetic analysis using the major gene plus polygene mix model. The histogram of the frequency distribution and skewness of the flowering time of the F_2 population in the D × E combination from two parents with a 10-d difference in character neared zero,

Table 2. Akaike's information criterion (AIC) values of 24 genetic models.

Model	Implication of the model	Florescence	
		D × E	X × E
A-1	1MG-AD	5569.145	8540.259
A-2	1MG-A	5396.736	8608.366
A-3	1MG-EAD	5382.204	8541.198
A-4	1MG-NCD	5528.457	8814.882
B-1	2MG-ADI	5349.09	**8079.218**
B-2	2MG-AD	5361.477	8498.067
B-3	2MG-A	5527.405	8762.563
B-4	2MG-EA	5377.494	8645.312
B-5	2MG-CD	5370.891	8566.295
B-6	2MG-EAD	5368.891	8564.366
C-0	PG-ADI	**5260.027**	**8194.998**
C-1	PG-AD	5325.37	8716.291
D-0	MX1-AD-ADI	**5264.028**	8198.998
D-1	MX1-AD-AD	5295.7	8332.073
D-2	MX1-A-AD	5314.679	8803.508
D-3	MX1-EAD-AD	5323.076	8803.505
D-4	MX1-NCD-AD	5500.917	8498.348
E-0	MX2-ADI-ADI	5267.075	**8040.305**
E-1	MX2-ADI-AD	**5272.584**	8272.831
E-2	MX2-AD-AD	5329.172	8400.191
E-3	MX2-A-AD	5296.003	8332.849
E-4	MX2-EA-AD	5315.21	8416.858
E-5	MX2-CD-AD	5333.697	8312.814
E-6	MX2-EAD-AD	5323.155	8328.87

A = additive; AD = additive-dominance; ADI = additive-dominance epistasis; CD = complete dominance; E = equal; EA = equally additive; EAD = equally additive-dominance; I = interaction; MG = major gene model; MX = major gene plus polygene mixed model; N = negative direction; NA = invalid; NCD = negatively complete dominance; PG = polygene model.
Underlined text indicates the minimum AIC value.

indicating that the trait fit the standard normal distribution and was controlled by minor polygenes. At the same time, the slightly skewed normal distribution and kurtosis deviated zero (−0.32) of the F_2 population in X × E from two parents with a 4-d difference in character suggested that there are major genes in the genetic basis of this trait.

Genetic model analysis of flowering time. According to the AIC values (Monniaux 2017), three models containing C-0, D-0, and E-1 were selected as candidate models for the flowering time of D × E based on the AIC values of 24 genetic models of each hybridized combination (Table 2). Similarly, the candidate models for X × E were B-1, C-0, and E-0. The suitability tests of the candidate models of D × E reached a significant level (Table 3), and the model (C-0) with the smallest AIC value was regarded as the optimal model, which indicated that the flowering time of pansy under the genetic background from the parents with larger differences in character is regulated by polygenes with additive-dominant-epistatic effects. According to the same principles, the E-0 model with the smallest AIC value (Table 4) was considered the optimal model for X × E; that is, two major genes plus polygenes with additive-dominant-epistatic effects controlled the flowering time of pansy from parents with minor differences in character in this genetic setting.

Estimation of genetic parameters of the optimal model for pansy flowering time. Genetic parameters of the optimal models were calculated using the least-squares method. As shown in Table 5, the heritabilities of the polygenes controlling flowering time in D × E_F_2, D × E_D, and D × E_E were 26.06%, 28.29%, and 68.11%, respectively. The major genes significantly affected the flowering time for the X × E hybridized combination (Table 6), which was from the parents with a minor difference in character. The additive effects (d_a and d_b) and the dominant effects (h_a and h_b) of the two major genes were positive, indicating that the additive effects and dominant genes delayed pansy flowering. The ratio of the additive effect to the dominant effect of the two major genes revealed that the additive effect was smaller than the dominant effect. The interaction effects between the additive effects and the dominant effects of the two major genes were negative. Adverse effects were also found in the interaction between the additive effect of the first major gene and the dominant effect of the second, as well as in the interaction between the additive effect of the second major gene and the dominant effect of the first. This indicated that the interaction between the two major genes accelerates pansy flowering. Table 7 shows that the heritabilities of the flowering times of X × E_F_2 and X × E_E were high (58.69% and 76.98%, respectively). In the X × E_X population, the major genes possessed greater heritability than that of the polygenes. This suggested that genes, especially the major genes, mainly controlled the heredity of the flowering time of pansy in the X × E hybridized combination that came from parents with minor differences in character.

Discussion

The pansy is one of the most popular bedding flowers worldwide. Understanding the genetic control of flowering time is useful for

Table 3. Suitability tests of candidate models for D × E hybridized combinations.

Model	Generation	U_1^2	$P(U_1^2)$	U_2^2	$P(U_2^2)$	U_3^2	$P(U_3^2)$	${}_nW^2$	$P({}_nW^2)$	D_n	$P(D_n)$
C-0	P_1	0.02*	0.90	0.03*	0.85	0.07	0.79	0.06	0.81	0.12	0.73
	P_2	0.11	0.73	0.17	0.68	0.14	0.71	0.13	0.44	0.14	0.56
	F_1	0.16	0.68	0.14	0.71	0*	0.97	0.19	0.29	0.23	0.06
	F_2	0.1	0.75	0.01*	0.91	0.63	0.43	0.44	0.06	0.09	0.03*
	B_1	0.1	0.75	0.3	0.55	1.32	0.25	0.30	0.14	0.11	0.03*
	B_2	0.25	0.62	0.05	0.83	7.76	0*	0.51	0.04*	0.13	0.02*
D-0	P_1	0.02*	0.90	0.03	0.85	0.07	0.80	0.06	0.81	0.12	0.73
	P_2	0.11	0.74	0.17	0.68	0.14	0.71	0.13	0.44	0.14	0.56
	F_1	0.16	0.69	0.14	0.71	0*	0.97	0.18	0.29	0.23	0.06
	F_2	0.10	0.75	0.01*	0.92	0.68	0.41	0.44	0.06	0.09	0*
	B_1	0.10	0.75	0.37	0.54	1.45	0.23	0.30	0.14	0.11	0.02*
	B_2	0.25	0.62	0.04	0.84	7.55	0.01*	0.51	0.04	0.13	0.02*
E-1	P_1	0.03*	0.87	0.05	0.82	0.07	0.79	0.06	0.8	0.12	0.75
	P_2	0.26	0.61	0.37	0.54	0.20	0.65	0.16	0.37	0.15	0.47
	F_1	0.02*	0.90	0.02*	0.89	0*	0.95	0.16	0.36	0.21	0.11
	F_2	0.66	0.41	0.51	0.47	0.08	0.77	0.46	0.05	0.11	0*
	B_1	0.54	0.46	0.37	0.54	0.16	0.68	0.23	0.22	0.10	0.03
	B_2	5.62	0.02*	8.94	0*	7.71	0.01*	1.08	0*	0.19	0*

U_1^2, U_2^2, and $U3^2$ refer to the statistics of the uniformity test. ${}_nW^2$ refers to the statistics of the Smirnov test. D_n refers to the statistics of the Kolmogorov test. *Significance at 0.05.

Table 4. Suitability test results of the candidate models of the X × E hybridized combination.

Model	Generation	U_1^2	$P(U_1^2)$	U_2^2	$P(U_2^2)$	U_3^2	$P(U_3^2)$	${}_nW^2$	$P({}_nW^2)$	Dn	P (dN)
B-1	P_1	1.86	0.17	1.36	0.24	0.38	0.54	0.29	0.15	0.2	0.11
	P_2	1.61	0.2	2.23	0.14	1.11	0.29	0.34	0.11	0.21	0.1
	F_1	6.67	0.01*	7.05	0.08	0.38	0.54	0.97	0*	0.35	0*
	F_2	10.31	0*	5.11	0.02*	11.51	0*	1.46	0*	0.13	0*
	B_1	8.03	0*	6.43	0.01*	0.69	0.41	0.94	0*	0.15	0*
	B_2	3.96	0.05	9.44	0*	21.01	0*	1.35	0*	0.15	0*
C-0	P_1	0*	0.96	0.07	0.79	0.75	0.4	0.11	0.56	0.15	0.43
	P2	0.11	0.74	0.22	0.64	0.35	0.55	0.16	0.37	0.15	0.4
	F_1	0.34	0.56	0.11	0.74	0.87	0.35	0.24	0.21	0.21	0.1
	F_2	0.59	0.44	1.17	0.28	1.82	0.18	0.56	0.03	0.09	0*
	B_1	0.01*	0.91	0.05	0.82	0.23	0.63	0.22	0.23	0.08	0.03*
	B_2	5.58	0.02*	5.18	0.02*	0*	0.97	3.81	0*	0.25	0*
E-0	P_1	0*	0.96	0.07	0.79	0.74	0.39	0.11	0.56	0.15	0.43
	P_2	0.11	0.74	0.22	0.64	0.35	0.55	0.16	0.37	0.15	0.4
	F_1	0.34	0.56	0.11	0.74	0.87	0.35	0.24	0.21	0.21	0.1
	F_2	0.06	0.81	0.17	0.68	0.55	0.46	0.22	0.24	0.06	0.04*
	B_1	0*	0.95	0.02*	0.90	0.07	0.79	0.22	0.23	0.09	0.02*
	B_2	1.30	0.25	0.97	0.32	0.23	0.63	1.12	0*	0.15	0*

U_1^2, U_2^2, and $U3^2$ refer to the statistics of the uniformity test. ${}_nW^2$ refers to the statistics of the Smirnov test. D_n refers to the statistics of the Kolmogorov test. *Significance at 0.05.

Table 5. Second-order genetic parameters of the optimal model for the flowering time of the D × E hybridized combination.

Second-order genetic parameter	D × E_F_2	D × E_D	D × E_E
σ^2_{mg}			
h^2_{mg} (%)			
σ^2_{Pg}	5.86	6.57	35.89
h^2_{Pg} (%)	26.36	28.65	68.67

σ^2_{mg} = major gene variance; h^2_{mg} = major gene heritability; σ^2_{pg} = polygene variance; h^2_{pg} = polygene heritability.

breeding cultivars with appropriate flowering times. Our investigation indicated that the flowering time of pansies displayed continuous and normal distributions in populations exhibiting complex trait characteristics. The same phenomenon has been observed in many other plants, including *Arabidopsis* (Zhang et al. 2003), rice (Yano et al. 2001), rapeseed (Xu et al. 2016), soybean (Lin et al. 2021), pumpkin (Abbas et al. 2022), and *Chrysanthemum ×morifolium* (Zhao et al. 2023). Recent studies have revealed that flowering time is tuned by multiple genes, including *FT*, *FLH*, *FLC*, *VIN3*, *LFY*, *SOC1*, *AP1*, *FVE*, *FY*, *FLD*, *PEP*, and *HAD5* (Adrian et al. 2010; Chong and Stinchcomb 2019; Huang et al. 2021; Seedat et al. 2013; Takagi et al. 2023; Wang et al. 2016; Xie et al. 2024). The number and allelic variations that affect flowering time and whether there are some genes with larger effects among these variant alleles are the most important concerns for breeders regarding a particular breeding germplasm. Based on the investigation of the flowering time of pansy and using the major gene plus polygene mixed inheritance analysis, we found that the flowering time of pansy was controlled by multiple genes with minor effects in some cases, such as under the D × E genetic background, or by major genes with minor polygenes in other cases, such as in the genetic setting of X × E.

If major genes (QTLs) are identified and precisely mapped, then it would be convenient to perform marker-assisted selection breeding and directional introgression. Therefore, the mining of major QTLs has attracted increasing attention from breeders (Abbas et al. 2022). A genetic analysis demonstrated that major genes were relatively easy to detect in genetic populations derived from parents with minor phenotypic differences. In contrast, only minor polygenic genes were detected in the genetic populations produced by the hybridization of two parents with large phenotypic differences. Therefore, choosing germplasms with minor phenotypic differences as hybrid parents to generate genetic populations instead of traditional QTL mapping, which adopts parents with different characteristics to produce genetic populations, is a feasible strategy for major QTL mapping and mining. Recently, a rapid multi-QTL mapping (RapMap) method proposed by Zhang et al. (2021) was used to successfully identify eight rice grain-size genes by using F_2 gradient populations constructed from accessions with minor phenotypic differences, thus confirming the findings of this study.

Flowering induction involves several genetic pathways such as the autonomous, vernalization, photoperiod, and gibberellin (Chong and Stinchcomb 2019; Lin et al. 2021; Mouradov et al. 2002; Takagi et al. 2023; Xie et al. 2024; Yang et al. 2024). Therefore, plant flowering is influenced by both the internal physiological state and external environmental factors (Jung and Müller 2009; Putterill et al. 2004), including genetic and environmental factors such as temperature, light, water, fertilizer, and diseases (Balcerowicz 2021; Choudhary et al. 2022; Niu et al. 2000; Oh and Runkle 2016; Takagi et al. 2023; Zeng et al. 2006). In the present study, we found that weather conditions significantly influenced pansy flowering. The flowering of plants accelerated under sunny and warm weather but was delayed during low temperature and cloud days. This led to the clustering of plant flowering and affected the precise correspondence between phenotype and genotype, which may have affected the precise mapping of QTLs and the isolation of major genes. Providing stable environmental conditions or generating genetically permanent populations, such as double haploid and recombinant inbred lines, and investigating the phenotype for several years are vital to obtaining ideal phenotype data for flowering.

Table 6. First-order genetic parameters of the optimal model of the flowering time of the X × E hybridized combination.

First-order genetic parameter	Estimated value	First-order genetic parameter	Estimated value
d_a	4.37	j_{ba}	−9.77
d_b	4.37	l	−1.92
h_a	5.15	[h]	
h_b	6.87	[d]	
i	−0.41	d_a/h_a	0.85
j_{ab}	−8.05	d_b/h_b	0.64

σ^2_{mg} = major gene variance; h^2_{mg} = major gene heritability; σ^2_{pg} = polygene variance; h^2_{pg} = polygene heritability.

d = additive effect of major genes; d_a = additive effect of the first major gene; d_b = additive effect of the second major gene; h = dominant effect of the major genes; h_a = dominant effect of the first major gene; h_b = dominant effect of the second major gene; i = additive × additive effect between two major genes; j_{ab} = additive (a) × dominant (b) effect; j_{ba} = additive (b) × dominant (a) effect; l = dominant × dominant effect between two major genes; d_a/h_a = the dominant degree of the first major gene; d_b/h_b = the dominant degree of the second major gene.

Table 7. Second-order genetic parameters of the optimal model for the flowering time of the X × E hybridized combination.

Second-order genetic parameter	X × E_F_2	X × E_X	X × E_E
σ^2_{mg}	24.44	17.39	79.52
h^2_{mg} (%)	58.69	35.72	76.98
σ^2_{Pg}		14.10	6.58
h^2_{Pg} (%)		28.95	6.37

σ^2_{mg} = major gene variance; h^2_{mg} = major gene heritability; σ^2_{pg} = polygene variance; h^2_{pg} = polygene heritability.

Conclusions

Our investigation showed that the flowering time of pansies is a typical complex characteristic displaying continuous and normal distributions in segregated populations. A genetic analysis using a major gene plus polygene mixed genetic model indicated that in the genetic background hybridized by two parental inbred lines, D and E, with large differences in flowering time, the flowering time was controlled by minor polygenes with additive-dominant-epistatic effects, resulting in low heritability. In the genetic setting of the two parents, X and E, which differed slightly in phenotype, two major and minor polygenes exerting additive-dominant-epistatic effects governed the flowering time, leading to high heritability.

References Cited

Abbas HMK, Zhou YY, Huang HX, Qamar MT, Wang MM, Lu S, Xu C, Liu Z, Wu TQ, Zhong YJ. 2022. QTL mapping, whole genome resequencing, and marker-assisted selection provide basics of early flowering in pumpkin. Plant Breed. 141(2):266–276. https://doi.org/10.1111/pbr.12996.

Adrian J, Farrona S, Reimer JJ, Albani MC, Coupland G, Turck F. 2010. cis-regulatory elements and chromatin state coordinately control temporal and spatial expression of FLOWERING LOCUS T in *Arabidopsis*. Plant Cell. 22(5): 1425–1440. https://doi.org/10.1105/tpc.110.074682.

Balcerowicz M. 2021. Coming into bloom: A light-sensitive transcription factor complex tells roses when to flower. Plant Physiol. 186(2): 812–813. https://doi.org/10.1093/plphys/kiab124.

Brightbill CM, Sung S. 2022. Temperature-mediated regulation of flowering time in *Arabidopsis thaliana*. aBIOTECH. 3(1):78–84. https://doi.org/10.1007/s42994-022-00069-2.

Cho L-H, Yoon J, An G. 2017. The control of flowering time by environmental factors. Plant J. 90(4):708–719. https://doi.org/10.1111/tpj.13461.

Chong VK, Stinchcombe JR. 2019. Evaluating population genomic candidate genes underlying flowering time in *Arabidopsis thaliana* using T-DNA insertion lines. J Hered. 110(4): 445–454. https://doi.org/10.1093/jhered/esz026.

Choudhary A, Kumar A, Kumar U, Choudhary R, Kumar R, Jat R, Nidhibahen P, Hatamleh AA, Al-Dosary MA, Al-Wasel YA, Rajagopal R, Ravindran B. 2022. Various fertilization managements influence the flowering attributes, yield response, biochemical activity and soil nutrient status of Chrysanthemum (*Chrysanthemum morifolium* Ramat.). Sustainability. 14(8):4561. https://doi.org/10.3390/su14084561.

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C, Coupland G. 2007. FT protein movement contributes to long-distance signaling in floral induction of *Arabidopsis*. Science. 316(5827):1030–1033. https://doi.org/10.1126/science.1141752.

Du X, Wang H, Liu J, Zhu X, Mu J, Feng X, Liu H. 2022. Major gene with polygene inheritance analysis of shoot architecture traits in *Viola cornuta*. Sci Hortic. 303:111204. https://doi.org/10.1016/j.scienta.2022.111204.

Ehrenreich IM, Hanzawa Y, Chou L, Roe JL, Kover PX, Purugganan MD. 2009. Candidate gene association mapping of arabidopsis flowering time. Genetics. 183(1):325–335. https://doi.org/10.1534/genetics.109.105189.

Gai J, Wang J. 1998. Identification and estimation of a QTL model and its effects. Theor Appl Genet. 97(7):1162–1168. https://doi.org/10.1007/s001220051005.

Gai J, Zhang Y, Wang J. 2003. Genetic system of quantitative traits in plants (in Chinese). Science Press, Beijing, China.

Han B, Huang S, Huang G, Wu X, Jin H, Liu Y, Xiao Y, Zhou R. 2023. Genetic relatedness and association mapping of horticulturally valuable traits for the *Ceiba* plants using ddRAD sequencing. Hortic Plant J. 9(4):826–836. https://doi.org/10.1016/j.hpj.2022.01.006.

Hayama R, Yokoi S, Tamaki S, Yano M, Shimamoto K. 2003. Adaptation of photoperiodic control pathways produces short-day flowering in rice. Nature. 422(6933):719–722. https://doi.org/10.1038/nature01549.

Hori K, Matsubara K, Yano M. 2016. Genetic control of flowering time in rice: Integration of Mendelian genetics and genomics. Theor Appl Genet. 129(12):2241–2252. https://doi.org/10.1007/s00122-016-2773-4.

Huang L, Min Y, Schiessl S, Xiong X, Jan HU, He X, Qian W, Guan C, Snowdon RJ, Hua W, Guan M, Qian L. 2021. Integrative analysis of GWAS and transcriptome to reveal novel loci regulation flowering time in semi-winter rapeseed. Plant Sci. 310:110980. https://doi.org/10.1016/j.plantsci.2021.110980.

Jung C, Müller AE. 2009. Flowering time control and applications in plant breeding. Trends Plant Sci. 14(10):563–573. https://doi.org/10.1016/j.tplants.2009.07.005.

Kessler JR, Hagan A, Jr, Cobb P. 1999. Pansy production and marketing. Southeast Floric. July/August:29–39. https://hortscans.ces.ncsu.edu/uploads/p/a/pansy_pr_51e448e796b25.pdf.

Kuittinen H, Sillanpää M, Savolainen O. 1997. Genetic basis of adaptation: Flowering time in *Arabidopsis thaliana*. Theor Appl Genet. 95(4):573–583. https://doi.org/10.1007/s001220050598.

Lin X, Liu B, Weller JL, Abe J, Kong F. 2021. Molecular mechanisms for the photoperiodic regulation of flowering in soybean. J Integr Plant Biol. 63(6):981–994. https://doi.org/10.1111/jipb.13021.

Monniaux M, McKim SM, Cartolano M, Thévenon E, Parcy F, Tsiantis M, Hay A. 2017. Conservation vs divergence in LEAFY and APETALA1 functions between *Arabidopsis thaliana* and *Cardamine hirsuta*. New Phytol. 216(2): 549–561. https://doi.org/10.1111/nph.14419.

Mouradov A, Cremer F, Coupland G. 2002. Control of flowering time: Interacting pathways as a basis for diversity. Plant Cell. 14(Suppl): S111–S130. https://doi.org/10.1105/tpc.001362.

Niu G, Heins RD, Cameron AC, Carlson WH. 2000. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of pansy (*Viola ×wittrockiana*). J Am Soc Hortic Sci. 125(4):436–441. https://doi.org/10.21273/JASHS.125.4.436.

Oh W, Runkle ES. 2016. Flowering and morphological responses of petunia and pansy as influenced by lamp type and lighting period to provide long days. Korean J HST. 34(2):207–219. https://doi.org/10.12972/kjhst.20160021.

Putterill J, Laurie R, Macknight R. 2004. It's time to flower: The genetic control of flowering time. Bioessays. 26(4):363–373. https://doi.org/10.1002/bies.20021.

Seedat N, Dinsdale A, Ong EK, Gendall AR. 2013. Acceleration of flowering in *Arabidopsis thaliana* by Cape Verde Islands alleles of FLOWERING H is dependent on the floral promoter FD. J Exp Bot. 64(10):2767–2778. https://doi.org/10.1093/jxb/ert120.

Shen P, Gao S, Chen X, Lei T, Li W, Huang Y, Li Y, Jiang M, Hu D, Duan Y, Li M, Li J. 2020. Genetic analysis of main flower characteristics in the F_1 generation derived from intraspecific hybridization between *Plumbago auriculata* and *Plumbago auriculata f. alba*. Sci Hortic. 274:109652. https://doi.org/10.1016/j.scienta.2020.109652.

Song X, Xu Y, Gao K, Fan G, Zhang F, Deng C, Dai S, Huang H, Xin H, Li Y. 2020. High-density genetic map construction and identification of loci controlling flower-type traits in chrysanthemum (*Chrysanthemum* × *morifolium* Ramat. Hortic Res. 7(1):108–1265. https://doi.org/10.1038/s41438-020-0333-1.

Song X, Zhao X, Fan G, Gao K, Dai S, Zhang M, Ma C, Wu X. 2018. Genetic analysis of the corolla tube merged degree and the relative number of ray florets in chrysanthemum (*Chrysanthemum* × *morifolium* Ramat.). Sci Hortic. 242:214–224. https://doi.org/10.1016/j.scienta.2018.07.010.

Sun X, Liu L, Zhi X, Bai J, Cui Y, Shu J, Li J. 2019. Genetic analysis of tomato internode length via mixed major gene plus polygene inheritance model. Sci Hortic. 246:759–764. https://doi.org/10.1016/j.scienta.2018.11.044.

Takagi H, Hempton AK, Imaizumi T. 2023. Photoperiodic flowering in *Arabidopsis*: Multilayered regulatory mechanisms of CONSTANS and the florigen FLOWERING LOCUS T. Plant Commun. 4(3):100552. https://doi.org/10.1016/j.xplc.2023.100552.

Veerman A, van Zon JCJ. 1965. Insect pollination of pansies (*Viola* spp.). Entomologia Exp Applicata. 8(2):123–134. https://doi.org/10.1111/j.1570-7458.1965.tb00847.x.

Wang N, Chen B, Xu K, Gao G, Li F, Qiao J, Yan G, Li J, Li H, Wu X. 2016. Association mapping of flowering time QTLs and insight into their contributions to rapeseed growth habits. Front Plant Sci. 7(7):338. https://doi.org/10.3389/fpls.2016.00338.

Warner RM, Erwin JE. 2006. Prolonged high-temperature exposure differentially reduces growth and flowering of 12 *Viola ×wittrockiana* Gams. cvs. Sci Hortic. 108(3):295–302. https://doi.org/10.1016/j.scienta.2006.01.034.

Wu X, Zhao X, Gao K, Tian Y, Zhang M, Anderson NO, Dai S. 2023. Heterosis and mixed genetic analysis of flowering traits in cross breeding of

day-neutral *Chrysanthemum* (Asteraceae). Agronomy. 13(8):2107. https://doi.org/10.3390/agronomy13082107.

Xie H, Li X, Sun Y, Lin L, Xu K, Lu H, Cheng B, Xue S, Cheng D, Qiang S. 2024. DNA methylation of the autonomous pathway is associated with flowering time variations in *Arabidopsis thaliana*. IJMS. 25(13):7478. https://doi.org/10.3390/ijms25137478.

Xu L, Hu K, Zhang Z, Guan C, Chen S, Hua W, Li J, Wen J, Yi B, Shen J, Ma C, Tu J, Fu T. 2016. Genome-wide association study reveals the genetic architecture of flowering time in rapeseed (*Brassica napus* L.). DNA Res. 23(1):43–52. https://doi.org/10.1093/dnares/dsv035.

Yang M, Lin W, Xu Y, Xie B, Yu B, Chen L, Huang W. 2024. Flowering-time regulation by the circadian clock: From *Arabidopsis* to crops. The Crop J. 12(1):17–27. https://doi.org/10.1016/j.cj.2023.09.002.

Yano M, Kojima S, Takahashi Y, Lin H, Sasaki T. 2001. Genetic control of flowering time in rice, a short-day plant. Plant Physiol. 127(4):1425–1429. https://doi.org/10.1104/pp.010710.

Ye Y, Wu J, Feng L, Ju Y, Cai M, Cheng T, Pan H, Zhang Q. 2017. Heritability and gene effects for plant architecture traits of crape myrtle using major gene plus polygene inheritance analysis. Sci Hortic. 225(1):335–342. https://doi.org/10.1016/j.scienta.2017.06.065.

Zeng Q, Zhao Z, Zhao S. 2006. Signaling pathways of plant flowering time regulation (in Chinese). Genetics. 28(8):1031–1036.

Zhang H, Ransom C, Ludwig P, van Nocker S. 2003. Genetic analysis of early flowering mutants in Arabidopsis defines a class of pleiotropic developmental regulator required for expression of the flowering-time switch flowering locus C. Genetics. 164(1):347–358. https://doi.org/10.1093/genetics/164.1.347.

Zhang J, Zhang D, Fan Y, Li C, Xu P, Li W, Sun Q, Huang X, Zhang C, Wu L, Yang H, Wang S, Su X, Li X, Song Y, Wu ME, Lian X, Li Y. 2021. The identification of grain size genes by RapMap reveals directional selection during rice domestication. Nat Commun. 12(1):5673. https://doi.org/10.1038/s41467-021-25961-1.

Zhao ZH, Zhang YG, Gao K, Tian YK, Zhang QL, Fang ZJ, Wang S, Liu H, Ji YS, Dai SL. 2023. Variation and correlation analysis of florescence and main ornamental traits of *Chrysanthemum* × *morifolium* Ramat. varieties. Plant Sci J. 41(2):214–223. https://doi.org/10.11913/PSJ.2095-0837.22172.