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The quantitative-genetic and QTL architecture of trait integration and modularity in *Brassica rapa* across simulated seasonal settings

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Within organisms, groups of traits with different functions are frequently modular, such that variation among modules is independent and variation within modules is tightly integrated, or correlated. Here, we investigated patterns of trait integration and modularity in *Brassica rapa* in response to three simulated seasonal temperature/photoperiod conditions. The goals of this research were to use trait correlations to understand patterns of trait integration and modularity within and among floral, vegetative and phenological traits of *B. rapa* in each of three treatments, to examine the QTL architecture underlying patterns of trait integration and modularity, and to quantify how variation in temperature and photoperiod affects the correlation structure and QTL

architecture of traits. All floral organs of *B. rapa* were strongly correlated, and contrary to expectations, floral and vegetative traits were also correlated. Extensive QTL co-localization suggests that covariation of these traits is likely due to pleiotropy, although physically linked loci that independently affect individual traits cannot be ruled out. Across treatments, the structure of genotypic and QTL correlations was generally conserved. Any observed variation in genetic architecture arose from genotype × environment interactions (GEIs) and attendant QTL × E in response to temperature but not photoperiod.

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Introduction

Throughout the natural world, biological systems tend to be modular; organisms are composed of recognizable units that differ in development, structure and function (Wagner et al., 2007; Klingenberg, 2008). Modularity refers to the degree of connectedness; a module is connected internally but independent from other modules (Wagner, 1996). Morphologically, modules are relatively independent groups of phenotypic traits, whereas traits within modules act in an integrated, or coordinated, manner, with coordination arising from interactions among the processes that produce the traits (Cheverud, 1996; Klingenberg, 2008). Evolutionarily, unconnected modules may respond independently to selection and follow different adaptive paths (Wagner, 1996), whereas integration of traits within modules often represents a trade-off; integration reduces the occurrence of maladaptive trait combinations, but may also limit the response of individual traits to selection (Wagner, 1996; Klingenberg, 2008).

The floral organs of plants are commonly viewed as integrated traits. Flowers are composed of multiple organs that frequently act in a coordinated manner to carry out the functions of pollinator attraction, pollen

donation and pollen receipt. Given that the singular function of flowers is reproduction, the size and shape of floral organs is frequently coordinated and populations often maintain strong genotypic correlations among floral traits (Conner and Via, 1993; Oneil and Schmitt, 1993; Carr and Fenster, 1994; Conner and Sterling, 1995; Juenger et al., 2000; van Kleunen and Ritland, 2004; Ashman and Majetic, 2006; Brock and Weinig, 2007). One theory for the evolution of floral trait correlations is via natural selection by pollinators on floral phenotypes (Berg, 1960). This theory predicts that plants with specialist pollinators will have highly correlated floral organ sizes, with correlations arising by selection for floral dimensions that fit the dimensions of the pollinator, whereas plants with generalist pollinators are predicted to have less strongly correlated floral traits. However, empirical studies have shown that the relationship between pollinator specificity and the level of covariation among floral traits is not as consistent as predicted by Berg (Conner and Sterling, 1995; Armbruster et al., 1999; Brock and Weinig, 2007), suggesting that other factors may also affect floral trait correlations.

Genetically, several mechanisms may underlie floral trait correlations. If pollinator efficiency has contributed to increased floral trait correlations, selection may have favored specific combinations of alleles at unlinked loci, or 'adaptive character complexes' (Armbruster and Schwaegerle, 1996), resulting in linkage disequilibrium (LD) among physically unlinked genes. Alternatively, covariation of traits may arise from a common develop-

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mental or genetic architecture. For example, correlations among traits may arise because a pleiotropic gene affects variation in several traits (Lande, 1980), as in the ABC model of plant development, where B-class genes affect the development of both petals and stamens (Weigel and Meyerowitz, 1994). From the ABC model for organ identity, one might also predict that correlations for size are stronger between organs residing in adjacent floral whorls than organs in non-adjacent whorls. Empirical research suggests that the genetic mechanisms underlying floral trait correlations may differ among species. All floral organs were equally highly correlated in Mimulus guttatus and Mimulus micranthus (Carr and Fenster, 1994), Phlox drummondii (Waitt and Levin, 1993), Arabidopsis thaliana (Juenger et al., 2000, 2005; Brock and Weinig, 2007) and Brassica nigra (Conner and Sterling, 1995), and QTL mapping and analysis of segregating progenies with extensive generations of recombination suggested that pleiotropic genes (or physically linked loci) were primarily responsible for floral trait correlations in Arabidopsis (Juenger et al., 2000; Conner, 2002). However, in Raphanus raphanistrum and Brassica napus, filament and corolla traits were more strongly correlated than other floral traits, potentially as a consequence of pollinator-mediated selection and LD of physically unlinked genes (Conner and Sterling, 1995). Given these results, patterns of floral trait correlations and their underlying genetic mechanisms may be species-specific.

As floral and leaf traits have a common developmental origin (Ratcliffe et al., 1999), they may also co-vary; however, floral, vegetative and other types of traits have different functions, may have undergone selection for independent development, and may therefore comprise separate modules. Berg's theory of pollinator selection proposes an explanation for the independence of floral and vegetative traits (Berg, 1960); because vegetative traits may respond plastically to environmental variation, plants that buffer the development of floral organs from that of vegetative organs may have more consistent floral organ sizes that better fit the dimensions of specialist pollinators, leading to increased rates of pollination, and ultimately, more independence of floral and vegetative traits (Berg, 1960). Relative to plants with specialist pollinators, this theory predicts that plants with generalist pollinators will experience less selection for consistent floral organ sizes and will have less independent floral and vegetative traits (Berg, 1960). Empirical studies have shown that the degree of independence of floral and vegetative traits is not well predicted by pollination syndrome; modularity of floral and vegetative organs was equally pronounced in species with unspecialized vs specialized pollination syndromes (Armbruster et al., 1999). More generally, several empirical studies have found that floral and vegetative traits are modular, such that traits within floral or vegetative modules were correlated, whereas floral and vegetative traits were generally uncorrelated (Conner and Via, 1993; Conner and Sterling, 1996; Juenger et al., 2005; Ashman and Majetic, 2006; but see Brock and Weinig, 2007), and QTL mapping in a population of recombinant inbred lines (RILs) of Arabidopsis revealed that floral and vegetative traits had largely independent genetic architectures (Juenger et al., 2005). In sum, integration/modularity may depend on genetic, ecological and evolutionary factors that are specific to each species.

It is also noteworthy that the expression of many developmental pathways (such as flowering time, shade avoidance) depends on environmental cues, such that the expression of integration/modularity may vary by environment (Waitt and Levin, 1993; Pigliucci and Marlow, 2001; Conner et al., 2003; Brock and Weinig, 2007). For example, in Phlox drummondii, the correlation structure among traits differed with different nutrient availability (Waitt and Levin, 1993), in Raphanus raphinistrum, the correlation structure among floral traits differed between field and greenhouse environments (Conner et al., 2003), and in A. thaliana, changes in vernalization, season length and light composition affected patterns of trait correlation structure (Pigliucci and Marlow, 2001; Brock and Weinig, 2007). Also of relevance to the current study, photoperiod and temperature may have indirect effects on floral meristem development and floral organ identity genes in A. thaliana (Okamuro et al., 1993, 1996), and such organ-specific effects may be one mechanism by which environment could influence integration/ modularity. More generally, these results suggest that patterns of trait integration and modularity may be sensitive to environmental variation, but few studies have used more than a single environment.

In this study, we used a population of 150 RILs to understand the quantitative-genetic and QTL architecture of trait integration and modularity in Brassica rapa, and to asses how this genetic architecture changes across three simulated seasonal settings that the species naturally encounters (see Materials and methods). We were specifically interested in quantifying: (1) patterns of trait integration within flowers, and if floral organs in adjacent whorls show stronger integration than those in non-adjacent whorls as might be expected if genes affecting floral organ size act pleiotropically in adjacent whorls similar to the effects of ABC class genes; (2) the degree of modularity between floral, vegetative and phenological traits; (3) the effect of seasonally variable abiotic factors on the expression of integration/ modularity and (4) the genetic mechanisms underlying trait integration/modularity and the response to environmental variation.

Materials and methods

Study system

We investigated the genetic basis of trait integration and modularity in *Brassica rapa* and the effect of environmental variation on these patterns. *B. rapa* is an insectpollinated, oilseed and vegetable crop (Prakash and Hinata, 1980). Like other members of the Brassicaceae, flowers of *B. rapa* have distinct (unfused) floral organs, including four sepals, four petals, six stamens (four long + two short), and a compound pistil of two carpels. The distinct floral organs make this species well suited to examining the structure of bivariate correlations between floral organs and, specifically, the relative strength of correlations between organs in different whorls.

The original native range of *B. rapa* is thought to have extended across Eurasia from the Western Mediterranean to Central Asia, and wild individuals of the species still grow throughout this region (Gomez Campo, 1999).

Many crops were domesticated from this wild progenitor independently in several locations across Eurasia (Zhao et al., 2005), including varieties cultivated for oil (B. rapa subsp. oleifera), as root vegetables (B. rapa subsp. rapa, or turnip), and as leafy vegetables (B. rapa subsp. chinensis, or pak choi, and *B. rapa* subsp. *pekinensis*, or Chinese cabbage). Given that *B. rapa* was domesticated in many regions and is cultivated in numerous locations worldwide, this species is capable of surviving across a wide range of environmental conditions. Further sources of environmental variation arise from agricultural practices; most leafy vegetables and oilseed varieties are planted as spring or fall annuals, whereas root vegetables such as turnips are planted as fall or winter annuals and biennials. As this species encounters such a wide range of abiotic variation, it is well suited to understanding how integration and modularity of floral, vegetative and phenological traits respond to the environment. Across locations and seasons where B. rapa is cultivated, two main environmental factors that vary are temperature and photoperiod. We studied responses to three different combinations of temperature and photoperiod characteristic of habitats that B. rapa occupies, including: (1) long days, warm temperatures, which are experienced by spring or summer annuals (such as pak choi planted in the spring), (2) long days, cool temperatures, which are experienced by overwintering biennial crops that flower in the spring (such as turnips planted in fall in Europe) and (3) short days, cool temperatures, which are experienced by fall or winter annuals (such as Chinese cabbage or pak choi planted in the fall). We did not examine short photoperiods and warm temperatures, as this combination of conditions is unlikely to exist in any of the locations where *B. rapa* grows.

The genotypes used in this study were RILs derived from a cross between two highly inbred genotypes of B. rapa. The parents of the RILs were R500, a cultivated seed oil genotype, and IMB211, a rapid cycling genotype that may approximate a weedy member of the species; this cross may therefore be representative of gene flow occurring between cultivated genotypes and their wild neighbors, and can be used to investigate the genetic regions that are responsible for floral, vegetative and phenological trait variation between these two types of populations. Furthermore, the intensity of selection for integration/modularity may have varied in these parents (and between cultivars and wild genotypes in general), and this population of RILs is therefore of interest to investigate integration/modularity in *B. rapa*. To form the RILs, the two parents were crossed, the F1 generation was selfed, and the progeny were advanced by single seed descent to the S6 generation to form 150 RILs (Iniguez-Luy et al., 2009).

Experimental design and growth conditions

Six growth-chamber compartments (PGC-9/2 with Percival Advanced Intellus Environmental Controller, Percival Scientific, Perry, IN, USA) were used to simulate seasonal settings. As previous research using the same model of growth chamber and similar numbers of *B. rapa* individuals revealed that plants caused photosynthesisinduced drawdowns of CO_2 that affected floral morphology (Edwards *et al.*, 2009), ventilation was increased in each growth-chamber compartment by adding two additional exhaust vents and an intake fan. This modification doubled the number of air exchanges to maintain CO_2 at or above 375 p.p.m. For all growth chambers, light intensity during light cycles was maintained at a photosynthetic photon flux density of around $500 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$, and the vapor pressure deficit was maintained between 0.45 and 1.65 (45–70% relative humidity).

One replicate of each of the 150 RILs and the two parental genotypes were grown in each of the six growth-chamber compartments. The growth chambers were set to: (1) WL represents warm temperature (24 °C), long photoperiod (14 h/10 h light/dark cycles), (2) CL represents cool temperature (12 °C), long photoperiod (14 h/10 h light/dark cycles) and (3) CS represents cool temperature (12 °C), short photoperiod 10 h/14 h light/ dark cycles). Each treatment occupied two of the six growth chambers at one time, and this planting design was temporally replicated three times, totaling six replicates of each genotype in each treatment. The treatments were rotated among growth chambers so that each treatment occupied each growth-chamber compartment once.

For each replicate of each genotype, we planted three seeds that were cold/dark stratified for 3 days at $4^{\circ}C$ and then placed immediately into growth chambers set to the three treatments, with genotypes fully randomized within each chamber. After germination, seedlings were thinned to one plant. Plants were watered regularly to maintain moist soil conditions.

Phenotypic trait measurements

Plants were checked daily for germination, which was scored when the seed coat opened and the radicle became visible. All germinated plants were checked daily for bolting, which was scored when buds differentiated from the apical meristem. At bolting, one young, fully expanded leaf was removed from all bolting plants and scanned. Leaf area was measured from the scanned image using ImageJ (Rasband, 1997-2007). Once a plant had bolted, it was checked every morning for flowering, which was scored when sepals opened and petals became visible or when a flower bud senesced prior to opening. After flowering, each plant was checked for flower maturity, which was recorded every afternoon at 1400 hours for plants in which the anthers on the third and fourth flowers of the main stem dehisced and began to shed pollen. At flower maturity, the third and fourth flowers were removed and placed in 75% ethanol for subsequent dissection, the length of the plants' stem was measured, and the collection date was recorded. As some plants aborted flowers (that is, the flower buds senesced prior to opening), we recorded the number of aborted flowers and collected the first two viable flowers when the third and fourth flowers were not viable (generally not later than the 10th flower). To estimate phenology, we recorded the number of days from germination to flowering (days to flowering) and the number of days from flowering to the collection of the flowers (collection interval), which estimates the length of time necessary for a plant to produce viable flowers. The vegetative traits included in this study were leaf area and stem length.

Preserved flowers were dissected under a dissecting microscope (Nikon SMZ800, Nikon Corporation, Tokyo,

Japan) and digitally photographed. As one of our goals was to understand patterns of integration in adjacent and non-adjacent floral whorls, we measured multiple traits from the pistil, stamen and petal whorls. Floral organ sizes were measured from the digital image using ImageJ (Rasband, 1997-2007); measured traits included style length, ovary length, short anther length (that is, the length of anther on a representative short stamen), short filament length (that is, the length of filament on a representative short stamen), long anther length (that is, the length of anther on a long stamen), long filament length (that is, the length of filament on a long stamen), petal blade length, petal claw length, petal width and petal area. Measurements of the two flowers from each individual were averaged for all data analysis, except petal area, which was calculated on only one flower because of the extended time needed for this measurement. From the measurements of individual floral organs, we calculated three composite measurements that estimate floral allometry: (1) herkogamy, or total pistil length minus long filament length, (2) stamen exsertion, or long filament length minus petal claw length and (3) pistil exsertion, or total pistil length minus petal claw length.

Statistical analyses

Within each treatment, we used restricted maximum likelihood (REML in PROC MIXED, SAS ver. 9.2) to estimate the random effects of genotype and temporal block on each phenotypic trait. The variance components estimated from this analysis were used to calculate the ratio $V_{\rm G}/V_{\rm P}$ where $V_{\rm G}$ is the among-genotype variance component of a trait in each treatment and $V_{\rm P}$ is the total of all estimated variance components of a trait in each treatment.

To test for genotypic differences in the response to treatment and estimate genotypic values, we carried out a mixed-model nested analysis of variance (ANOVA) over all three treatments using restricted maximum likelihood (PROC MIXED, SAS ver. 9.2). We evaluated the fixed effect of treatment and the random effects of genotype, chamber nested within treatment, and genotype × treatment interaction (GEI) on all measured traits. A significant genotype effect was interpreted as genetic differences in mean trait expression, a significant treatment effect was interpreted as phenotypic plasticity (or trait sensitivity) among treatments, and a significant interaction effect was interpreted as genetic variation in plasticity.

Using the full ANOVA model, we estimated the genotypic values for each trait in each treatment using best linear unbiased predictors (Robinson, 1991; Littell *et al.*, 2006). To assess the level of integration and modularity of traits, best linear unbiased predictors of genotypic values in each treatment were used to estimate genotypic correlations among traits within each treatment (SAS PROC CORR, SAS ver. 9.2). The significance values of all correlations were corrected for multiple comparisons by controlling the false discovery rate (Benjamini and Hochberg, 1995). Best linear unbiased predictors of genotypic values in each treatment were also used to estimate r_{GE} , the genotypic correlation of each trait across treatment pairs (for example, across WL/CL, WL/CS, CL/CS; SAS PROC CORR). Estimates

of $r_{\rm GE}$ indicate the extent to which the same genetic loci have phenotypic expression and alleles have the same function across treatments; estimates of r_{GE} approaching one suggest that the same genetic loci are expressed and alleles have similar effects across the two treatments, whereas estimates approaching 0 suggest that different genetic loci are expressed or alleles that affect trait variation differ in function across the two treatments (Fry et al., 1996; Gurganus et al., 1998; Vieira et al., 2000). To determine whether the r_{GE} values for each trait across each pair of treatments were significantly different from both 0 and 1, we carried out a mixed-model nested ANOVA using the full model as specified above (evaluating the fixed effect of treatment and the random effects of genotype, chamber nested within treatment, and genotype × treatment interaction), but comparing two treatments at a time (PROC MIXED, SAS ver. 9.2); $r_{\rm GE}$ of a trait across each treatment pair was interpreted as significantly different than 1 when the genotype × treatment interaction was significant, and significantly different from 0 when the among-genotype variance was significant (Gurganus et al., 1998; Vieira et al., 2000).

Prior to analysis, we evaluated the response variables for normality and homoscedasticity. The assumptions of normality for ANOVA were not met for some traits, and these were transformed as follows: style length, petal blade length, and petal width were square-root transformed; ovary length, stem length, petal area and leaf area were log-10 transformed; days to flowering was inverse transformed and short and long anther length, long filament length and petal claw length were transformed to the 1.5 power. We carried out all ANOVA, correlation and QTL-mapping analyses using both nontransformed and transformed data, but we present only the results of non-transformed data because the outcome of significance tests was largely unaffected by transformation (not shown).

QTL mapping

The linkage map used in this study was described previously by Iniguez-Luy et al. (2009) and is composed of 224 RFLP and microsatellite markers spanning 10 linkage groups, with an average marker density of 5.7 cM per marker. QTL mapping of genotypic estimates of each trait in each treatment was carried out using composite interval mapping as implemented in Windows QTL Cartographer ver. 2.5 (Wang et al., 2007). To control for effects of variation segregating elsewhere in the genome, we identified co-factors using a forward-backward regression model and a 10-cM window; a maximum of 10 co-factors was selected for inclusion in the mapping model. We scanned for QTL at 2-cM intervals across the *B. rapa* genome. The genome-wide significance threshold of the likelihood ratio (LR) test statistic for QTL was determined for each trait using 1000 permutations (Churchill and Doerge, 1994), with a type I error rate of 0.05. We also tested for QTL using a type I error rate of 0.075 to evaluate the presence of marginally significant QTL that might affect the interpretation of environmentspecific QTL effects (such as $\hat{Q}TL \times E$ interactions). The 2-LOD support limits were calculated as $LOD = 0.217 \times LR$ (Weber et al., 2001). Closely neighboring QTL, between which LR values dropped below the significance threshold but for which support intervals overlapped, were only considered as separate QTL when additive effects reversed sign; otherwise, only QTL with the largest LR values were retained.

We compared QTL expression of traits within treatments to evaluate the genetic basis of trait integration and modularity and compared QTL expression among treatments to determine the effects of treatment on QTL expression. A given QTL was deemed to affect multiple traits or the same trait across treatments when the 2-LOD support intervals overlapped. To determine whether alleles at QTL were sensitive to treatments, we carried out analyses of QTL×treatment interactions for each significant QTL using single marker, two-way ANOVAs (PROC GLM, SAS ver. 9.2). To differentiate the effects of temperature and photoperiod on QTL expression, these analyses were carried out for all pairwise combinations of treatments in which the QTL was detected (for example, if the QTL was detected in CL, we evaluated $OTL \times$ treatment interactions in CL/CS and CL/WL). For these analyses, we evaluated the fixed effects of treatment, the genotype at the marker nearest to each detected QTL, and the marker × treatment interaction. Given the low power of this analysis, we used a 0.1 type I error rate.

Finally, we carried out two-dimensional genome scans to detect pairs of QTL that interact epistatically using R/qtl (Broman *et al.*, 2003). For this test, we scanned at 1-cM steps within each interval. Significance thresholds were determined by performing 1000 permutations and using a 0.05 type I error rate.

Results

Quantitative genetics and correlations within treatments Within each treatment, all traits demonstrated highly significant effects of genotype (P<0.01; Table 1). Although temporal block was also included as a factor in these ANOVAs, we did not detect a significant effect of this factor (results not shown). The ratios of genotypic to total phenotypic variance in each treatment (V_G/V_P), or broad-sense heritability, ranged from 0.1 to 0.68. In general, floral, vegetative and composite traits had larger V_G/V_P (0.28–0.68), phenological traits had smaller V_G/V_P (0.14–0.54) and the number of aborted flowers had the smallest V_G/V_P (0.1–0.2; Table 1). The magnitude of V_G/V_P ratios was generally largest in the CL and smallest in the WL environment.

To assess the patterns of integration and modularity within and among floral, vegetative and phenological traits, we estimated genotypic correlations between each pair of traits in each treatment. Consistent with prior studies, floral traits were strongly positively correlated within each treatment (r = 0.39 - 0.97, P < 0.0001; Figure 1). Given that LD between physically distant loci is disrupted in RILs, these correlations suggest that either pleiotropy or physical linkage between proximate loci underlies the observed correlations. Adjacent floral whorls were not more strongly correlated than nonadjacent whorls; for example, the average correlation between pistil and stamen traits was 0.61 (range 0.45-0.78), and the average correlation between pistil and petal traits was 0.62 (range 0.45-0.76), and this was consistent across treatments. The number of aborted flowers was negatively correlated with all floral length traits (that is smaller floral organ size was associated with increased floral abortion; r = -0.20 to -0.47, P = 0.01 to < 0.0001; Figure 1).

Contrary to hypothesized modularity, the two vegetative traits were positively correlated with all floral traits (r = 0.19-0.72, P = 0.02 to <0.0001; Figure 1). Vegetative traits were also marginally negatively correlated with the number of aborted flowers (decreasing plant size was weakly correlated with increased floral abortion; r = -0.15 to -0.27, P = 0.07-0.0008; Figure 1). The two phenological traits showed varying degrees of modularity; days to flowering was not correlated with floral or

Table 1 Means and quantitative genetic partitioning of morphological, vegetative and phenological traits in each of three treatments

Treatment		CL			CS			WL	
Trait	Mean (s.e.)	V_G (s.e.)	V_G/V_P	Mean (s.e.)	V_G (s.e.)	V_G/V_P	Mean (s.e.)	V_G (s.e.)	V_G/V_P
Style length	2.069 (0.032)	0.079 (0.011)**	0.53	1.901 (0.032)	0.056 (0.008)**	0.58	1.896 (0.032)	0.086 (0.012)**	0.49
Ovary length	4.719 (0.057)	0.280 (0.039)**	0.54	3.993 (0.057)	0.170 (0.024)**	0.51	3.894 (0.057)	0.205 (0.029)**	0.51
Short anther length	2.161 (0.033)	0.106 (0.0140)**	0.68	2.147 (0.032)	0.077 (0.010)**	0.60	2.200 (0.032)	0.056 (0.008)**	0.54
Short filament length	3.464 (0.070)	0.375 (0.052)**	0.57	3.235 (0.070)	0.2314 (0.033)**	0.48	2.501 (0.069)	0.136 (0.020)**	0.41
Long anther length	2.246 (0.031)	0.092 (0.012)**	0.68	2.181 (0.031)	0.0745 (0.010)**	0.63	2.192 (0.031)	0.055 (0.007)**	0.59
Long filament length	4.572 (0.082)	0.289 (0.040)**	0.54	4.387 (0.082)	0.226 (0.031)**	0.56	4.027 (0.082)	0.183 (0.027)**	0.44
Petal blade length	5.697 (0.096)	0.523 (0.070)**	0.61	5.273 (0.096)	0.327 (0.045)**	0.55	4.175 (0.095)	0.195 (0.029)**	0.40
Petal claw length	2.872 (0.063)	0.122 (0.017)**	0.59	2.816 (0.063)	0.105 (0.014)**	0.54	2.920 (0.063)	0.063 (0.011)**	0.28
Petal width	5.059 (0.106)	0.6134 (0.081)**	0.65	4.633 (0.105)	0.478 (0.064)**	0.61	3.132 (0.105)	0.201 (0.029)**	0.42
Petal area	27.818 (0.776)	49.083 (6.743)**	0.58	23.547 (0.775)	32.358 (4.483)**	0.54	13.539 (0.771)	8.208 (1.237)**	0.36
Flowers aborted	1.070 (0.251)	2.537 (0.692)**	0.18	0.649 (0.249)	0.967 (0.262)**	0.20	0.791 (0.247)	0.838 (0.276) [§]	0.10
Leaf area	1.951 (0.835)	2.954 (0.399)**	0.53	2.698 (0.833)	7.841 (1.006)**	0.65	12.340 (0.829)	64.309 (8.262)**	0.59
Stem length	27.503 (1.037)	37.356 (5.071)**	0.59	24.817 (1.036)	37.356 (5.071)**	0.65	22.815 (1.033)	44.612 (5.643)**	0.60
Days to flowering	63.190 (1.968)	29.234 (6.076)**	0.19	72.941 (1.965)	62.813 (9.274)**	0.36	38.853 (1.961)	39.298 (5.346)**	0.54
Collection interval	6.739 (0.577)	4.734 (1.423)*	0.14	5.626 (0.575)	9.211 (1.763)**	0.32	1.750 (0.572)	3.627 (0.545)**	0.37
Herkogamy	2.202 (0.081)	0.198 (0.031)**	0.40	1.498 (0.081)	0.139 (0.020)**	0.49	1.755 (0.081)	0.193 (0.029)**	0.37
Stamen exsertion	1.707 (0.048)	0.081 (0.012)**	0.38	1.575 (0.048)	0.054 (0.008)**	0.41	1.112 (0.047)	0.076 (0.011)**	0.43
Pistil exsertion	3.908 (0.083)	0.250 (0.038)**	0.44	3.072 (0.082)	0.170 (0.024)**	0.51	2.866 (0.0820)	0.217 (0.033)**	0.36

Abbreviations: CL, cool temperature long photoperiod; CS cool temperature short photoperiod; V_G , among-genotypic variance; V_G/V_P among-genotypic variance divided by total phenotypic variance; WL, warm temperature long photoperiod. P < 0.01, *P < 0.001, *P < 0.001.

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	1	0.52**	0.51**	0.53**	0.53**	0.48**	۲ 0.70**	۲ 0.50**	0.52**	۲ 0.62**	-0.25§	0.54**	0.25§	-0.05	-0.14	0.62**	0.31**	0.74**	
style length		0.46** 0.52**	0.52** 0.56**	0.46** 0.45**	0.52** 0.58**	0.46** 0.50**	0.69** 0.62**	0.45** 0.54**	0.51**	0.60** 0.58**	-0.23§ -0.25§	0.49** 0.53**	0.22§ 0.38**	0.00 0.17	-0.13 -0.13	0.58** 0.68**	0.32** 0.26§	0.71**	
	0		0.70**	0.68**	0.71**	0.75**	0.75**	0.73**	0.53**	0.70**	-0.30*	0.57**	0.30*	-0.20‡	-0.31*	0.55**	0.53**	0.81**	
ovary length		1	0.73** 0.68**	0.69** 0.63**	0.76** 0.72**	0.78** 0.76**	0.76** 0.75**	0.73** 0.76**	0.56**	0.70** 0.66**	-0.31* -0.31*	0.52** 0.49**	0.24§ 0.37**	-0.09 0.13	-0.29* -0.20‡	0.45** 0.60**	0.57**	0.75** 0.82**	
abort opthor longth		2	ſ	0.72**	0.95**	0.72**	0.80**	0.69**	0.71**	0.80**	-0.42**	0.69**	0.29*	-0.08	-0.40**	0.29*	0.49**	0.55**	
Short anther length				0.52**	0.97**	0.56**	0.65**	0.61**	0.52**	0.62**	-0.43	0.63**	0.49**	0.03	-0.44**	0.23	0.30*	0.63**	
short filament length			e de la composición de		0.69**	0.81**	0.71** 0.66**	0.72** 0.71**	0.59** 0.54**	0.69**	-0.38** -0.40**	0.49**	0.21§ 0.19†	-0.16	-0.32** -0.31*	0.18‡	0.61**	0.52**	
J		<u>م. </u>			0.55**	0.79**	0.59**	0.67**	0.33**	0.49**	-0.42**	0.32**	0.24§	0.02	-0.26§	0.10	0.60**	0.47**	
long anther length				1	dh.	0.73** 0.71**	0.81** 0.81**	0.70** 0.69**	0.73** 0.70**	0.81** 0.79**	-0.38** -0.41**	0.71** 0.72**	0.33** 0.30*	-0.11 0.02	-0.36** -0.39**	0.35** 0.31*	0.48** 0.47**	0.60** 0.57**	
						0.58**	0.69**	0.65**	0.55**	0.66**	-0.45**	0.64**	0.53**	0.06	-0.41**	0.54**	0.29**	0.66**	
long filament length			A				0.74**	0.87**	0.52* 0.45**	0.68**	-0.34	0.57**	0.36**	-0.06 0.11	-0.37**	-0.02	0.80**	0.48**	
							0.71**	0.82**	0.41**	0.59**	-0.30**	0.37**	0.37**	0.18‡	-0.24§	0.09	0.79**	0.54**	
petal blade length			F		F		ЛL	0.65**	0.77	0.93	-0.32	0.63	0.37	-0.06	-0.30	0.45	0.52**	0.70**	
							طللللهـ م الأهر	0.66**	0.75**	0.90**	-0.31**	0.44**	0.43**	0.14	-0.19‡	0.46**	0.47**	0.70**	
petal claw length		$\mathcal{L}_{\mathcal{A}}$? "				-IIIh	0.42**	0.57**	-0.40**	0.61**	0.31**	0.03	-0.38**	0.00	0.38**	0.25§	
										0.92**	-0.43	0.44	0.28*	-0.01	-0.38	0.30	0.29	0.56**	
petal width		1.5		P		7		در ب		0.93**	-0.28*	0.54**	0.26§	-0.11	-0.21‡	0.40**	0.31*	0.55**	
											-0.30*	0.64**	0.35**	-0.10	-0.28*	0.40	0.50**	0.67**	
petal area		35-55		.						մհ	-0.28* -0.25§	0.62** 0.45**	0.34**	-0.05 0.03	-0.28* -0.16	0.39**	0.48**	0.64**	
	2.5		12.2			·		- -				-0.27*	-0.20‡	0.18‡	0.68**	-0.08	-0.13	-0.15	
flowers aborted	•	•		•		•	•	•	•	•		-0.24§ -0.21§	-0.19‡ -0.15	0.17‡ 0.13	0.66** 0.68**	-0.13 -0.16	-0.07 -0.06	-0.17 -0.18‡	
	2						22		5				0.36**	-0.01	-0.34**	0.28*	0.33**	0.46**	
stem length			1 C 6	.	्र रह.							_ all h_	0.38** 0.53**	0.269 0.39**	-0.31* -0.27*	0.16 0.49**	0.35** 0.17‡	0.37** 0.53**	
leaf area				6					. A.		• • •			0.26§	-0.30*	0.07	0.29*	0.24§	
					7									0.249	-0.27 -0.22§	0.00 0.27§	0.23§ 0.24§	0.14	
days to flowering	2. S.	186		See.		No.		See.			کے ا	•,.0	• £	Ъ	0.07	-0.22§	0.09	-0.15	
	: 8, jí	S	<u>, </u>	5 P		Se. 3	<u>, 8, 5</u>	x. , 3	in 9		• ŝ.	کنی ک	, or a s	<u></u>	0.02	0.07	0.31**	0.24§	
collection interval				.	, de						- 84			and a state	h	0.01	-0.17‡ -0.14	-0.09	
																-0.04	0.00	-0.04	
herkogamy					. 2		. : ?				• • 5		. •		•	14	-0.14 -0.14	0.81**	
nonogamy		<u>کې کې</u>		.				305					• 7			, Alling	-0.17‡	0.82**	
stamen exsertion											. 1	1			. 4	. 1818.	dll	0.45** 0.47**	
																	_ الله	0.43**	
pistil exsertion		J 5					25	2	63		•••	:X-97	-	દુ 'હું	- 4			allh i	
													• •					، حطالالللك	

Figure 1 Correlation coefficients and significance of correlations among traits within treatments. Pearson correlation coefficients of correlations among traits within the CL (upper), CS (middle) and WL (bottom) treatments are indicated above the diagonal, with correlations that are significantly different than zero after false discovery rate correction indicated. Histograms of each trait in the CL treatment are shown on the diagonal, and plots of the bivariate correlation among pairs of traits in the CL treatment are shown below the diagonal; histograms and plots are shown only for the CL treatment because correlations are highly similar in all three treatments. *P < 0.05, *P < 0.01, *P < 0.001, *P < 0.001.

composite traits, marginally positively correlated with number of aborted flowers (that is delayed flowering was marginally associated with increased floral abortion; r = 0.13 - 0.18, P = 0.1 - 0.03; Figure 1), and positively correlated with vegetative traits in all treatments (laterflowering plants were larger; r = 0.24-0.31, P = 0.004 to < 0.0001) except for leaf area in CL (r = -0.01; Figure 1). By contrast, collection interval was marginally to strongly negatively correlated with most floral traits (except style length and petal width), strongly positively correlated with number of aborted flowers (r = 0.65 - 0.68, P < 0.0001), negatively correlated with vegetative traits (smaller plants took longer to produce viable flowers once flowering had been initiated, r = -0.09 to -0.44, P = 0.27 to < 0.0001; Figure 1), and uncorrelated with days to flowering (Figure 1).

Herkogamy (total pistil length minus long filament length) was positively correlated with pistil traits but not

filament traits. Stamen exsertion (long filament length minus petal claw length) was positively correlated with both filament and petal claw traits. Pistil exsertion (total pistil length minus petal claw length) was very strongly positively correlated with both pistil traits and petal claw length. In general, for all classes of traits, the correlation structure and magnitude of correlation coefficients were similar across all treatments (Figure 1).

Quantitative genetics and correlations among treatments Most traits demonstrated highly significant GEI (P < 0.0001; Table 2) except collection interval (P = 0.026) and the number of aborted flowers (P = 0.22). Despite the significant GEI, the effect of genotype remained highly significant for all traits (P < 0.0001; Table 2). To measure the relative variance attributable to genotype and GEI, we divided the GEI variance by the among-genotype

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Table 2 Quantitative gen standard error (in parenti	etic partitioning of variati neses) and significance of	on in floral, vegetative and 1 effects	eproductive timing traits i	n <i>B. rapa</i> RILs in three treat	ments, including variance o	components of each effect,
Trait	Style length	Ovary length	Short anther length	Short filament length	Long anther length	Long filament length
Random effects (Z) Chamber (treatment) Genotype Genotype × treatment Residual	$\begin{array}{c} 0.002 \ (0.001)^{\ddagger} \\ 0.053 \ (0.008)^{**} \\ 0.021 \ (0.003)^{**} \\ 0.065 \ (0.002)^{**} \end{array}$	0.009 (0.004) [‡] 0.173 (0.024)** 0.046 (0.007)** 0.190 (0.007)**	0.003 (0.001) [§] 0.067 (0.009)** 0.015 (0.002)** 0.047 (0.002)**	0.017 (0.007) [§] 0.186 (0.027)** 0.071 (0.010)** 0.223 (0.008)**	0.002 (0.001) [‡] 0.071 (0.009)** 0.010 (0.002)** 0.039 (0.001)**	0.029 (0.011) [§] 0.203 (0.028)** 0.048 (0.007)** 0.186 (0.006)**
Fixed effects (F) Treatment	df F F _{2, 23.7} 14.87**	df F F _{2, 20.4} 97.29**	df F F _{2, 21.3} 1.17	$\begin{array}{cc} \mathrm{df} & \mathrm{F} \\ \mathrm{F}_{2,\ 20.1} & 70.59^{**} \end{array}$	df F F _{2, 19.7} 2.56	df F $F_{2, 17}$ 14.27*
Significant genotype × treat contrasts	WL/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS
Trait	Petal blade length	Petal claw length	Petal width	Petal area	Flowers aborted	Leaf area
Random effects (Z) Chamber (treatment) Genotype Genotype × treatment Residual	0.038 (0.015) [§] 0.266 (0.038)** 0.093 (0.012)** 0.254 (0.009)**	$^{0.019}_{0.03}$ (0.007) $^{0.019}_{0.037}$ (0.012) $^{**}_{0.017}$ (0.003) $^{***}_{0.090}$ (0.003) $^{***}_{0.090}$ (0.003) $^{***}_{0.090}$	$\begin{array}{c} 0.046 (0.018)^{\$} \\ 0.345 (0.047)^{**} \\ 0.099 (0.013)^{**} \\ 0.255 (0.009)^{**} \end{array}$	2.180 (0.878)** 21.528 (3.083)** 8.287 (1.102)** 23.018 (0.786)**	$\begin{array}{c} 0.250 & (0.117)^{\ddagger} \\ 1.409 & (0.245)^{**} \\ 0.11 & (0.145) \\ 7.299 & (0.248)^{**} \end{array}$	2.995 (1.135) [§] 10.259 (1.999)** 15.345 (1.517)** 14.444 (0.480)**
Fixed effects (F) Treatment	df F F _{2, 178} 84.34**	df F F _{2, 16.1} 0.71	df F F _{2, 17.5} 117.8**	df F F _{2, 19.3} 11.43**	df F F _{2, 14.5} 0.87	df F F _{2, 21.7} 53.95*
Significant genotype × treat contrasts	CL/CS WL/CL WL/CS	WL/CL WL/CS	WL/CL WL/CS	WL/CL WL/CS	ML/CL	CL/CS WL/CL WL/CS
Trait	Stem length	Days to flowering	Collection interval	Herkogamy	Stamen exsertion	Pistil exsertion
Random effects (Z) Chamber (treatment) Genotype Genotype × treatment Residual	4.632 (1.759) [§] 34.074 (4.371)** 6.361 (0.868)** 20.414 (0.68)**	20.835 (7.790) [§] 33.542 (4.950)** 10.726 (2.059)** 62.137 (2.097)**	$\begin{array}{c} 1.599 & (0.634)^{\$} \\ 5.3686 & (0.821)^{**} \\ 0.7516 & (0.388)^{\dagger} \\ 15.8354 & (0.545)^{**} \end{array}$	$\begin{array}{c} 0.030 & (0.012)^{\$} \\ 0.112 & (0.018)^{**} \\ 0.065 & (0.01)^{**} \\ 0.222 & (0.008)^{**} \end{array}$	$\begin{array}{c} 0.01 & (0.004)^{\$} \\ 0.051 & (0.008)^{**} \\ 0.02 & (0.003)^{**} \\ 0.02 & (0.003)^{**} \\ 0.09 & (0.003)^{**} \end{array}$	$\begin{array}{c} 0.03 & (0.012)^{\$} \\ 0.1477 & (0.022)^{**} \\ 0.0638 & (0.01)^{**} \\ 0.256 & (0.009)^{**} \end{array}$
Fixed effects (F) Treatment	$\begin{array}{cc} df & F \\ F_{2,\ 16.6} & 6.55^{\$} \end{array}$	df F F _{2, 15.7} 84.96**	df F F _{2, 15.5} 23.40**	$\begin{array}{cc} df & F \\ F_{2,\ 17.6} & 21.67^{**} \end{array}$	df F _{2, 17.2} 51.04**	F F F _{2, 17.6} 52.59**
Significant genotype × treat contrasts	WL/CL WL/CS	CL/CS WL/CL WL/CS	ML/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS	CL/CS WL/CL WL/CS
Abbreviations: CL, cool to $^{\ddagger}P < 0.05$, $^{\$}P < 0.01$, * $P < 0.0$	emperature long photoper 001, **P<0.0001.	iod; CS cool temperature sho	rt photoperiod; RIL, recom	binant inbred line; WL, war	m temperature long photop	eriod.

Heredity

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variance (Gurganus *et al.*, 1998), which ranged from 0.13 to 0.38 (except for leaf area, which was 1.50), indicating that although a significant portion of variation was attributable to GEI for most traits, a larger proportion of variation was attributable to among-genotype differences.

To further assess whether the genetic architecture of a given trait changed across environments, we estimated genotypic correlations (r_{GE}) and performed ANOVAs for pairs of treatments. Overall, values of r_{GE} were high (0.77–0.99) for most traits, with the exception of leaf area (0.38–0.47; Table 3). For style length, ovary length, short filament length, long filament length, petal blade length, petal claw length, petal width, petal area, flowers aborted, stem length, collection interval and stamen exsertion across CL/CS, flowers aborted across WL/CS, and flowers aborted and stem length across WL/CS, r_{GE} estimates were significantly different than 0 and not or only moderately (P > 0.01) significantly different from 1 (that is, significant genotype effect but non-significant GEI; Table 3), indicating that common loci affected variation and that each allele at a locus had a similar function for these traits across these treatment pairs. For all other comparisons, and more specifically for most comparisons involving WL, estimates of r_{GE} were significantly different than both 0 and 1 (that is, both genotype and GEI effects were highly significant; Table 3), indicating that some different loci affect variation across treatment pairs and/or that some alleles have different functional effects across treatment pairs. These results suggest that for many traits, the expression of loci and the effects of alleles were more conserved across treatments with the same temperatures (yet different photoperiods) and less conserved across treatments with different temperatures.

Table 3 Pearson correlation coefficients of across-treatment geno-
typic correlations ($r_{\rm GE}$) for each trait

Trait	$r_{\rm GE} \ CL \ vs \ CS$	$r_{\rm GE}$ WL vs CL	$r_{\rm GE}$ WL vs CS
Style length	0.93 ^{NS}	0.73**	0.76**
Ovary length	0.93^{\ddagger}	0.85**	0.86**
Short anther length	0.93*	0.85**	0.88**
Short filament length	0.91^{\ddagger}	0.78**	0.77**
Long anther length	$0.95^{\$}$	0.91**	0.92**
Long filament length	0.94^{\ddagger}	0.83**	0.86*
Petal blade length	0.93^{\ddagger}	0.77**	0.78**
Petal claw length	0.96 ^{NS}	0.89**	0.89**
Petal width	0.94^{NS}	0.81**	0.83**
Petal area	0.93 ^{NS}	0.81**	0.83**
Flowers aborted	0.99 ^{NS}	0.99^{\ddagger}	0.99^{NS}
Leaf area	0.42**	0.47**	0.39**
Stem length	0.95 ^{NS}	0.86**	0.90^{NS}
Days to flowering	$0.86^{\$}$	0.86**	0.88*
Collection interval	0.97^{NS}	$0.97^{\$}$	0.98^{*}
Herkogamy	$0.86^{\$}$	0.69**	0.69**
Stamen exsertion	0.91^{\ddagger}	0.74**	0.83**
Pistil exsertion	$0.89^{\$}$	0.76**	0.78**

Abbreviations: ANOVA, analysis of variance; CL, cool temperature long photoperiod; CS cool temperature short photoperiod; NS, not significant; WL, warm temperature long photoperiod.

All correlations are significantly different from zero (P < 0.0001). *P*-values indicated below are from tests of significance of the genotype × treatment interaction term from ANOVA analyses of pairs of environments and indicate whether cross-environment correlations are significantly different from 1.

 $^{\ddagger}P < 0.1, ^{\ddagger}P < 0.05, ^{\$}P < 0.01, ^{*}P < 0.001, ^{**}P < 0.0001.$

Patterns of main-effect QTL expression within each treatment

The genome-wide scan detected 181 significant QTL, 61 of which were detected in CL, 61 were detected in CS and 59 were detected in WL (Figure 2; Appendix).

To evaluate the QTL architecture underlying the strongly positive genotypic correlations among floral traits, we investigated patterns of QTL co-localization among floral organs within each treatment. Consistent with the strongly positive genotypic correlations (Figure 1), almost all floral QTL affected multiple traits, and this pattern was consistent in each of the three treatments. For example, a QTL detected at \sim 45 cM on chromosome 1 in CL affected seven of the 10 measured floral traits, or in other words, seven of the eight floral QTL detected on chromosome 1 co-localized, and similarly strong patterns of co-localization were observed on most chromosomes (Figure 2). Overlapping floral QTL always had the same direction of additive effects, and QTL from all combinations of floral whorls overlapped. QTL of organs in adjacent whorls did not overlap with greater frequency than those for organs in non-adjacent whorls; for example, style length and ovary length QTL co-localized with 11 stamen QTL (adjacent whorls) and 12 petal QTL (non-adjacent whorls) in CS, and, coincidentally, with seven stamen QTL (adjacent whorls) and nine petal QTL (non-adjacent whorls) in both CL and WL.

To assess the relationship among floral, vegetative and reproductive timing traits, we investigated patterns of co-localization of QTL. Consistent with strongly positive correlations between floral and vegetative traits (Figure 1), most QTL for vegetative traits co-localized with QTL from one or more floral organs from the same treatment (for example, QTL for floral traits and stem length co-localized at $\sim 60 \text{ cM}$ on chromosome 1 in all three treatments; Figure 2; Appendix). Consistent with a non-significant correlation between days to flowering and floral traits (Figure 1), only a small number of QTL for days to flowering co-localized with floral traits (Figure 2; Appendix). Days to flowering, however, was positively correlated with vegetative traits and had QTL with the same direction of additive effects that colocalized (Figures 1 and 2; Appendix). Consistent with the negative correlation between collection interval and both floral and vegetative traits (Figure 1), QTL for collection interval and both floral and vegetative traits co-localized in all three treatments, and the direction of additive effects of collection interval QTL were opposite those of floral and vegetative QTL (Figure 2; Appendix).

We next compared patterns of QTL expression of composite traits (herkogamy, stamen exsertion and petal exsertion) with those of their underlying floral organs to assess whether their genetic architecture was shared with one or both organs. Herkogamy (total pistil length minus long filament length) was positively correlated with pistil traits but not filament traits (Figure 1), and correspondingly, QTL for herkogamy often co-localized with pistil QTL but not filament QTL (for example, herkogamy QTL co-localized with pistil QTL but not stamen QTL at ~50 cM on chromosome 1 in CL; Figure 2; Appendix). In contrast, stamen exsertion (long filament length minus petal claw length) was positively correlated with both underlying organs (Figure 2; Appendix), and stamen exsertion QTL co-localized with both petal and stamen QTL in all three treatments (Figure 2; Appendix). Similarly, pistil exsertion (total pistil length minus petal claw length) was positively correlated with both underlying traits (Figure 1) and pistil exsertion QTL co-localized with both petal and pistil QTL in all three treatments (Figure 2; Appendix).



Figure 2 QTL detected for traits measured in three treatments. The length of bars designate the range of 2-LOD support limits for each QTL, with the peak of the QTL indicated. Solid bars indicate QTL that are significant using a 0.05 type I error rate and dashed bars indicate QTL that are significant using a 0.075 type I error rate.

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6	style length CS CL WI	ovary length CS CL WL	short anther length CS CL WI	short filament length CS CL WL	long anther length CS CL WL	long filament length CS CL WI	petal blade length CS CL WI	petal claw length CS CL WI	petal width CS CL WI	petal area CS CL WI	flowers aborted CS CL WI	leaf area CS CL WI	stem length CS CL WI	days to flowering CS CL WI	collection interval	herk- ogamy CS CL WI	stamen exsertion CS CL WI	pistil exsertion CS CL WL
0 10 20 30 40 50 60 90 100 110 120 130 0 130 0 130 0 100 100 100	+++	+++++++++++++++++++++++++++++++++++++++	+++	+	+ + ++ + +	+	+	+	++	++		4	+		+ +	+		+
7 0 10 20 30 40 50 60 70 80 90 0	++	+ +	+	++	+			++										+
8 0 10 20 30 40 50	++		-				+			+						++		
9 0 10 20 		++ +		+		+		+++						+	+†	Ļ	+	+
10 0 10 20 30 40 50 60 70 80 90)	+									<u>+</u> +					+ +		

Figure 2 Continued.

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Patterns of main-effect QTL expression across treatments

Consistent with estimates of r_{GE} that were significantly different than 0 for most traits (significant amonggenotype effect; Table 3), QTL from all three treatments co-localized for a trait in many cases, and often explained a large percentage of variance (>10%) for a trait in at least one treatment (Figure 2; Appendix).

Despite the large magnitude of most estimates of r_{GE} we nevertheless detected many across-environment correlations that were significantly different than one, particularly across WL/CS or WL/CL (Table 3), suggesting that somewhat different loci contribute to trait expression across environments with differing temperatures. Using a 0.1 type I error rate, 15 QTL demonstrated significant $QTL \times E$ for pistil, stamen, petal, vegetative traits and days to flowering (Appendix). We did not detect significant QTL × E for flowers aborted (Appendix), consistent with expectations given that $r_{GE} = 1$ for this trait. In all but one instance, $QTL \times E$ was detected across WL/CL or WL/CS (Appendix), indicating that QTL expression was in fact most sensitive to temperature. We examined the additive effects of these QTL to determine the cause of the significant interaction, and all were due to changes in the magnitude of additive effects (and not sign) across treatments (data not shown).

Epistatically interacting QTL

In the two-dimensional genome scans for QTL × QTL epistasis, only five instances of loci with significant epistatic effects were detected. Four of these (for petal width-WL, petal area-WL, herkogamy-WL and pistil exsertion-CS) were detected between marker BRMS006 on the top of chromosome 8 and marker pX139cH on the top of chromosome 10. The fifth (style length-WL) was detected between marker fito137 in the middle of chromosome 3 and marker pX139cH on the top of chromosome 10.

Discussion

Patterns of integration and modularity

Previous research has shown that floral traits are usually significantly correlated in hermaphroditic plant species, and that plants with zygomorphic flowers have more strongly integrated floral organs than actinomorphic species (Ashman and Majetic, 2006). Despite the fact that Brassicaceae have actinomorphic flowers, previous research in the family revealed that floral traits are frequently highly correlated (Conner and Sterling, 1995; Juenger et al., 2000, 2005; Brock and Weinig, 2007). In the current study, floral traits were highly correlated despite the fact that LD between physically distant loci was reduced by recombination during RIL formation; this suggests that pleiotropic loci (or LD between physically proximate loci) contributed to floral trait integration. The high frequency with which floral QTL co-localized further supports the hypothesis of pleiotropy because it is unlikely that genes that independently affect the size of different floral organs would always be in such close proximity. Previous studies in Arabidopsis also suggested that pleiotropy was likely to be responsible for floral trait covariation (Conner, 2002; Juenger et al., 2005). Interestingly, we did not find stronger correlations between floral organs in adjacent whorls vs non-adjacent whorls; thus, any pleiotropic effects on quantitative variation in floral organ size appear to be uniform throughout the flower, in contrast to the expression pattern of ABC genes, which affect qualitative variation in floral organ identity in adjacent whorls.

Evolutionarily, correlations observed in this study suggest that allometry of floral organs may be genetically or developmentally constrained in B. rapa, and, more specifically, that a response to selection on one floral trait may be accompanied by corresponding responses in other floral traits. This correlation could act as a relevant constraint in this species given that previous research in B. rapa has shown that the allometry of floral organs (herkogamy) strongly affects the rate of reproduction and inbreeding (Brock et al., in review). That said, research in natural populations of close relatives, R. raphanistrum and B. napus, revealed that filament and corolla traits were more strongly correlated than other floral organs, and these enhanced correlations presumably arose from evolutionary responses to pollinatormediated selection (Conner and Sterling, 1995). It is parsimonious to assume that the initial genetic mechanisms underlying floral development, namely pleiotropy or LD between physically proximate loci, are conserved within this clade, as they appear to determine floral organ size in A. thaliana, B. rapa and B. nigra. Thus, a short-term constraint may exist on floral evolution in B. rapa, but if the behavior of other members of the clade is any guide, then modifiers may arise that enable independent responses of floral organs to selection.

Results of this study also revealed strong genotypic correlations and frequent co-localization of QTL between floral and vegetative traits of *B. rapa*, suggesting that pleiotropy or LD between physically proximate genes may also be responsible for covariation of the floral and vegetative traits examined in this study. These genotypic and QTL associations again suggest that measured floral and vegetative traits may not evolve completely independently over at least the short-term, assuming that the genetic architecture of the genotypes studied here is representative of the segregating variation of this species. As the parents of the RILs used in this study were a cultivated seed oil genotype (R500) and a rapid cycling (imb211) genotype that may approximate a weedy member of the species, these RILs may be representative of segregating variation for some crosses occurring between cultivated genotypes and their wild neighbors. One interesting avenue for future research would be to assess patterns of modularity of floral and vegetative traits in a more diverse selection of cultivated and wild genotypes of *B. rapa* to determine the extent to which the results of this study are representative of species-wide patterns of floral integration and modularity.

In contrast to the results of this study, previous research has found that floral and vegetative modules are generally not significantly correlated in plants (Ashman and Majetic, 2006). For example, previous studies in the Brassicaceae found that floral and vegetative organs were uncorrelated (Conner and Sterling, 1996; Juenger *et al.*, 2005), shared few common QTL (Juenger *et al.*, 2005), and therefore represented separate modules (but see Brock and Weinig, 2007). Variation in floral and vegetative traits in *B. rapa* is thus less modular than has been found previously in other Brassicaceae

species. One possible explanation for these differences among studies is that vegetative traits vary in the extent to which they are modular. For instance, in *P. drummondii*, plant height, biomass and the number of nodes and branches were correlated with floral traits, whereas leaf traits were not (Waitt and Levin, 1993); the choice of vegetative traits could influence the interpretation of modularity. In this study, sampling different vegetative traits may have revealed different patterns of modularity in *B. rapa*. Another possible reason for experimental differences is that modularity of floral and vegetative organs is not ubiquitous, and may depend more on the evolutionary history and genetic architecture of each species than previously realized.

The patterns of modularity between phenological and floral or vegetative traits varied. Collection interval, or the time elapsed from first flowering until several viable flowers developed, was negatively correlated with floral and vegetative traits and positively correlated with the number of aborted flowers. Thus, the longer the collection interval (or the longer it took to produce a viable flower), the smaller the floral and vegetative organs were, and the more frequently flowers were aborted; potentially, collection interval may therefore be indicative of overall plant vigor. The QTL that colocalized for collection interval, floral traits and vegetative traits may therefore be loci that have a general affect on the overall vigor of the plant. The other phenological trait, days to flowering, was not correlated with floral traits but was significantly positively correlated and had QTL that co-localized with vegetative traits. This relationship between flowering time and vegetative traits is consistent with previous research that found that laterflowering plants are generally larger (Bolmgren and Cowan, 2008), likely because they allocate resources to vegetative growth longer than early-flowering plants. These QTL may directly regulate days to flowering, but only indirectly affect vegetative size by determining the duration of time available to grow prior to reproduction. However, another possibility is that these QTL have direct mechanistic affects in tissues throughout the plant (that is, directly affect flowering time and vegetative organ size). An increase in flowering time, however, did not translate into larger floral organ size. Interestingly, it thus appears that the genetic mechanisms linking flowering time to vegetative traits are independent from those that link vegetative and floral traits.

Composite traits showed differing patterns of QTL architecture in relation to component traits. Herkogamy, which was previously found to be a strong indicator of the rate of self-pollination in *B. rapa* in the field (Brock et al., in review), was positively correlated and had QTL that co-localized with pistil traits but not filament traits. Thus, in the controlled settings investigated in this experiment, variation in pistil traits more strongly affected herkogamy, and hence, may have a stronger affect on the rate of self-pollination in B. rapa in these conditions. However, these results may be environmentdependent, as stamen traits more strongly affected herkogamy in a field setting (Brock et al., in review). In contrast, stamen exsertion and pistil exertion were correlated and had QTL that co-localized with both underlying traits. Previous studies of pollination efficiency in Raphanus found that the extent to which pistils and stamens were exserted had an effect on the rate of reproduction; genotypes with the most exserted stamens had the most number of pollen grains removed, and genotypes with intermediate pistil exsertion had the highest probability of successful fertilization (Conner *et al.*, 1995). The results of this study suggest that variation in both component traits underlying stamen exsertion or pistil exsertion affect the rate of successful fertilization. These patterns suggest that multiple traits (pistil, stamen or corolla length) could control the degree of organ exsertion and hence the rate of outcrossing, whereas the underlying trait (pistil or stamen length) most strongly affecting herkogamy and hence the rate of inbreeding in *B. rapa* may vary depending on the environmental setting.

Response of genotypes to differences in temperature and photoperiod

Variance explained by the effect of genotype was typically much greater than that explained by GEI, and this result was supported by QTL that co-localized in all three treatments for most traits. Nonetheless, GEI effects were significant for most traits. r_{GE} was generally greater across treatments with the same temperature (but differing photoperiod) than across treatments with the same photoperiod (but differing temperatures). These results suggest that common genetic loci affected trait variation and that alleles had the same functional effects across treatments with the same temperature (in CL vs CS), whereas differences existed in the causal genetic loci or functional effects of alleles across treatments with different temperatures (in most comparisons involving WL). This significant temperature effect is in agreement with results of research on reproductive traits in other species (Jermstad et al., 2003; Hedhly et al., 2005; Schmuths et al., 2006). Also consistent with the finding that GEI was due to differential sensitivity to temperature, all but one $QTL \times E$ interaction was in response to temperature.

One implication of the large effects of temperature detected in this study is that plants growing as fall and winter annuals and as biennials in natural environments may have trait expression similar to each other, but different from spring or summer annuals. The large natural differences in temperature environments that B. rapa experiences across its wide Eurasian distribution, coupled with GEI in response to temperature, may have ecological implications in that different genotypes may be favored in different temperature environments. These results are important because they suggest that future temperature changes associated with climate change may favor specific genotypes. In particular, genotypes may vary in the success of fertilization by pollinators depending on floral responses to temperature; thus, any future temperature changes associated with climate change may therefore exert strong selective pressures that shape patterns of genetic and phenotypic diversity across species ranges.

Conclusions and future research

We found that floral traits were highly integrated in *B. rapa* and that floral, vegetative and phenological traits were generally not as modular as has been previously found in the Brassicaceae. To assess whether the patterns of trait integration and modularity revealed in this study

are representative of those found across the species, future research will focus on understanding the patterns of correlations among traits in a diverse sampling of cultivated and wild genotypes of B. rapa. Results of this study also revealed that large numbers of QTL colocalized for many traits with different functions, suggesting that pleiotropic or closely physically linked genes control variation in many different traits. To further understand the genetic basis of trait variation in B. rapa, future research will focus on fine-mapping QTL identified in this study, starting with genomic regions that contain multiple floral QTL of large effect. Fine-mapping efforts will be facilitated by results of the B. rapa genome project (Kim et al., 2009), which has generated genomic information useful for marker development and selection of candidate genes. Fine mapping of floral QTL may be complementary to research carried out under the floral genome project; the floral genome project identified loci affecting floral development and qualitative variation in floral organ identity across angiosperms, whereas our research aims to identify loci affecting quantitative variation in floral organ size. A further goal of fine-mapping efforts will be to understand whether pleiotropic or tightly linked genes control variation in floral traits and to functionally characterize genetic variants controlling floral quantitative trait variation in *B. rapa*.

Conflict of interest

The authors declare no conflict of interest.

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Appendix

Results of composite interval QTL mapping in *Brassica rapa* RILs. The position, 2-LOD support intervals, likelihood ratio (LR) test statistic, additive effect of the imb211 allele, percent variance explained and closest marker are indicated for each significant QTL detected in this study, organized by trait, position and

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treatment as shown in Figure 2. ### before a trait name indicates marginal QTL that were significant at the P = 0.075 level. QTL that demonstrate significant QTL × environment interactions (QTL × E) across pairs of treatments, and the level of significance for these interactions, are also indicated ($^{\dagger}P < 0.1$, $^{\ddagger}P < 0.05$, $^{\$}P < 0.01$).

Trait–treatment	Position in cM (2-LOD intervals)	LR	Additive effect	% Variance explained	Closest marker	QTL that demonstrate significan $QTL \times E$ across treatment pairs
Chromosome 1						
Style length–CS	39.66 (38.25-43.22)	44.148	-0.097	18.248	fito019d	
Style length-CL	41.83 (38.25-43.22)	38.319	-0.101	15.373	fito101a	
Style length-WL	43.22 (34.56-50.6)	37.516	-0.109	13.803	pW108aE	
Style length-WL	68.54 (62.24–71.28)	19.575	0.075	6.292	pX128dX	WL/CL^{\dagger}
Short anther length–CL	56.77 (50.6-62.24)	15.181	-0.071	6.209	fito222	
Short filament length-CL	43.22 (30.99–50.77)	14.019	-0.160	6.851	pW108aE	WL/CL^{\dagger}
Short filament length-CL	68.54 (62.24–91.28)	13.822	0.159	6.434	pX128dX	
Short filament length-WL	68.54 (67.92-81.28)	28.216	0.150	11.600	pX128dX	
Long anther length–CL	41.66 (32.56–62.24)	20.036	-0.073	7.068	fito101a	
Long anther length–WL	58.77 (30.99-62.24)	18.769	-0.067	7.883	fito222	
Petal blade–CS	39.66 (30.99-44.6)	33.953	-0.182	12.456	fito019d	
Petal blade–CL	39.66 (34.56-44.6)	34.553	-0.217	12.441	fito019d	WL/CL^{\ddagger}
Petal blade–WL	39.66 (26.99–48.6)	21.728	-0.136	8.990	fito019d	See above
Petal claw–CS	0.67 (0.01–15.89)	14.150	-0.068	4.401	pW249dX	
Petal width–CS	39.66 (32.56–50.6)	26.052	-0.183	8.517	fito019d	
Petal width–CL	41.66 (38.25–60.77)	23.741	-0.202	8.480	fito101a	
Petal width–WL	39.66 (32.56–44.6)	29.924	-0.172	11.601	fito019d	
Petal area–CS	39.66 (32.56–44.6)	32.213	-1.693	12.275	fito019d	
Petal area–CL	41.66 (32.56–50.77)	31.085	-1.966	12.094	fito101a	
Petal area–WL	39.66 (32.56–44.6)	32.843	-1.285	14.047	fito019d	
Leaf area–WL	39.66 (24.6-43.22)	12.818	-1.207	7.126	fito019d	
Stem length–CS	0.01 (0.01–7.86)	14.996	-1.514	5.734	pW190aH	
Stem length–WL	0.67 (0.01–7.86)	15.323	-1.337	4.844	pW249dX	
Stem length–CS	50.77 (43.22-62.24)	34.799	-2.253	14.739	pX136bE	
Stem length–CL	44.6 (38.25–60.77)	36.122	-2.131	14.115	pW216aH	
Stem length–WL	50.77 (43.22-60.77)	47.521	-2.478	17.022	pX136bE	
Days to flowering–WL	39.66 (24.99–50.77)	14.473	-1.335	5.162	fito019d	

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Trait–treatment	Position in cM (2-LOD intervals)	LR	Additive effect	% Variance explained	Closest marker	QTL that demonstrate significant QTL \times E across treatment pairs
Herkogamy–CS	52.77 (38.25-62.24)	19.946	-0.103	8.534	pX136bE	
Herkogamy–CL	50.77 (44.6-62.24)	22.591	-0.127	9.892	pX136bE	
Herkogamy–WL	52.77 (50.6-62.24)	38.876	-0.155	15.804	pX136bE	
Stamen exsertion–WL	68.54 (63.92–87.28)	20.746	0.069	7.656	pX128dX	
Pistil exsertion–WL	52.77 (38.25–62.24)	24.404	-0.129	10.415	pX136bE	
Chromosome 2	104.00 (00.0F, 11F.0F)	00.041	0.1(0	10 202	V107 V	
Ovary length -CS	104.89 (90.05-117.85)	22.941 12.076	0.162	10.292	pX10/aX	
Ovary length_CS	100.09 (90.03 - 129.03) 135 85 (123 85 - 135 85)	12 883	-0.1098	4.090	pW2050H	
Long filament length-CL	15.46 (9.37–26.58)	12.653	-0.130	5.748	pX139eH	
Long filament length–WL	96.05 (86.04–106.66)	21.030	0.137	7.532	pW205bH	
Petal blade-CL	115.42 (104.89–129.85)	13.365	0.160	6.102	pW249aX	
Petal claw–WL	14.91 (11.37–26.58)	14.100	-0.067	5.348	fito338a	
Pistil exsertion–CS	117.42 (96.05–117.85)	13.666	0.096	5.630	pW249aX	
Pistil exsertion–WL	117.42 (104.89–129.85)	13.685	0.092	5.005	pW249aX	
Chromosome 3				ć		
Style length–WL	55.73 (46.39–59.48)	17.797	-0.064	6.087	pW214aX	
Ovary length-CS	54.59 (51.33-59.48)	25.979	-0.133	10.536	pW214aX	
WI	79.83 (70.78-94.49)	10.991	-0.119	6.724 4.017	fito109D	
Short anther length_CS	22 01 (2 01 - 42 4)	14 530	-0.003	7 126	nX139aH	
Short anther length–CL	118.52 (108.21 - 124.62)	23.841	-0.087	8.179	fito413	
Short filament length–CS	63.48 (54.59–76.61)	12.702	-0.129	5.976	pW147bH	
Long anther length–WL	30.86 (26.01–46.39)	19.001	-0.065	7.457	pX144bE	
Long anther length-CL	58.25 (46.39-69.45)	15.345	-0.065	5.246	pX141cE	
Long anther length-CL	118.52 (108.87–128.2)	22.613	-0.083	7.969	fito413	
Long filament length-CS	55.73 (54.59–66.06)	22.798	-0.201	9.753	pW214aX	
Long filament length–CL	61.48 (51.33–70.78)	13.908	-0.166	7.401	pX141cE	
Petal blade-CS	75.72 (65.48–92.49)	14.105	-0.118	5.172	fito071d	
Petal width_CS	54 59 (42 4-68 06)	13 824	-0.003 -0.134	4.478	pW147D11 pW214aX	
Petal width–WL	40.4 (26.01–52.59)	14.191	-0.104	5.193	pW189aH	
Petal width–CS	142.71 (138.7–161.05)	18.059	0.151	5.785	fito434	
Petal width-WL	145.76 (132.2–161.05)	15.013	0.117	5.770	pW169aX	
Petal area–CS	54.59 (44.39-66.06)	17.058	-1.218	6.334	pW214aX	
Petal area–WL	35.21 (0.01-44.39)	13.634	-0.768	5.709	pX144bE	
Stem length-CS	58.25 (44.39–70.78)	14.227	-1.361	5.102	pX141cE	
###Stem length-CL	61.48 (54.59–70.78)	12.208	-1.316	5.182	pX141cE	
Dava to flowering CI	39.48 (34.39-73.72) 44.39 (31.83 55.73)	18.529	-1.558	0.035 10.802	pX141CE	
Herkogamy_CS	44.39 (31.83-33.73)	16 317	-1.895 -0.115	6 500	pW174CA pW189aH	
Herkogamy–WL	40.4(31.83-44.39)	17.725	-0.097	6.224	pW189aH	
Stamen exsertion–CS	55.73 (46.39–69.45)	13.586	-0.056	7.297	pW214aX	
Pistil exsertion-WL	55.73 (46.39–59.48)	17.005	-0.104	6.509	pW214aX	
Chromosome 4						
Short anther length-CS	47.35 (28.01–58.53)	13.772	-0.057	4.945	pW120dX	
Short anther length-CL	49.35 (37.39–58.53)	22.018	-0.081	8.140	pW120dX	
Long anther length–CS	47.35 (28.01–58.53)	13.111	-0.055	4.677	pW120dX	
Long anther length–CL	47.35 (38.52–58.53)	18.930	-0.069	6.525	pW120dX	
Long filament length-CS	53.35 (37.39-64.62)	13.728	-0.110	6.124	pX129dX	
Potal claw CS	57 35 (47.01-79.62)	13.433	-0.105	4.948	pX129dX	
Petal claw-CL	53.35 (47.01-60.63)	29.217	-0.115	11.974	pX129dX	
Stem length-CL	96.09 (80.3–106.09)	24.013	-1.768	9.403	pW178bE	
Herkogamy–CS	69.62 (60.53-80.3)	16.314	0.093	6.741	pW246fX	WL/CS^{\ddagger}
Pistil exsertion-CS	67.62 (58.53–79.62)	20.220	0.134	8.621	pW246fX	WL/CS^{\ddagger}
Chromosome 5						
Short filament length-WL	98.67 (85.84–103.94)	13.447	0.088	5.117	pW143aE	
Chromosome 6						
Style length-CS	27.86 (17.5–37.59)	23.386	-0.073	9.232	pW160bH	
Style length-CL	27.86 (19.5–33.27)	39.796	-0.105	15.227	pW160bH	
Style length–WL	29.86 (25.5–48.59)	15.522	-0.064	5.647	pW160bH	
Ovary length CI	72.54 (63.4-94.15) 78 15 (67.00, 09.15)	31.303	-0.150	13.608	BRIVISU26b	
Ovary length_WI	76.13 (07.09-96.13) 57 ()3 (42 59_67 (0)	24.003 27 071	-0.107	9.274 9.9 <u>4</u> 7	fito423	
Short anther length_CL	0.01 (0.01–12.01)	13.243	0.064	4.780	pW227aE	
					I	

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(Continued)

Short anther length CS 65.8 (634-70.54) 27.99 -0.097 12.506 fito277 Short anther length-CL 65.4 (616-70.54) 27.191 -0.070 8.220 pV2219aE Short anther length-CL 0.01 (0.01-10.01) 15.36 0.127 70.043 pV227aE Short altament length-CL 0.01 (0.01-10.01) 12.10 0.168 4.8375 pV227aE Short altament length-CL 0.01 (0.01-10.01) 12.10 0.168 4.8375 pV227aE Long anther length-CL 56.4 (63.4-92.15) 77.62 pV219aE WL/CS ¹ Long anther length-CL 25.86 (16.01-33.27) 15.074 -0.073 15.36 pV219aE WL/CS ¹ Long anther length-CL 56.56 (53.70.54) 16.076 0.070 5.397 pV219aE WL/CS ¹ Peal blade-CS 37.11 (6.01-40.59) 13.03 -0.017 15.98 MM200B MM20BE Peal daw-CL 25.5 (17.5.27) 20.217 -0.017 6.470 BKM8026b ML/CL ¹ Peal daw-CL 25.5 (17.5.27) 20.217<	Trait-treatment	Position in cM (2-LOD intervals)	LR	Additive effect	% Variance explained	Closest marker	QTL that demonstrate significant $QTL \times E$ across treatment pairs
Short anhwe length-C1. 65.4 (61.97-02.54) 27.190 -0.073 9.2.03 pW219aE Short anhwe length-C2. 0.01 (0.01-0.00) 13.05 0.124 7.043 pW227AE short filament length-C2 0.01 (0.01-0.00) 13.05 0.124 7.043 pW227AE methods in length-C1 0.01 (0.01-0.00) 13.05 0.124 7.043 pW227AE short filament length-C2 0.01 (0.01-0.00) 13.045 0.128 7.703 pW227AE short filament length-C1 25.5 (1.01-37.99) 13.702 -0.100 6.692 pW100bH long anther length-C2 0.01 (0.01-0.00) 13.183 0.063 5.771 pW227AE long anther length-C2 6.56 (1.01-37.99) 13.702 -0.103 5.757 pW223AE long anther length-C2 6.56 (1.01-37.99) 13.702 -0.103 5.757 pW223AE long anther length-C2 6.56 (1.01-37.99) 13.702 -0.103 5.757 pW23AE long anther length-C2 6.56 (1.01-37.94) 16.076 -0.070 15.355 pW23AE long anther length-C2 7.415 (3.03-92.15) 13.484 0.008 14.075 pW23AE long anther length-C3 7.415 (3.03-92.15) 13.484 0.0188 14.074 pW23AE long anther length-C4 7.415 (3.03-92.15) 14.188 -0.107 5.928 BKNSC2ab long anther length-C4 7.415 (3.03-92.15) 14.188 -0.107 5.928 BKNSC2ab long anther length-C5 7.415 (3.03-92.15) 14.188 -0.107 5.928 BKNSC2ab long anther length-C5 7.415 (3.03-92.15) 14.080 -0.146 6.789 pW23AE long anther length-C5 7.415 (3.03-92.15) 14.080 -0.146 6.789 pW13AE Petal data-C5 6.54 (4.319-85.15) 16.000 -0.146 6.789 pW13AE Petal data-C1 2.258 (1.07-57.35) 15.25 0.2021 -0.071 6.470 BKNSC2ab Petal vidth-C1 2.586 (1.57.375) 13.252 -0.0271 6.470 BKNSC2ab Petal vidth-C1 4.258 (1.02-61.35) 18.120 -0.124 12.279 Hit0.27 Petal vidth-C1 4.258 (1.02-61.35) 18.100 -1.268 5.860 pW130bH H Petal vidth-C1 4.258 (1.02-61.35) 18.100 -1.268 5.860 pW130bH H Petal vidth-C1 4.054 (0.14-7.15) 13.1225 -0.227 PW100bH H Petal vidth-C1 4.054 (0.14-7.5) 13.1225 -0.237 14.270 BKNSC2ab PW1040H WL/C5 -0.158 6.160 PW130bH WL/C5 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.160 -0.159 8.1	Short anther length-CS	65.56 (63.4–70.54)	32.793	-0.097	12.506	fito227	
Short anther length-WL 6 54 (60.63–70.54) 23.314 -0.070 8.2.20 pW2/9.6E short illument length-C4 WL 0.01 0.001–10.01) 13.35 0 124 7.248 pW227.6E short illument length-C4 WL 0.01 0.001–10.01) 12.124 0.088 6.435 pW227.6E bort fillument length-C5 65.4 (57.63–92.15) 17.622 -0.135 7.575 pW227.6E Long anther length-C5 65.4 (57.63–92.15) 17.622 -0.135 0.063 5.775 pW227.6E Long anther length-C5 65.4 (57.63–92.15) 17.622 -0.135 0.063 5.775 pW227.6E Long anther length-C5 65.4 (57.63–92.15) 17.622 -0.135 0.063 5.777 pW219.6E Long anther length-C5 65.4 (57.63–92.15) 17.622 -0.135 17.67 pW219.6E Long anther length-C5 65.4 (53.46.31–83.15) 37.633 -0.012 0.1457 pW219.6E Long anther length-C5 65.4 (53.46.31–33.15) 37.633 -0.012 0.1457 pW219.6E Long anther length-C5 65.4 (53.46.31–33.15) 37.633 -0.012 0.1457 pW219.6E Long anther length-C5 65.4 (53.09–83.15) 88.090 -0.016 6.578 pW219.6E Petal black-C5 7.257 13.14 (1.98–63.15) 82.0421 -0.018 6.640 file.227 here long liment length-C5 7.257 (1.57–32.77 2.23.20) -0.148 6.640 file.227 here long liment length-C5 7.258 (0.75–32.77 2.23.00 -0.1486 6.640 file.227 here long liment length-C5 7.258 (0.75–32.77 2.23.00 -0.1486 6.640 file.227 here long liment length-C5 7.258 (0.75–32.77 2.23.00 -0.1486 6.640 file.227 here long liment length-C5 7.258 (0.75–32.77 2.23.00 -0.128 5.6477 horos68 Feal volth-C1 7.258 (0.75–32.77 2.23.00 -0.128 5.6477 horos68 Here longth-C1 8.258 (0.610–37.59) 14.589 -0.128 5.677 horos68 Here longth-C1 8.258 (0.610–37.59) 14.589 -0.128 5.677 horos68 Here longth-C1 8.258 (0.610–37.59) 14.589 -0.128 5.678 BWN5026b Here longth-C1 8.258 (0.610–37.59) 14.589 -0.125 5.678 BWN5026b Here length-C1 8.558 (0.513 -0.148 -1.586 BWN5026b Here longth-C1 8.258 (0.610–37.59) 14.599 -0.255 5.028 pW100H1 Here longth-C1 8.258 (0.610–37.59) 14.599 -0.255 5.028 pW100H1 Here longth-C1 8.258 (0.610–37.59) 14.599 -0.255 5.028 pW100H1 Here longth-C1 8.258 (0.610–37.59) 14.599 -0.355 5.028 pW100DX Here longth-C	Short anther length–CL	65.4 (61.95–70.54)	27.190	-0.093	9.203	pW219aE	
abort nament englen-C1 000 001-1000 12.200 0.124 7483 pri227aE with Short filament length -C2 001 001-1000 12.2124 0.088 6.453 pri227aE block filament length -C3 0.654 (57.3-92.5) 17.022 0.108 0.6692 pri260 WL/CS ⁺ Long anther length -C3 0.01 0001-1000 15.183 0.063 5.771 pri27aB WL/CS ⁺ Long anther length -C3 0.654 (63.4-82.15) 37.623 -0.102 14.357 pri27aB WL/CS ⁺ Long anther length -C4 0.654 (63.4-82.15) 37.623 -0.102 14.357 pri27aB WL/CS ⁺ Long anther length -C5 0.654 (63.4-82.15) 37.623 -0.102 14.357 pri27aB WL/CS ⁺ Long anther length -C5 0.554 (53.0-73.72) 15.074 -0.073 5.136 pri27aB WL/CS ⁺ Long anther length -C5 0.554 (53.0-73.72) 15.074 -0.073 5.136 pri27aB WL/CS ⁺ Head blade-C5 0.554 (53.0-73.72) 15.074 -0.079 5.330 pri27aB WL/CS ⁺ Petal blade-C5 0.554 (53.0-73.757 26.217 -0.107 9.330 pri27aB WL/CS ⁺ Petal claw-CL 2.555 (17.5-37.79) 15.356 -0.113 4.437 pri27aB WL/CS ⁺ Petal claw-CL 2.556 (53.9-73.15) 18.827 -0.107 9.330 pri27aB WL/CS ⁺ Petal claw-CL 0.554 (53.9-73.15) 18.827 -0.127 0.421 12.799 ftb027 Petal claw-CL 0.554 (53.9-73.15) 13.5125 -0.241 12.279 ftb027 Petal vidth -C1 0.554 (53.9-73.15) 13.5125 -0.241 12.279 ftb027 Petal vidth -C1 0.554 (53.9-73.15) 13.5123 -0.241 12.799 ftb027 Petal vidth -C1 0.554 (53.9-73.15) 13.2422 -0.250 11.090 pri27a WL/CS ⁺ Petal vidth -C1 0.554 (53.9-73.15) 13.2422 -0.251 11.400 pri27a WL/CS ⁺ Petal vidth -C1 0.544 (53.09-76.15) 13.277 204 11.279 ftb027 Petal vidth -C1 0.554 (53.9-76.15) 13.277 204 11.279 ftb027 Petal vidth -C1 0.554 (53.9-76.15) 13.277 12.218 BLNNE026b WL/CC ⁺ Petal vidth -C1 0.545 (63.9-76.15) 13.777 12.775 12.228 BLNNE026b WL/CC ⁺ Petal vidth -C1 2.236 (17.5-33.27) 23.240 -1.988 10.772 pri160H WL/CC ⁺ Petal vidth -C1 2.246 (19.9-66.15) 23.773 -1.775 12.228 BLNNE026b WL/CC ⁺ Petal vidth -C1 2.245 (63.9-66.15) 23.773 -1.775 12.228 BLNNE026b WL/CC ⁺ Petal vidth -C1 2.254 (63.9-66.15) 23.773 -1.775 12.228 BLNNE026b WL/CC ⁺ Petal vidth -C1 2.256 (17.5-33.27) 13.577 0.065 4.588 BLNO026b WL/CC ⁺ Petal vidth	Short anther length–WL	65.4 (60.63–70.54)	23.314	-0.070	8.220	pW219aE	
mms 0.01 <th< td=""><td>Short filament length_CI</td><td>0.01 (0.01 - 10.01) 0.01 (0.01 - 10.01)</td><td>15.365</td><td>0.124</td><td>7.043</td><td>pW227aE pW227aE</td><td></td></th<>	Short filament length_CI	0.01 (0.01 - 10.01) 0.01 (0.01 - 10.01)	15.365	0.124	7.043	pW227aE pW227aE	
Short filament length-C1 25.0 (20.1-327.59) 13.702 -0.160 6.692 $pV120hF$ W1/C5 ² Long anther length-C3 0.01 (0.01-0.01) 15.183 0.063 5.771 $pV120hF$ W1/C5 ² Long anther length-C4 0.01 (0.01-0.01) 15.183 0.003 5.771 $pV121hF$ W1/C5 ² Long anther length-C3 6.54 (0.3-42.15) 37.653 -0.102 14.547 $pV21hF$ W1/C5 ⁴ Long anther length-C3 6.54 (0.3-42.15) 37.653 -0.102 14.547 $pV21hF$ W1/C5 ⁴ Long anther length-C4 6.54 (0.10-75.15) 10.000 -0.008 15.071 $pV121hF$ W1/D6F Long anther length-C5 74.15 (0.30-9.215) 14.188 -0.107 15.293 BRM5026b Petal blade-C5 6.54 (0.10-88.15) 18.660 -0.146 6.789 $pV21hF$ W1/D6F Petal blade-C5 6.54 (0.10-88.15) 18.660 -0.146 6.789 $pV21hF$ H Petal claw-C4 25.5 (0.7-5.727) 26.217 -0.107 9.303 $pV10hF$ H Petal claw-C4 25.7 (0.5-14.757) 18.369 -0.112 5.677 $pV110hF$ H Petal claw-C4 25.7 (0.5-14.757) 18.369 -0.112 5.677 $pV110hF$ H Petal claw-C4 25.7 (0.5-14.751) 18.369 -0.112 5.677 $pV110hF$ H Petal vidth-C4 6.54 (0.50-6.709) 30.239 -0.220 11.090 $pV219hE$ W1/C4 ⁵ Petal vidth-C5 7054 (0.5-7.759) 18.369 -0.112 5.677 $pV110hF$ H Petal vidth-C4 6.54 (0.50-6.709) 30.239 -0.220 11.090 $pV219hE$ W1/C4 ⁵ Petal vidth-C4 6.54 (0.50-6.709) 30.239 -0.220 11.090 $pV219hE$ W1/C4 ⁵ Petal vidth-C4 6.54 (0.50-6.15) 25.773 -1.775 11.222 BRM5026b W1/C4 ⁵ Petal vidth-C4 7284 (0.10-9.151) 25.773 -1.775 11.202 BRM5026b W1/C4 ⁵ Petal vidth-C4 7254 (0.10-6.151) 25.773 -1.775 11.202 BRM5026b W1/C4 ⁵ Petal vidth-C4 80.15 (0.3-112.15) 14.880 -1.488 6.822 BRM5026b W1/C4 ⁵ Petal vidth-C4 80.15 (0.3-112.15) 14.880 -1.488 6.822 BRM5026b W1/C4 ⁵ Petal vidth-C4 80.15 (0.3-112.15) 14.880 -1.498 10.722 $pV160hH$ W1/C4 ⁵ Petal vidth-C4 80.15 (0.3-112.15) 14.880 -0.385 6.609 $pV219hE$ 41.725 Petal area-C4 7234 (0.00-8.151) 13.600 0.325 6.609 $pV120hF$ 40.1/C5 Petal area-C1 82.56 (0.00-7.99) 13.31 -0.05 1.488 0.522 BRM5026b PU1/C5 Petal area-C1 82.56 (0.00-7.99) 13.31 -0.05 6.991 BRM5010 0.1/C5 Petal area-C1 82.15 (0.2-1.71) 14.880 -0.05 6.992 BRM5026b PU1/C5 Petal area-C1 82.15 (0.2-1.75) 11.486 0.05 1.478 PV200F P	###Short filament length_WL	0.01 (0.01 - 10.01) 0.01 (0.01 - 10.01)	12.124	0.088	4.835	pW227aE pW227aE	
Short filament length-CS of 4 (27.63-92.15) 17.622 -0135 7.575 $pV229aE$ WL/CS ² Long anther length-CL 25.86 ($6.01-3.27$) 15.074 -0.073 5.136 $pV160bH$ Long anther length-CL 65.66 ($6.01-3.27$) 15.074 -0.073 5.136 $pV129aE$ Long anther length-CL ($6.55.6$ ($6.01-3.27$) 15.074 -0.073 5.136 $pV129aE$ Long anther length-CL ($6.55.6$ ($6.01-3.27$) 15.074 -0.073 5.295 $pV219aE$ Long anther length-CL ($6.55.6$ ($6.01-3.27$) 13.0176 -0.070 5.395 $pV219aE$ Long anther length-CL ($6.55.6$ ($7.5-32.7$) 25.217 -0.107 5.298 $pV219aE$ Peal black-CS ($7.5-32.7$) 25.217 -0.107 5.308 $pV160bH$ Peal black-CS ($7.5-32.7$) 10.366 -0.186 5.509 $pV160bH$ Peal black-CS ($7.5-32.7$) 10.366 -0.186 5.509 $pV160bH$ Peal daw-VL ($7.54.6$ ($7.5-32.7$) 10.366 -0.186 5.509 $pV160bH$ Peal daw-VL ($7.5.6$ ($7.5-32.7$) 10.366 -0.186 5.509 $pV160bH$ Peal daw-VL ($7.5.6$ ($7.5-32.7$) 25.217 -0.107 5.308 $pV160bH$ Peal daw-VL ($7.5.6$ ($7.5-32.7$) 25.207 -0.220 $pV160bH$ WL/CF Peal daw-VL ($7.5.6$ ($7.5-32.7$) 25.207 -0.220 $pV160bH$ WL/CF Peal daw-VL ($7.5.6$ ($7.5-32.7$) 25.207 -0.220 $pV160bH$ WL/CF Peal availt-CL ($7.5.6$ ($7.5-32.7$) 25.207 -0.220 $pV160bH$ WL/CF Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ WL/CC Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ WL/CC Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ $PV200H$ $PV200H$ $PV200H$ Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ $PV20H$ $PV20H$ $PV20H$ Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ $PV20H$ $PV20H$ $PV20H$ Peal availt-CL ($7.5.6$ ($7.5.6$) $pV100H$ $PV20H$	Short filament length–cl	25.5 (16.01–37.59)	13.702	-0.160	6.692	pW160bH	
Long anther length $\leq S$ 0.01 (001-1001) 15.183 0.063 5.771 pW227aE Long anther length $\leq S$ 654 (63.4+82.15) 37.633 -0.102 14.547 pW219aE Long anther length $\leq S$ 654 (63.4+82.15) 37.633 -0.102 14.547 pW219aE Long anther length $\leq S$ 654 (63.4+82.15) 37.633 -0.102 14.547 pW219aE Long anther length $\leq S$ 654 (63.4+82.15) 33.840 -0.038 14.071 BKM5026b Long anther length $\leq S$ 7.17 (53.4+92.15) 33.840 -0.038 14.071 BKM5026b Petal chave $\leq S$ 7.27 (53.2+7.21) 14.137 -0.107 3.030 pW160BH Petal chave $\leq S$ 7.05 (64.6) (63.0+88.15) 18.690 -0.146 6.789 pW219aE Petal chave $\leq S$ 7.05 (64.6) (63.0+88.15) 18.690 -0.146 6.789 pW219aE Petal chave $\leq S$ 7.05 (64.6) (53.6) 13.6827 -0.077 6.670 BKM5026b Petal chave $\leq S$ 7.05 (64.6) (53.6) 15 16.827 -0.077 6.670 BKM5026b Petal chave $\leq S$ 7.05 (64.6) 37.675 16 16.827 -0.077 6.670 BKM5026b Petal dwidth $\leq C$ 7.05 (63.4-76.15) 35.125 -0.424 12.709 fac227 W1/C5 ⁴ Petal width $\sim C$ 7.05 (63.4-76.15) 35.125 -0.241 12.709 fac227 W1/C5 ⁴ Petal width $\sim C$ 7.05 (64.04.7-6.15) 35.125 -0.241 12.709 fac227 W1/C5 ⁴ Petal width $\sim C$ 7.25 (60.0+9.615) 28.737 -1.775 11.000 pV110aH ###764al width $\sim C$ 7.25 (60.0+9.615) 28.73 -1.775 12.023 BKM5026b W1/C1 ⁴ ###764al width $\sim C$ 7.25 (60.0+9.615) 28.73 -1.775 12.023 BKM5026b W1/C1 ⁴ ###566m length $\sim C$ 7.25 (60.0+9.615) 28.73 -1.775 12.023 BKM5026b W1/C1 ⁴ ###566m length $\sim C$ 7.25 (60.0+9.615) 28.31 -1.365 5.028 BKM5026b W1/C1 ⁵ Petal area $\sim C$ 7.25 (60.0+9.615) 28.31 -1.365 5.028 BKM5026b W1/C1 ⁵ Petal area $\sim C$ 7.25 (60.0+9.615) 12.827 -1.775 12.023 BKM5026b W1/C1 ⁵ Petal area $\sim C$ 7.25 (60.0+9.615) 12.827 -1.755 12.040 BKM5026b W1/C1 ⁵ Petal area $\sim C$ 7.25 (60.0+9.615) 12.424 -0.118 4.072 PW10bA Hird cognitor $\sim C$ 7.25 (60.0+9.155) 13.517 -0.58 4.582 BKM5026b $\sim C10etcinn interval \sim W 82.15 (0.27-12.15 14.882 -1.666 7.508 BKM5026b\sim C10etcinn interval \sim W 82.15 (0.27-12.15 14.826 -0.668 BKM5026b\sim C10etcinn interval \sim W 84.25 (27.27.28.25 -0.0136 0.051 BKM5026b\sim W1/C55 PM1000 -1.25$	Short filament length-CS	65.4 (57.63–92.15)	17.622	-0.135	7.575	pW219aE	WL/CS^{\dagger}
Long anther length-CL 2586 (16.01-33.27) 15.074 -0.073 5.136 pW160bH Long anther length-CL 65.65 (1.02-70.35) 10.076 -0.073 5.136 pW120aE Long anther length-CL 65.65 (1.02-70.35) 10.076 -0.073 5.395 pW120aE Long anther length-CL 65.65 (1.02-70.35) 10.076 -0.073 5.395 pW120aE Long anther length-CL 65.65 (1.02-70.35) 10.076 -0.073 5.395 pW120aE Peal blade-CS 63.72 (1.0.01-0.059) 13.013 -0.113 4.437 fbt0.068 Peal blade-CS 63 (4.60.9-88.15) 18.690 -0.146 6.799 pW2194E Peal blade-CS 63 (4.60.9-88.15) 18.690 -0.146 6.799 pW2194E Peal blade-CS 63 (4.60.9-86.15) 10.827 -0.071 6.470 BRM502ab Peal blade-CS 64 (6.00-86.15) 10.827 -0.071 6.470 BRM502ab Peal blade-CS 64 (6.00-96.15) 10.827 -0.071 6.470 BRM502ab Peal vidth-VL 255 (0.75-52.7) 13.36 -0.186 5.650 pW160bH Peal vidth-VL 327 (1.75-46.79) 30.239 -0.230 11.090 pW2194E W1/CS ⁴ Peal vidth-VL 327 (1.75-46.79) 30.239 -0.230 11.090 pW2194E W1/CS ⁴ Peal vidth-VL 61.95 (94.03-73.17) 23.240 -0.198 bW1/CS ⁴ Peal vidth-VL 61.95 (94.03-73.17) 23.240 -0.988 (5.82 BRM502ab W1/CS ⁴ Peal vidth-VL 61.95 (94.03-74.15) 12.422 -0.111 4.613 pX1194E W1/CS ⁴ Peal vidth-VL 61.95 (94.03-74.15) 12.422 -0.111 4.613 pX1194E W1/CS ⁴ Peal vidth-VL 61.95 (94.03-74.15) 12.422 -0.118 6.828 BRM502ab W1/CS ⁴ Peal vidth-VL 61.95 (94.03-74.15) 13.690 -0.580 (5.63.28 pW160bH W1/CS ⁴ Peal vidth-VL 61.95 (96.01-74.15) 13.690 -0.581 6.800 7.965 BRM502ab W1/CS ⁴ Peal vidth-VL 61.95 (96.01-74.15) 13.697 0.352 (6.64.78 pW202b W1/CS ⁴ Peal vidth-VL 63 (5.70.9-64.15) 13.690 0.321 (6.778 pW20bK Collection interval-WL 63 (5.70.9-64.95) 13.100 1265 7.806 fbt0.372 Pint exertion-CL 49.03 (21.5-76.39) 13.517 0.028 4.998 BRM502ab Crosses 7 Sive length-CL 40.03 (21.5-77.63) 13.517 0.038 4.999 BW1502b Collection interval-WL 654 (5.70.9-64.95) 13.109 0.051 4.0328 6.099 pW219aE Herkogamy-VI, 49.03 (29.5-64.99) 24.544 0.0133 9.551 fbt0.348 Ovary length-CL 40.36 (21.5-77.91) 13.367 0.038 4.9228 BRM502b Crosses 7 Sive length-CL 40.03 (21.5-77.91) 15.77 0.005 4.4886 fbt0.101b Herkog	Long anther length–CS	0.01 (0.01-10.01)	15.183	0.063	5.771	pW227aE	
Long anther length C1 is 05.4 for 0.4 solutions of the set of the	Long anther length–CL	25.86 (16.01–33.27)	15.074	-0.073	5.136	pW160bH	
$ \begin{array}{c} \label{eq:constraints} \begin{array}{l} \mbox{Ling} (f) \\ \mbox{Ling} (f) \\\mbox{Ling} (f) \\\mbox{Ling} (f) \\\mbox{Ling} (f)$	Long anther length CI	65.4 (63.4-82.15) 65.56 (51.03, 70.54)	37.633	-0.102	14.547	pW219aE	
$ \begin{array}{c} \mbox{Lengthament length-CS} 7.115 (63.00-92.15) 14.188 -0.107 5.923 BKMS026 \\ \mbox{Petal blade-CS} 8.51 (7.65.27) (60.01-659) 13.013 -0.013 4.347 ficto608 \\ \mbox{Petal blade-CS} 8.51 (7.65.27) (20.01-659) 13.001 -0.013 -0.013 4.347 ficto608 \\ \mbox{Petal claw-CL} 2.55 (7.5-32.7) 26.217 -0.107 9.330 pW160bH \\ \mbox{Petal claw-CL} 2.55 (7.5-32.7) 16.366 -0.186 5.560 pW160bH \\ \mbox{Petal claw-WL} 7.415 (63.09-96.15) 16.327 -0.071 6.470 BKMS026b \\ \mbox{Petal width-CL} 2.58 (07.5-37.59) 16.366 -0.186 5.560 pW160bH \\ \mbox{Petal width-CL} 5.46 (3.09-67.09) 32.29 -0.220 111.09 pW160bH \\ \mbox{WL}/CS^1 \\ \mbox{Petal width-CL} 5.46 (3.09-67.09) 32.29 -0.220 111.09 pW160bH \\ \mbox{WL}/CL^1 \\ \mbox{Petal width-CL} 5.46 (3.09-67.09) 32.29 -0.220 111.09 pW160bH \\ \mbox{WL}/CL^1 \\ \mbox{Petal width-CL} 5.46 (3.09-67.09) 32.273 -1.775 12.023 \\ \mbox{Petal width-CL} 5.46 (3.09-67.09) 32.29 -0.250 \\ \mbox{Petal width-CL} 5.256 (6.10-61.59) 12.482 -0.111 \\ \mbox{Atin area-CL} 2.256 (6.10-61.59) 13.640 \\ \mbox{Petal area-CL} 2.256 (6.10-61.59) 13.647 \\ \mbox{Petal area-CL} 2.256 (6.10-61.59) 13.647 \\ \mbox{Petal area-CL} 2.256 (6.10-61.59) 13.647 \\ \mbox{Petal area-CL} 2.257 (7.54-94.15) 12.05 1 12.87 \\ \mbox{Collection interval-WL} 6.54 (7.03-9-0.15) 13.647 \\ \mbox{Collection interval-WL} 6.54 (7.03-9-0.15) 13.647 \\ \mbox{Collection interval-WL} 6.54 (7.03-9-0.15) 13.647 \\ \mbox{Petal area-CL} 2.253 (7.57.63) 19.738 \\ \mbox{Collection interval-WL} 6.54 (7.03-9-0.15) 13.647 \\ \mbox{Petal area-CL} 2.253 (7.05-4-9.15) 12.872 \\ \mbox{Petal area-CL} 2.253 (7.05-6-9.9) 15.917 \\ \mbox{Classicn interval-WL} 6.42 (7.05-6-9.9) 21.88 \\ \m$	Long anther length–WL	74 15 (72 54–92 15)	33 840	-0.070 -0.088	14 071	BRMS026b	
Petal blade-CS 32.7 (16.01-40.59) 13.013 -0.113 4.437 fito088 Petal blade-CS 65.41 (63.09-81.5) 18.600 -0.136 6.789 pW160bH Petal claw-CS 70.514 (61.9-86.15) 20.420 -0.088 6.600 fito227 Petal claw-CS 70.514 (61.9-86.15) 20.420 -0.088 6.600 fito227 Petal vidth-CL 25.86 (77.5-37.99) 16.366 -0.116 5.650 pW160bH Petal width-CL 6.54 (63.09-67.19) 30.222 -0.211 11.091 pW129.26 WL/C3 ¹ Petal width-CS 72.54 (63.09-67.19) 30.222 -0.211 11.091 pW129.26 WL/C1 ¹ Petal atoa-CS 72.54 (63.09-96.15) 28.733 -1.775 12.023 BWN5026b WL/C1 ¹ Petal atoa-CS 72.54 (63.09-96.15) 13.810 -1.584 6.532 BWN5026b WL/C3 ¹ Stem length-CL 80.15 (61.3-102.15) 14.882 -1.666 7.965 BRM5026b Collection interval-VL 80.15 (23.76.31) 17.3	Long filament length–CS	74.15 (63.09–92.15)	14.188	-0.107	5.928	BRMS026b	
Petal blade-CS 65.4 (63.09-88.15) 18.690 -0.146 6.789 pW219aE Petal claw-CL 255 (17.52.27) 20.217 -0.107 9.330 pW160bH Petal claw-CS 70.54 (61.95-86.15) 20.420 -0.088 6.600 fits227 Petal width-CL 23.86 (17.5-37.59) 16.366 -0.186 5.650 pW160bH Petal width-CS 70.54 (63.47-6.15) 35.125 -0.241 12.009 fits227 WL/CS ³ Petal width-CL 6.54 (63.09-64.09) 32.23 -0.230 11.090 pW160bH WL/CS ³ Petal width-CL 6.54 (63.09-64.09) 32.23 -1.280 11.090 pW1602b WL/CL ³ Petal area-CL 72.54 (63.09-64.19) 12.452 -1.663 16.3728 WL/CL ³ Stem length-CL 25.86 (16.01-37.59) 13.531 -1.465 5.262 pW160bH Stem length-CL 82.63 (10.3-74.15) 13.660 0.21 6.478 pW120bL Collection interval-VL 6.14 (67.03-80.15) 13.607 0.385	Petal blade-CS	32.7 (16.01-40.59)	13.013	-0.113	4.437	fito068	
Petal claw-CL 25 (17.5–32.7) 26.217 -0.107 9.330 pW160bH Petal claw-WL 74.15 (63.09–66.15) 16.827 -0.071 6.470 BRN50226 Petal with-CL 25.86 (17.5–37.59) 16.862 -0.122 5.477 fitod6bH Petal with-CL 6.460 0.152 -0.211 12.709 BRN50226 WL/CS ⁴ Petal with-CL 6.45 (63.09–67.09) 30.239 -0.250 11.090 PW12b48 WL/CL ⁴ ##farteat with-WL 0.15 (49.07.5–33.27) 23.240 -1.988 10.772 PW160bH WL/CL ⁴ Petal area-CL 27.24 (63.09–61.13 27.73 -1.775 12.023 BRM5026b WL/CS ⁴ Leaf area-CL 25.4 (63.09–61.13 15.460 5.360 BRM5026b WL/CS ⁴ Sem length-CL 25.1 (10.3–10.21) 13.811 1.266 5.366 BRM5026b Collection interval-VL 20.1 (10.3–10.21) 13.882 -1.666 7.806 BRM5026b Collection interval-CS 6.95 (97.03–41.15) 12.672	Petal blade–CS	65.4 (63.09-88.15)	18.690	-0.146	6.789	pW219aE	
Preak claw-WL 20.34 (61.93–66.15) 20.420 -0.088 6.600 BRX/S1226b Preak with-CL 25.86 (17.5–37.59) 16.366 -0.186 5.650 pW160bH Preak with-WL 32.7 (17.5–36.59) 16.366 -0.186 5.650 pW160bH Preak with-WL 64.37 (65.9–6.79) 32.9 -0.220 11.020 pW219aL WL/CL ³ ###Preak with-WL 61.95 (49.03–74.15) 12.422 -0.111 4.613 pW119dV Preak with-CL 6.54 (65.09–66.15) 28.773 -1.775 12.023 BRMS026b WL/CL ⁴ Preak area-CL 72.54 (65.09–66.15) 12.857.73 -0.238 65.80 BRMS026b WL/CL ⁴ Stem length-CL 80.15 (51.03–61.51) 13.80 -1.58 65.028 BRMS026b WL/CL ⁴ Stem length-CL 80.15 (51.03–61.51) 13.067 0.556 6.478 BRMS026b Collection interval-WL 634 (37.93 24.311 -0.016 BRMS026b Collection interval-WL 6434 (37.94 10.936 6.478	Petal claw–CL	25.5 (17.5–32.7)	26.217	-0.107	9.330	pW160bH	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Petal claw-CS	70.54 (61.95-86.15)	20.420	-0.088	6.600	fito227	
Petal width-WL 327 (1/5-46.30) 14.689 -0.122 5.477 Finologia Petal width-CS 704 (63.4-76.15) 35.125 -0.2301 10.900 pW194. WL/CS ¹ Petal width-CL 6.54 (63.09-67.19) 30.239 -0.2501 11.090 pW194. WL/CS ¹ Petal area-CL 2.786 (17.5-33.27) 23.240 -1.988 10.772 pW106H WL/CS ¹ Petal area-CS 72.54 (63.09-96.15) 16.940 -1.548 6.582 BRMS026b WL/CS ¹ Leaf area-CS 58.63 (51.07-41.59) 13.531 -1.365 5.028 PW1608H WL/CS ¹ Stem length-CL 2.856 (16.01-37.59) 13.531 -1.466 7.965 BRMS026b WL/CS ¹ Collection interval-WL 82.15 (20.7-14.14) 12.63 -1.479 6.416 BRMS026b WL/CS ¹ Pistil exsertion-CL 49.03 (21.5-57.63) 19.287 -0.131 9.066 pW127.4E Pistil exsertion-CL 49.03 (21.5-57.63) 19.287 -0.131 9.066 pW127.4E	Petal width_CI	74.13 (03.09-90.13) 25.86 (17.5-37.59)	16.627	-0.071 -0.186	6.470 5.650	pW160bH	
Petal width-CS 70.54 (63.4–76.15) 35.125 -0.241 12.709 fluzz WL/CS ³ ###Petal width-WL 6.19 5 (49.05–70.9) 30.299 -0.250 11.00 pW129aE WL/CS ³ ###Petal width-WL 6.19 5 (49.05–74.15) 12.422 -0.111 4.613 pM19dX WL/CL ³ Petal area-CS 7.254 (63.09–66.15) 28.773 -1.775 12.023 RRMS02b WL/CL ³ Stem length-CL 28.66 (16.01–37.59) 18.110 12.65 7.806 fito378b WL/CS ³ Stem length-CL 80.15 (51.03–102.15) 14.882 -1.666 7.965 RRMS02b Collection interval-WL 6.29 (57.03–74.15) 13.607 0.38 6.609 pW127aE Fistil exsertion-CL 49.03 (20.5–76.3) 19.738 -0.131 8.147 pW127aE Fistil exsertion-CL 49.03 (20.5–76.3) 19.738 -0.131 8.147 pW127aE Fistil exsertion-CL 49.03 (20.5–76.3) 19.738 -0.136 9.812 BRMS040 Style length-CS	Petal width–WL	32.7 (17.5–46.59)	14.689	-0.100	5.477	fito068	
Petal width-CL 654 (63.09-67.09) 30239 -0.250 11.090 pVL/9LE WL/CL ¹ Petal area-CL 27.86 (175-33.27) 2422 -0.111 4.613 pV1194X Petal area-CL 72.84 (63.09-96.15) 16.940 -1.588 10.772 pW106H WL/Cl ¹ Leaf area-CL 72.84 (63.09-96.15) 16.940 -1.548 6.582 BKMS026b WL/Cl ² Leaf area-CS 58.63 (51.07-61.95) 13.531 -1.365 5.028 pW106H WL/CS ² Stem length-CL 80.15 (51.07-10.218) 13.069 0.521 6.478 BKMS026b Collection interval-WL 82.15 (52.7-112.44) 12.633 -1.479 6.416 BKMS026b Collection interval-WL 49.03 (21.5-57.63) 19.278 -0.131 9.066 pW127aE Pistil exsertion-CL 49.03 (21.5-57.63) 19.278 -0.133 9.616 pW127aE Style length-CS 4.01 (0.01-17.3) 14.896 0.661 6.990 BKMS040 Ovary length-CL 2.01 (0.01-17.3) 14.89	Petal width–CS	70.54 (63.4–76.15)	35.125	-0.241	12.709	fito227	WL/CS [§]
###Petal width-WL $(61.95 (49.03-74.15)$ 12.422 -0.111 4.613 $pW130bH$ WL/CL^1 Petal area-CL $27.86 (3.09-96.15)$ 22.200 -1.775 12.023 $BRM5026b$ WL/CL^1 Petal area-CS $72.54 (63.09-96.15)$ 16.940 -1.548 6.582 $BRM5026b$ WL/CS^1 Leaf area-CS $58.63 (51.03-61.95)$ 18.110 1.265 7.806 $fm0.37bb$ WL/CS^1 Stem length-CL $82.53 (22.712.44)$ 12.633 -1.4365 5.028 $pW130bH$ Stem length-CL $80.15 (51.03-102.15)$ 14.882 -1.666 7.965 $BRM5026b$ Collection interval-WL $65.4 (57.03-80.15)$ 13.607 0.385 6.690 $pW219aE$ Herkogamy-WL $49.03 (39.59-61.95)$ 24.311 -0.111 8.147 $pW127aE$ Pistil exsertion-CL $82.15 (70.54-94.15)$ 12.872 -0.136 9.812 $BRM5040$ Style length-CS $4.01 (0.01-17.3)$ 14.896 0.061 6.990 $BRM5040$ Style length-CL $2.01 (0.01-17.3)$ 13.375 0.633 3060 $pW1304E$ Short intamer length-CL $6.82 (72.87-96.88)$ 13.375 0.633 3060 $pW1304E$ Short intamer length-CL $6.82 (72.87-96.88)$ 13.375 0.633 3060 $pW1304E$ Short intamer length-CL $6.82 (72.87-96.88)$ 13.375 0.063 3.806 $pW1304E$ Short intamer length-CL $6.82 (72.87-96.88)$ 13.375 0.063 3.980 pW	Petal width-CL	65.4 (63.09-67.09)	30.239	-0.250	11.090	pW219aE	WL/CL^{\ddagger}
Petal area-CJ. 27.86 (17.5-33.27) 23.240 -1.988 10.722 pW100bH WL/CL' Petal area-CS 72.54 (63.09-96.15) 16.940 -1.548 6.582 BKM5026b WL/CS' Leaf area-CL 2.54 (63.09-96.15) 16.940 -1.548 6.582 BKM5026b WL/CS' Stem length-CL 25.86 (16.01-37.59) 13.331 -1.365 5.028 pW106bH WL/CS' Stem length-CL 61.95 (57.03-74.15) 13.069 0.521 6.478 pW200bX Collection interval-WL 65.4 (57.03-74.15) 13.069 0.521 6.478 pW200bX Collection interval-WL 65.4 (57.03-80.15) 13.607 0.385 6.699 pW127aE Pistil exsertion-CL 49.03 (21.5-57.63) 19.738 -0.111 8.147 pW127aE Pistil exsertion-CL 82.15 (70.54-94.15) 12.872 -0.136 6.990 BRM5020b Ciromosome 7 50yle length-CS 4.01 (0.01-17.3) 14.896 0.061 6.990 BRM5040 Style length-CL 2.01 (0.01-17.3) 14.896 0.061 6.940 BRM5040	###Petal width–WL	61.95 (49.03–74.15)	12.422	-0.111	4.613	pX119dX	
Pretai area-CS 72:54 (6:3.09-96.15) 25.7/3 -1.7/5 12.023 BKMS020b WL/CS* Leaf area-CS 58:63 (51.03-61.95) 18:110 1.265 7.806 fit.037b WL/CS* Stem length-CL 25:86 (3:03-61.95) 18:110 1.265 7.806 fit.037b WL/CS* Stem length-CL 80:15 (51.03-102.15) 14:882 -1.666 7.965 BKMS026b Collection interval-WL 64:37:03-80.15) 13:007 0.385 6.690 pW219aE Herkogamy-WL 49:03 (21.5-87.63) 19:738 -0.131 9.066 pW127aE Pistil exsertion-CL 49:03 (21.5-87.63) 19:738 -0.136 9.812 BKMS040 Style length-CS 4.01 (0.01-17.3) 14:896 0.061 6.990 BKMS040 Ovary length-CS 47:23 (25.82-56.99) 15:917 0.108 4.928 BKMS040 Ovary length-CL 20:10 (0.01-17.3) 13:57 0.063 3.980 pW130cE Short anther length-CL 56:99 (42.28-56.99) 15:917 0.109 7.263 fit.0348 Short filament length-CL 66:892 (Petal area–CL	27.86 (17.5–33.27)	23.240	-1.988	10.772	pW160bH	WL/CL ⁺
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Petal area-CS	72.54 (63.09-96.15)	28.773	-1.775	12.023	BRMS026b	WL/CS^*
$ \begin{array}{c} \label{eq:construct} \begin{tabular}{ c c c c c c c c c c c c c c c c c c c$	Leaf area-CL	72.34 (63.09-96.13) 58 63 (51 03-61 95)	18.940	-1.346 1 265	0.362 7.806	fito378b	WL/CL^{\dagger}
	Stem length-CL	25.86 (16.01-37.59)	13.531	-1.365	5.028	pW160bH	WE/ C0
###Stem length-WL $82.15\ (22.7-112.44)$ $12.633\ -1.479\$ $6.478\$ pW20abx Collection interval-WL $65.4\ (57.03-80.15)\$ $13.607\$ $0.385\$ $6.690\$ pW19aE Herkogamy-WL $49.03\ (21.5-57.63)\$ $19.738\$ $-0.111\$ $8.147\$ pW127aE Pistil essertion-CL $82.15\ (70.54-94.15)\$ $12.872\$ $-0.130\$ $9.812\$ BRMS040 Chromosome 7 Style length-CS $4.01\ (0.01-17.3)\$ $14.896\$ $0.061\$ $6.990\$ BRMS040 Ovary length-CL $2.01\ (0.01-17.3)\$ $14.896\$ $0.061\$ $6.990\$ BRMS040 Ovary length-WL $40.90\$ $(25.82-65.99)\$ $5.917\$ $0.103\$ $9.651\$ fio.348 Short anther length-UL $56.99\$ $(22.94-70.87)\$ $7.065\$ $7.010\$ $9.055\$ pW13OcE Short anther length-VL $9.61\$ $2.97-96.88\$ $13.825\$ $-0.166\$ $7.501\$ fio.348 Short anther length-VL $86.82\$ $72.97-96.88\$ $13.825\$ $9.005\$ pW13OcE <	Stem length-CL	80.15 (51.03-102.15)	14.882	-1.666	7.965	BRMS026b	
	###Stem length-WL	82.15 (32.7-112.44)	12.633	-1.479	6.416	BRMS026b	
Collection interval-WL 65.4 (57.03-80.15) 13.607 0.385 6.690 pW217aE Herkogamy-WL 49.03 (39.59-61.95) 24.311 -0.111 8.147 pW127aE Pistil exsertion-CL 82.15 (70.54-94.15) 12.872 -0.136 9.812 BRM5026b Chromosome 7 Style length-CS 4.01 (0.01-17.3) 14.896 0.061 6.990 BRM5040 Style length-CL 2.01 (0.01-17.3) 14.896 0.061 6.990 BRM5040 Ovary length-CS 4.72.3 (25.82-56.99) 15.917 0.109 7.263 fito348 Ovary length-CL 56.99 (43.23-74.23) 13.375 0.063 3.9551 fito348 Short filament length-CL 56.99 (43.23-74.23) 13.375 0.063 3.905 pW130cE Short filament length-CL 86.82 (72.87-96.88) 13.825 -0.166 7.501 fito101b Short filament length-CL 86.82 (72.87-96.88) 13.825 -0.120 9.005 pX101cH Long anther length-CL 86.82 (72.87-96.88) 13.825 -0.168 0.7501 fito101b Hill and ther length-CL 86.82 (72.87-96.88) 13.825 -0.168 0.7501 fito101b Hill and ther length-CL 86.82 (72.87-96.88) 13.825 -0.168 0.7501 fito101b Hill and the length-CL 86.82 (72.87-96.88) 13.825 -0.168 0.7501 fito101b Hill and ther length-CL 86.82 (72.87-96.88) 13.825 -0.168 0.7501 fito101b Hill and ther length-CL 86.82 (72.87-96.88) 12.503 -0.088 8.428 fito101b Hill and ther length-CL 86.82 (72.87-96.88) 21.503 -0.088 8.428 fito101b Hill and ther length-CL 86.82 (72.87-96.99) 21.891 0.085 7.034 fito348 Petal claw-CS 43.23 (36.96-56.99) 21.891 0.085 7.034 fito348 Petal claw-CL 47.23 (36.96-56.99) 21.891 0.085 fito348 Petal claw-CL 96.88 (84.82-96.9) 15.932 -1.475 6.010 pW150cH Stem length-CL 96.88 (84.82-96.9) 15.932 -1.475 6.010 pW150cH Days to flowening-CS 96.88 (84.82-96.9) 15.932 -1.475 6.010 pW150cH Pistl exsertion-VL 19.42 (16.01-30.62) 16.442 0.1006 6.015 pW146aH Style length-WL 0.01 (0.01-2518) 19.053 -0.066 6.254 BRM5006 Style length-WL 53.19 (3.11-87.19) 15.744 -0.	Collection interval–CS	61.95 (57.03–74.15)	13.069	0.521	6.478	pW200bX	
Interkögamj-WL 49.03 93.29-50.39 24.311 -0.111 8.14 PW127aE Pistil exsertion-CL 82.15 (70.54-94.15) 12.872 -0.136 9.812 BRM5040 Chromosome 7 Style length-CL 2.01 0.01-17.3) 13.517 0.058 4.928 BRM5040 Ovary length-CS 47.23 (25.82-56.99) 15.917 0.109 7.263 fito348 Ovary length-CL 2.01 0.01-17.3) 13.375 0.063 3.980 pW130cE Short anther length-CL 86.29 (25.82-56.99) 25.484 0.133 9.551 fito348 Short filament length-CL 86.82 (27.87-9.688) 13.825 -0.016 7.501 fito101b Long anther length-CL 86.82 (79.91-96.88) 21.003 -0.008 8.428 fito101b ###Long anther length-CL 86.82 (25.82-35.69) 26.090 0.109 10.685 fito348 Petal claw-CL 47.23 (36.96-56.99) 24.901 0.085 fito348 Petal claw-CL 47.23 (36.96-56.99) 24.901 0.085 <td>Collection interval–WL</td> <td>65.4 (57.03-80.15)</td> <td>13.607</td> <td>0.385</td> <td>6.690</td> <td>pW219aE</td> <td></td>	Collection interval–WL	65.4 (57.03-80.15)	13.607	0.385	6.690	pW219aE	
Fishil exertion-CL \$2.15 (70.54-94.15) 12.872 -0.136 9.812 BRM5026b Chromosome 7 Style length-CS 4.01 (0.01-17.3) 13.817 0.058 4.928 BRM5040 Style length-CS 4.01 (0.01-17.3) 13.517 0.058 4.928 BRM5040 Ovary length-CS 47.23 (25.82-56.99) 15.917 0.109 7.263 fito348 Ovary length-CL 40.96 (25.82-56.99) 25.484 0.133 9.551 fito348 Short anther length-CL 56.99 (43.23-74.23) 13.375 0.063 3.980 pW130cE Short filament length-CL 86.82 (72.87-96.88) 13.825 -0.166 7.501 fito101b Short filament length-WL 79.11 (70.08-96.82) 21.130 -0.120 9.005 pX101cH Long anther length-VL 86.82 (72.87-84.82) 12.007 -0.053 4.828 fito101b Petal claw-CS 43.23 (3.696-56.99) 2.600 0.109 10.685 fito348 Petal claw-CL 42.32 (3.696-56.99) 2.600 0.019 10.685 fito348 Petal claw-WL 28.62 (25.82-35.08)	Pistil exertion_CI	49.03 (39.39-61.93)	24.311 19.738	-0.111 -0.131	8.147 9.066	pw12/aE pW127aE	
$\begin{tabular}{lllllllllllllllllllllllllllllllllll$	Pistil exsertion–CL	82.15 (70.54–94.15)	12.872	-0.131	9.812	BRMS026b	
Style length-CS4.014.014.17.3)14.8960.0616.990BRMS040Style length-CL2.010.01-17.3)13.5170.0584.928BRMS040Ovary length-CS47.23(25.82-56.99)25.4840.1339.551fito348Short anther length-CL56.99(43.23-74.23)13.3750.0633.980pW130cEShort filament length-CL86.82(72.87-96.88)13.825-0.1667.501fito101bShort filament length-VL79.11(70.08-96.82)21.913-0.1209.005pX101cHLong anther length-CS56.99(22.67-87.87)15.7680.0705.324pW130cELong anther length-CL86.82(72.87-84.82)12.707-0.0534.886fito101b###Long anther length-CL86.82(72.87-84.82)12.707-0.0534.886fito348Petal claw-CL47.23(36.96-56.99)26.0900.10910.685fito348Petal claw-CL47.23(36.96-56.99)26.0900.105pW108aHStem length-CL96.88(84.82-96.9)15.932-1.4756.010pW150cHDays to flowering-CS96.88(84.82-96.9)15.932-1.4756.010pW150cHStem length-CL96.88(84.82-96.9)15.932-1.4756.010pW150cHChromosome &11.943(0.01-25.18)19.053-0.0666.264BRM5006Style length-WL0.010.01-25.1819.053	Chromosome 7						
Style length-CL2.01 (0.01-17.3)13.5170.0584.928BRM5040Ovary length-CS47.23 (25.82-56.99)15.9170.1097.263fito348Short anther length-CL56.99 (43.23-74.23)13.3750.0633.980pW130cEShort filament length-CL86.82 (72.87-96.88)13.825-0.1667.501fito101bShort filament length-CL86.82 (72.87-96.88)13.825-0.1667.501fito101bLong anther length-CL86.82 (79.97-96.88)21.913-0.1209.005pX101cHLong anther length-CL86.82 (79.97-96.88)21.503-0.0888.428fito101b###Long anther length-CL84.82 (72.87-84.82)12.707-0.0534.886fito101bPetal claw-CS43.23 (36.96-56.99)21.8910.085fito348Petal claw-CL47.23 (36.96-56.99)24.563-1.9859.994pW130cHStem length-CL86.88 (84.82-96.9)12.932-0.14756.010pW150cHStem length-CS96.88 (84.82-96.9)12.932-0.14756.010pW150cHDays to flowering-CS96.88 (88.296.9)19.008-2.0529.320pW150cHCL/CS [†] WL/CS [†] Pistil exsertion-CL56.99 (33.79-72.87)14.5660.1156.810pW130cEPistil exsertion-CL56.99 (33.79-72.87)14.5660.1156.810pW146aHStyle length-WL0.01 (0.01-25.18)19.053-0.0666.264BRMS006Style length-WL0.01 (0.01-25.	Style length–CS	4.01 (0.01-17.3)	14.896	0.061	6.990	BRMS040	
$\begin{array}{llllllllllllllllllllllllllllllllllll$	Style length-CL	2.01 (0.01–17.3)	13.517	0.058	4.928	BRMS040	
Ovary length-WL40.96 (25.82-56.99)25.4840.1339.551itto348Short anther length-CL86.82 (72.87-96.88)13.825-0.1667.501fitto101bShort filament length-WL79.11 (70.08-96.82)21.913-0.1209.005pX101cHLong anther length-CS56.99 (42.96-70.87)15.7660.0705.324pW130cELong anther length-CS86.82 (79.91-96.88)21.503-0.0888.428fitt0101b###Long anther length-CL86.82 (79.91-96.88)21.503-0.0888.428fitt011b###Long anther length-CL84.82 (72.87-84.82)12.707-0.0534.886fitt0348Petal claw-CL47.23 (36.96-56.99)26.0900.10910.685fitt0348Petal claw-CL47.23 (36.96-56.99)24.563-1.9859.994pW150cHStem length-CL96.88 (84.82-96.9)15.932-1.4756.010pW150cHStem length-CL96.88 (84.82-96.9)15.932-1.4756.010pW150cHDays to flowering-CS96.88 (88.82-96.9)19.008-2.0529.300pW150cHDays to flowering-CS96.88 (88.82-96.9)19.008-2.0529.300pW130cHPistil exsertion-WL19.82 (16.01-30.62)16.8420.1066.175fitt0105Pistil exsertion-CL56.99 (33.79-72.87)14.5660.1156.810pW146aHStyle length-WL53.19 (31.18-57.19)16.734-0.0656.005pW245bXPistil exsertion-CL51.09 (Ovary length–CS	47.23 (25.82–56.99)	15.917	0.109	7.263	fito348	
Short fillment length-CL 50-59 (45.25–4.25) 13.575 0.065 3.590 pW100E Short filament length-CL 86.82 (72.87–96.88) 13.825 -0.166 7.501 fito101b Short filament length-CL 86.82 (72.87–96.82) 21.913 -0.120 9.005 pX101cH Long anther length-CL 86.82 (79.91–96.88) 21.503 -0.088 8.428 fito101b ###Long anther length-LC 86.82 (79.91–96.88) 21.503 -0.088 8.428 fito101b Petal claw-CS 43.23 (36.96–56.99) 21.891 0.085 7.034 fito348 Petal claw-CL 47.23 (36.96–56.99) 26.090 0.109 10.685 fito348 Petal claw-CL 47.23 (36.96–56.99) 24.563 -1.985 9.994 pW150cH Stem length-CL 96.88 (84.82–96.9) 24.563 -1.985 9.994 pW150cH Stem length-CL 96.88 (84.82–96.9) 24.563 -1.985 9.994 pW150cH Days to flowering-CS 96.88 (88.82–96.9) 19.008 -2.052 9.320 pW150cH CL/CS [†] WL/CS [†] Herkogamy-WL 19.43 (0.01–33.4) 12.736 0.081 4.134 pW200cX Pistil exsertion-WL 19.82 (16.01–30.62) 16.842 0.106 6.175 fito105 Style length-VL 90.91 (0.01–25.18) 19.053 -0.066 6.264 BRMS006 Style length-VL 53.19 (31.18–57.19) 14.197 -0.055 4.580 pW146aH Style length-WL 53.19 (31.18–57.19) 14.734 -0.056 6.005 pW245bX Petal blade-CS 51.04 (46.07–57.19) 17.594 -1.524 6.760 pW146aH Style length-VL 0.01 (0.01–25.18) 19.053 -0.066 6.264 BRMS006 Herkogamy-CL 0.01 (0.01–25.18) 19.673 -0.065 6.055 pW245bX Petal larea-CS 49.04 (46.07–57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 0.01 (0.01–25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 0.01 (0.01–25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 46.07 (34.07–57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CS 46.07 (34.07–57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 46.07 (34.07–57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 46.07 (34.07–57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 46.07 (34.07–57.19) 15.872	Ovary length–WL	40.96 (25.82–56.99)	25.484	0.133	9.551	fito348	
Short filament length UL 79.11 (70.08-96.82) 21.913 -0.120 9.005 PX101CH Long anther length-CL 86.82 (79.91-96.88) 21.503 -0.088 8.428 fito101b ###Long anther length-UL 86.82 (79.91-96.88) 21.503 -0.088 8.428 fito101b ###Long anther length-WL 84.82 (72.87-84.82) 12.707 -0.053 4.886 fito101b Petal claw-CS 43.23 (36.96-56.99) 21.891 0.085 7.034 fito348 Petal claw-UL 27.23 (36.96-56.99) 21.891 0.085 7.034 fito348 Petal claw-UL 47.23 (36.96-56.99) 24.563 -1.985 9.994 pW150cH Stem length-CL 96.88 (84.82-96.9) 24.563 -1.985 9.994 pW150cH Stem length-CL 96.88 (84.82-96.9) 19.008 -2.052 9.320 pW150cH Days to flowering-CS 96.88 (88.82-96.9) 19.008 -2.052 9.320 pW150cH Therkogamy-WL 19.43 (0.01-33.4) 12.736 0.081 4.134 pW200cX Pistil exsertion-WL 19.82 (16.01-30.62) 16.842 0.106 6.175 fito105 Pistil exsertion-CL 56.99 (33.79-72.87) 14.566 0.115 6.810 pW130cE Chromosome 8 Style length-VL 0.01 (0.01-25.18) 19.053 -0.066 6.264 BRMS006 Style length-VL 0.01 (0.01-25.18) 19.053 -0.065 6.005 pW245bX Petal blade-CS 51.04 (46.07-57.19) 14.197 -0.055 4.580 pW146aH Style length-VL 53.19 (31.18-57.19) 16.734 -0.065 6.005 pW245bX Petal blade-CS 51.04 (46.07-57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 0.01 (0.01-25.18) 17.33 -0.092 6.728 fito429 Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CL 46.07 (34.07-57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 46.07 (34.07-57.19) 17.133 -0.092 6.728 fito429 Herkogamy-CL 46.07 (34.07-57.19) 17.133 -0.092 6.728 fito429 Herkogamy-CL 46.07 (34.07-57.19) 15.446 -0.103 6.884 pW120cX Pistil exsertion-CL 57.19 (36.07-57.19) 15.446 -0.103 6.884 pW120cX	Short filament length-CL	36.99 (43.25–74.23) 86.82 (72.87–96.88)	13.375	-0.063	3.960 7 501	fito101b	
Long anther length-CS56.99 $(42.96-70.87)$ 15.768 0.070 5.324 $pW130cE$ Long anther length-CL86.82 $(79.91-96.88)$ 21.503 -0.088 8.428fito101b###Long anther length-WL84.82 $(72.87-84.82)$ 12.707 -0.053 4.886fito101bPetal claw-CS43.23 $(36.96-56.99)$ 21.891 0.085 7.034 fito348Petal claw-CL47.23 $(36.96-56.99)$ 26.090 0.109 10.685 fito348Petal claw-WL28.62 $(25.82-35.08)$ 16.987 0.075 7.190 $pW108aH$ Stem length-CL96.88 $(84.82-96.9)$ 15.932 -1.475 6.010 $pW150cH$ Days to flowering-CS96.88 $(88.82-96.9)$ 19.008 -2.052 9.320 $pW150cH$ Days to flowering-CS96.88 $(88.82-96.9)$ 19.008 -2.052 9.320 $pW150cH$ Days to flowering-CS96.88 $(88.82-96.9)$ 19.008 -2.052 9.320 $pW130cE$ Chromosome 85tyle length-VL 19.43 $(0.01-33.4)$ 12.736 0.016 6.175 fito105Pistil exsertion-CL56.99 $(33.79-72.87)$ 14.566 0.115 6.810 $pW130cE$ Chromosome 8Style length-WL 0.01 $(0.01-25.18)$ 19.053 -0.066 6.055 $pW245bX$ Petal lade-CS 51.04 $(46.07-57.19)$ 17.594 -1.524 6.760 $pW146aH$ Style leng	Short filament length–WL	79.11 (70.08–96.82)	21.913	-0.120	9.005	pX101cH	
Long anther length-CL 86.82 (79.91–96.88) 21.503 -0.088 8.428 fito101b###Long anther length-WL 84.82 (72.87–84.82) 12.707 -0.053 4.886 fito101bPetal claw-CS 43.23 (36.96–56.99) 21.891 0.085 7.034 fito348Petal claw-CL 47.23 (36.96–56.99) 26.090 0.109 10.685 fito348Petal claw-CL 47.23 (36.96–56.99) 24.563 -1.985 9.994 pW108aHStem length-CS 96.88 ($84.82-96.9$) 15.932 -1.475 6.010 pW150cHDays to flowering-CS 96.88 ($84.82-96.9$) 15.932 -1.475 6.010 pW150cHDays to flowering-CS 96.88 ($88.82-96.9$) 19.008 -2.052 9.320 pW150cH CL/CS^{\dagger} Pistil exsertion-WL 19.43 ($0.01-33.4$) 12.736 0.081 4.134 pW200cXPistil exsertion-CL 56.99 ($3.79-72.87$) 14.566 0.115 6.810 pW130cEChromosome 8Style length-WL 0.01 ($0.01-25.18$) 19.053 -0.066 6.264 BRMS006Style length-WL 51.04 ($46.07-57.19$) 27.502 -0.171 8.002 pW245bXPetal lade-CS 49.04 ($46.07-57.19$) 27.502 -0.171 8.002 pW245bXPetal area-CS 49.04 ($46.07-57.19$) 17.594 -1.524 6.760 pW146aHHerkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 $pW345bX$ Petal a	Long anther length-CS	56.99 (42.96-70.87)	15.768	0.070	5.324	pW130cE	
###Long anther length-WL 84.82 (72.87-84.82) 12.707 -0.053 4.886 fito101bPetal claw-CS 43.23 (36.96-56.99) 21.891 0.085 7.034 fito348Petal claw-UL 47.23 (36.96-56.99) 22.6090 0.109 10.685 fito348Petal claw-WL 28.62 (25.82-35.08) 16.987 0.075 7.190 pW108aHStem length-CL 96.88 (84.82-96.9) 24.563 -1.985 9.994 pW150cHDays to flowering-CS 96.88 (84.82-96.9) 15.932 -1.475 6.010 pW150cHDays to flowering-CS 96.88 (84.82-96.9) 19.008 -2.052 9.200 pW150cHPistil exsertion-WL 19.43 ($0.01-33.4$) 12.736 0.081 4.134 pW200cXPistil exsertion-CL 56.99 ($33.79-72.87$) 14.566 0.115 6.810 pW130cEChromosome δ Style length-WL 0.01 ($0.01-25.18$) 19.053 -0.066 6.264 BRMS006Style length-WL 53.19 ($31.18-57.19$) 16.734 -0.065 6.005 pW146aHStyle length-WL 53.19 ($31.08-57.19$) 22.502 -0.171 8.002 pW245bXPetal blade-CS 51.04 ($46.07-57.19$) 22.502 -0.171 8.002 pW146aHHerkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.687 BRMS006Herkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.687 BRMS006Herkogamy-CL 0.01 ($0.07-57.19$) 17.54	Long anther length-CL	86.82 (79.91–96.88)	21.503	-0.088	8.428	fito101b	
Petal claw-CS 43.23 (36.96-56.99) 21.891 0.085 7.034 fito348Petal claw-CL 47.23 (36.96-56.99) 26.090 0.109 10.685 fito348Petal claw-WL 28.62 (25.82-35.08) 16.987 0.075 7.190 pW108aHStem length-CS 96.88 (84.82-96.9) 24.563 -1.985 9.994 pW150cHDays to flowering-CS 96.88 (88.82-96.9) 15.932 -1.475 6.010 pW150cHDays to flowering-CS 96.88 (88.82-96.9) 19.008 -2.052 9.320 pW150cH CL/CS^{\dagger} WL/CS [†] Herkogamy-WL19.43 (0.01-33.4) 12.736 0.081 4.134 pW200cXPistil exsertion-WL19.43 (0.01-30.62) 16.842 0.106 6.175 fito105Pistil exsertion-CL 56.99 (33.79-72.87) 14.566 0.115 6.810 pW130cEChromosome 8Style length-WL 0.01 (0.01-25.18) 19.053 -0.066 6.264 BRMS006Style length-WL 51.19 ($46.07-57.19$) 17.594 -1.524 6.760 pW146aHStyle length-WL 53.19 ($31.18-57.19$) 16.734 -0.065 6.005 pW245bXPetal area-CS 49.04 ($46.07-57.19$) 17.594 -1.524 6.760 pW146aHHerkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.687 BRM5006Herkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.68	###Long anther length–WL	84.82 (72.87-84.82)	12.707	-0.053	4.886	fito101b	
Petal claw-CL 47.25 (36.96-36.99) 20.90 0.109 10.885 10.636 Petal claw-WL 28.62 (25.82-35.08) 16.987 0.075 7.190 $pW1108H$ Stem length-CS 96.88 (84.82-96.9) 24.563 -1.985 9.994 $pW150cH$ Days to flowering-CS 96.88 (88.82-96.9) 19.008 -2.052 9.320 $pW150cH$ $CL/CS^{\ddagger} WL/CS^{\dagger}$ Herkogamy-WL 19.43 (0.01-33.4) 12.736 0.081 4.134 $pW200cX$ Pistil exsertion-WL 19.42 (16.01-30.62) 16.842 0.106 6.175 fito105Pistil exsertion-CL 56.99 (33.79-72.87) 14.566 0.115 6.810 $pW130cE$ Chromosome 8Style length-WL 0.01 ($0.01-25.18$) 19.053 -0.066 6.264 $BRMS006$ Style length-WL 53.19 ($31.18-57.19$) 14.197 -0.055 4.580 $pW146aH$ Style length-WL 53.19 ($31.18-57.19$) 16.734 -0.065 6.005 $pW245bX$ Petal blade-CS 51.04 ($46.07-57.19$) 27.502 -0.171 8.002 $pW245bX$ Petal area-CS 49.04 ($46.07-57.19$) 17.534 -7.660 $pW146aH$ Herkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.687 $BRMS006$ Herkogamy-CL 0.01 ($0.01-757.19$) 17.534 -7.660 $pW146aH$ Herkogamy-CL 46.07 ($34.07-57.19$) 17.9	Petal claw-CS	43.23 (36.96–56.99)	21.891	0.085	7.034	fito348	
Tetal traw-WL20.02 ($2.02-05.00^{\circ}$)10.05 -1.190° pW10011Stem length-CS96.88 ($84.82-96.9$)24.563 -1.985° 9.94pW150cHDays to flowering-CS96.88 ($84.82-96.9$)15.932 -1.475° 6.010pW150cHDays to flowering-CS96.88 ($84.82-96.9$)19.008 -2.052° 9.320pW150cHCL/CS [‡] WL/CS [†] Herkogamy-WL19.43 ($0.01-33.4$)12.736 0.081° 4.134pW200cXPistil exsertion-WL19.82 ($16.01-30.62$) 16.842° 0.106° 6.175° fito105Pistil exsertion-CL56.99 ($33.79-72.87$)14.566 0.115° 6.810° pW130cEChromosome 8Style length-CL49.04 ($46.23-57.19$)14.197^{\circ} -0.055° 4.580^{\circ}pW146aHStyle length-CL49.04 ($46.07-57.19$)12.502^{\circ} -0.171° 8.002° pW245bXPetal blade-CS51.04 ($46.07-57.19$)17.534^{\circ} -0.065° 6.05° pW146aHHerkogamy-CL0.01 ($0.01-25.18$)13.657^{\circ} 0.100° 5.687° BRMS006Herkogamy-CL0.01 ($0.01-25.18$)13.657^{\circ} 0.100° 5.687° BRMS006Herkogamy-CL46.07 ($34.07-57.19$)17.133^{\circ} -0.092° 6.728° fito429Herkogamy-CL46.07 ($34.07-57.19$)17.916^{\circ} -0.103° 6.884° pW120cXPistil exsertion-CL51.19 ($42.07-57.19$)23.714^{\circ} -0.155° 12.526°	Petal claw-CL Potal claw, WI	47.23 (36.96-56.99)	26.090 16.987	0.109	10.685	fit0348	
Stem length-CL96.88 (84.82-96.9)15.932 -1.475 6.010 pW150cHDays to flowering-CS96.88 (84.82-96.9)19.008 -2.052 9.320pW150cH CL/CS^{\ddagger} WL/CS [†] Herkogamy-WL19.43 (0.01-33.4)12.7360.0814.134pW200cXPistil exsertion-WL19.82 (16.01-30.62)16.8420.1066.175fito105Pistil exsertion-CL56.99 (33.79-72.87)14.5660.1156.810pW130cEChromosome 8Style length-WL0.01 (0.01-25.18)19.053 -0.066 6.264BRMS006Style length-CL49.04 (46.23-57.19)14.197 -0.055 4.580pW146aHStyle length-CL49.04 (46.23-57.19)14.197 -0.055 4.580pW245bXPetal blade-CS51.04 (46.07-57.19)22.502 -0.171 8.002pW245bXPetal area-CS49.04 (46.07-57.19)17.594 -1.524 6.760pW146aHHerkogamy-CL0.01 (0.01-25.18)13.6570.1005.687BRMS006Herkogamy-CS46.07 (34.07-57.19)17.133 -0.092 6.728fito429Herkogamy-CL46.07 (34.07-57.19)17.916 -0.114 7.770fito429Pistil exsertion-CS57.19 (34.07-57.19)13.446 -0.103 6.884pW120cXPistil exsertion-WL57.19 (36.07-57.19)15.872 -0.099 6.015pW245bX	Stem length_CS	26.62 (25.62–55.66) 96.88 (84.82–96.9)	24 563	-1.985	9 994	pW100a11 pW150cH	
Days to flowering-CS96.88 (88.82–96.9)19.008 -2.052 9.320PW150cH $CL/CS^{\ddagger} WL/CS^{\ddagger}$ Herkogamy-WL19.43 (0.01–33.4)12.7360.0814.134pW200cXPistil exsertion-WL19.82 (16.01–30.62)16.8420.1066.175fito105Pistil exsertion-CL56.99 (33.79–72.87)14.5660.1156.810pW130cEChromosome 8Style length-WL0.01 (0.01–25.18)19.053 -0.066 6.264BRMS006Style length-WL53.19 (31.18–57.19)14.197 -0.055 4.580pW146aHStyle length-WL53.19 (31.18–57.19)16.734 -0.065 6.005pW245bXPetal blade-CS51.04 (46.07–57.19)22.502 -0.171 8.002pW245bXPetal area-CS49.04 (46.07–57.19)17.594 -1.524 6.760pW146aHHerkogamy-CL0.01 (0.01–25.18)13.6570.1005.687BRMS006Herkogamy-CL0.01 (0.01–25.19)17.133 -0.092 6.728fito429Herkogamy-CL46.07 (34.07–57.19)17.133 -0.092 6.728fito429Herkogamy-CL46.07 (34.07–57.19)15.446 -0.103 6.884pW120cXPistil exsertion-CS57.19 (34.07–57.19)23.714 -0.155 12.526pW245bXPistil exsertion-WL57.19 (36.07–57.19)15.872 -0.099 6.015pW120cX	Stem length–CL	96.88 (84.82–96.9)	15.932	-1.475	6.010	pW150cH	
Herkogamy-WL19.43 $(0.01-33.4)$ 12.7360.0814.134pW200cXPistil exsertion-WL19.82 $(16.01-30.62)$ 16.8420.1066.175fito105Pistil exsertion-CL56.99 $(33.79-72.87)$ 14.5660.1156.810pW130cEChromosome 8Style length-WL0.01 $(0.01-25.18)$ 19.053-0.0666.264BRMS006Style length-CL49.04 $(46.23-57.19)$ 14.197-0.0554.580pW146aHStyle length-WL53.19 $(31.18-57.19)$ 16.734-0.0656.005pW245bXPetal blade-CS51.04 $(46.07-57.19)$ 22.502-0.1718.002pW245bXPetal area-CS49.04 $(46.07-57.19)$ 17.594-1.5246.760pW146aHHerkogamy-CL0.01 $(0.01-25.18)$ 13.6570.1005.687BRMS006Herkogamy-CL0.01 $(0.01-25.18)$ 13.6570.1005.687BRMS006Herkogamy-CL0.01 $(0.01-25.18)$ 13.6570.1005.687BRMS006Herkogamy-CS46.07 $(34.07-57.19)$ 17.133-0.0926.728fito429Herkogamy-CL46.07 $(34.07-57.19)$ 15.446-0.1036.884pW120cXPistil exsertion-CS57.19 $(34.07-57.19)$ 23.714-0.15512.526pW245bXPistil exsertion-CL51.19 $(42.07-57.19)$ 13.872-0.0996.015pW120cX	Days to flowering-CS	96.88 (88.82–96.9)	19.008	-2.052	9.320	pW150cH	$CL/CS^{\ddagger}WL/CS^{\dagger}$
Pistil exsertion-WL19.82 (16.01-30.62)16.8420.106 6.175 fito105Pistil exsertion-CL56.99 (33.79-72.87)14.5660.115 6.810 pW130cEChromosome 8Style length-WL0.01 (0.01-25.18)19.053 -0.066 6.264 BRMS006Style length-CL49.04 (46.23-57.19)14.197 -0.055 4.580 pW146aHStyle length-WL53.19 (31.18-57.19)16.734 -0.065 6.005 pW245bXPetal blade-CS51.04 (46.07-57.19)22.502 -0.171 8.002 pW245bXPetal area-CS49.04 (46.07-57.19)17.594 -1.524 6.760 pW146aHHerkogamy-CL0.01 (0.01-25.18)13.6570.1005.687BRMS006Herkogamy-CS46.07 (34.07-57.19)17.133 -0.092 6.728 fito429Herkogamy-CL46.07 (34.07-57.19)17.916 -0.114 7.770 fito429Pistil exsertion-CS57.19 (34.07-57.19)15.446 -0.103 6.884 pW120cXPistil exsertion-WL57.19 (36.07-57.19)15.872 -0.099 6.015 pW120cX	Herkogamy–WL	19.43 (0.01–33.4)	12.736	0.081	4.134	pW200cX	
Pistil exsertion-CL 56.99 (33.79-72.87) 14.566 0.115 6.810 pW130CE Chromosome 8 Style length-WL 0.01 (0.01-25.18) 19.053 -0.066 6.264 BRMS006 Style length-CL 49.04 (46.23-57.19) 14.197 -0.055 4.580 pW146aH Style length-WL 53.19 (31.18-57.19) 16.734 -0.065 6.005 pW245bX Petal blade-CS 51.04 (46.07-57.19) 22.502 -0.171 8.002 pW245bX Petal area-CS 49.04 (46.07-57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CS 46.07 (34.07-57.19) 17.133 -0.092 6.728 fito429 Herkogamy-CL 46.07 (34.07-57.19) 17.916 -0.114 7.770 fito429 Pistil exsertion-CS 57.19 (34.07-57.19) 15.446 -0.103 6.884 pW120cX Pistil exsertion-WL 57.19 (36.07-57.19) 13.872 -0.099 6.015 pW120cX	Pistil exsertion–WL	19.82 (16.01–30.62)	16.842	0.106	6.175	fito105	
Chromosome 8Style length-WL $0.01 (0.01-25.18)$ $19.053 -0.066$ 6.264 BRMS006Style length-CL $49.04 (46.23-57.19)$ $14.197 -0.055$ 4.580 $pW146aH$ Style length-WL $53.19 (31.18-57.19)$ $16.734 -0.065$ 6.005 $pW245bX$ Petal blade-CS $51.04 (46.07-57.19)$ $22.502 -0.171$ 8.002 $pW245bX$ Petal area-CS $49.04 (46.07-57.19)$ $17.594 -1.524$ 6.760 $pW146aH$ Herkogamy-CL $0.01 (0.01-25.18)$ $13.657 -0.100$ 5.687 BRMS006Herkogamy-CS $46.07 (34.07-57.19)$ $17.133 -0.092$ 6.728 fito429Herkogamy-CL $46.07 (34.07-57.19)$ $15.446 -0.103$ 6.884 $pW120cX$ Pistil exsertion-CL $51.19 (42.07-57.19)$ $23.714 -0.155$ 12.526 $pW245bX$ Pistil exsertion-WL $57.19 (36.07-57.19)$ $15.872 -0.099$ 6.015 $pW120cX$	Pistil exsertion-CL	56.99 (33.79-72.87)	14.566	0.115	6.810	pW130cE	
Style length=VVL $0.01 (0.01-25.18)$ $19.053 -0.066$ 6.264 BKM5006Style length=CL $49.04 (46.23-57.19)$ $14.197 -0.055$ 4.580 $pW146aH$ Style length=WL $53.19 (31.18-57.19)$ $16.734 -0.065$ 6.005 $pW245bX$ Petal blade=CS $51.04 (46.07-57.19)$ $22.502 -0.171$ 8.002 $pW245bX$ Petal area=CS $49.04 (46.07-57.19)$ $17.594 -1.524$ 6.760 $pW146aH$ Herkogamy=CL $0.01 (0.01-25.18)$ $13.657 -0.100$ 5.687 BRM5006Herkogamy=CS $46.07 (34.07-57.19)$ $17.133 -0.092$ 6.728 fito429Herkogamy=CL $46.07 (34.07-57.19)$ $15.446 -0.103$ 6.884 $pW120cX$ Pistil exsertion=CS $57.19 (34.07-57.19)$ $15.446 -0.103$ 6.884 $pW120cX$ Pistil exsertion=WL $57.19 (36.07-57.19)$ $15.872 -0.099$ 6.015 $pW120cX$	Chromosome 8		10.052	0.077	()()	DDMCOOL	
Style length-WL 53.19 ($31.18-57.19$) 14.127 -0.005 4.500 $pW140a11$ Style length-WL 53.19 ($31.18-57.19$) 16.734 -0.065 6.005 $pW245bX$ Petal blade-CS 51.04 ($46.07-57.19$) 22.502 -0.171 8.002 $pW245bX$ Petal area-CS 49.04 ($46.07-57.19$) 17.594 -1.524 6.760 $pW146aH$ Herkogamy-CL 0.01 ($0.01-25.18$) 13.657 0.100 5.687 BRM5006Herkogamy-CS 46.07 ($34.07-57.19$) 17.133 -0.092 6.728 fito429Pistil exsertion-CS 57.19 ($34.07-57.19$) 15.446 -0.103 6.884 $pW120cX$ Pistil exsertion-CL 51.19 ($42.07-57.19$) 23.714 -0.155 12.526 $pW245bX$ Pistil exsertion-WL 57.19 ($36.07-57.19$) 15.872 -0.099 6.015 $pW120cX$	Style length-WL	0.01 (0.01-25.18)	19.053 14 107	-0.066	6.264 4 580	DKW5006	
Petal blade-CS 51.04 (46.07-57.19) 22.502 -0.171 8.002 pW245bX Petal area-CS 49.04 (46.07-57.19) 17.594 -1.524 6.760 pW146aH Herkogamy-CL 0.01 (0.01-25.18) 13.657 0.100 5.687 BRMS006 Herkogamy-CS 46.07 (34.07-57.19) 17.133 -0.092 6.728 fito429 Pistil exsertion-CS 57.19 (34.07-57.19) 17.916 -0.114 7.770 fito429 Pistil exsertion-CL 51.19 (42.07-57.19) 15.446 -0.103 6.884 pW120cX Pistil exsertion-WL 57.19 (36.07-57.19) 15.872 -0.099 6.015 pW245bX	Style length–WL	53.19 (31.18-57.19)	16.734	-0.055 -0.065	6.005	pW245hX	
Petal area-CS49.04 (46.07-57.19)17.594-1.5246.760pW146aHHerkogamy-CL0.01 (0.01-25.18)13.6570.1005.687BRMS006Herkogamy-CS46.07 (34.07-57.19)17.133-0.0926.728fito429Herkogamy-CL46.07 (34.07-57.19)17.916-0.1147.770fito429Pistil exsertion-CS57.19 (34.07-57.19)15.446-0.1036.884pW120cXPistil exsertion-CL51.19 (42.07-57.19)23.714-0.15512.526pW245bXPistil exsertion-WL57.19 (36.07-57.19)15.872-0.0996.015pW120cX	Petal blade–CS	51.04 (46.07–57.19)	22.502	-0.171	8.002	pW245bX	
Herkogamy-CL0.01 (0.01-25.18)13.6570.1005.687BRMS006Herkogamy-CS46.07 (34.07-57.19)17.133-0.0926.728fito429Herkogamy-CL46.07 (34.07-57.19)17.916-0.1147.770fito429Pistil exsertion-CS57.19 (34.07-57.19)15.446-0.1036.884pW120cXPistil exsertion-CL51.19 (42.07-57.19)23.714-0.15512.526pW245bXPistil exsertion-WL57.19 (36.07-57.19)15.872-0.0996.015pW120cX	Petal area–CS	49.04 (46.07-57.19)	17.594	-1.524	6.760	pW146aH	
Herkogamy-CS46.07 (34.07-57.19)17.133-0.0926.728fito429Herkogamy-CL46.07 (34.07-57.19)17.916-0.1147.770fito429Pistil exsertion-CS57.19 (34.07-57.19)15.446-0.1036.884pW120cXPistil exsertion-CL51.19 (42.07-57.19)23.714-0.15512.526pW245bXPistil exsertion-WL57.19 (36.07-57.19)15.872-0.0996.015pW120cX	Herkogamy–CL	0.01 (0.01–25.18)	13.657	0.100	5.687	BRMS006	
Herkogamy-CL 46.0/ (34.07-57.19) 17.916 -0.114 7.770 fito429 Pistil exsertion-CS 57.19 (34.07-57.19) 15.446 -0.103 6.884 pW120cX Pistil exsertion-CL 51.19 (42.07-57.19) 23.714 -0.155 12.526 pW245bX Pistil exsertion-WL 57.19 (36.07-57.19) 15.872 -0.099 6.015 pW120cX	Herkogamy–CS	46.07 (34.07–57.19)	17.133	-0.092	6.728	fito429	
Pistil exsertion-CL 57.19 (94.07-57.19) 13.440 -0.105 0.804 pW120CX Pistil exsertion-CL 51.19 (42.07-57.19) 23.714 -0.155 12.526 pW245bX Pistil exsertion-WL 57.19 (36.07-57.19) 15.872 -0.099 6.015 pW120CX	Herkogamy–CL Bistil execution	46.07 (34.07-57.19)	17.916	-0.114	7.770	tito429	
Pistil exsertion–WL 57.19 (36.07–57.19) 15.872 –0.099 6.015 pW120cX	Pistil exsertion-CS	57.19 (34.07-37.19) 51 19 (42 07-57 19)	13.440 23.714	-0.103 -0.155	0.004	pw120cA pW245bX	
•	Pistil exsertion–WL	57.19 (36.07–57.19)	15.872	-0.099	6.015	pW120cX	

(Continued)						
Trait-treatment	Position in cM (2-LOD intervals)	LR	Additive effect	% Variance explained	Closest marker	QTL that demonstrate significant $QTL \times E$ across treatment pairs
Chromosome 9						
Ovary length–CL	36.64 (22.46-39.31)	13.365	-0.136	5.223	pW188cE	
Ovary length–CS	72.45 (69.65–76.89)	21.745	-0.175	8.779	pX119bX	
Ovary length–CL	72.45 (67.65–76.89)	15.395	-0.154	6.251	pX119bX	
Ovary length–CL	100.29 (91.38-107.79)	14.652	-0.138	5.789	pW246cX	
Short filament length–WL	14.46 (0.01-23.46)	19.844	-0.118	8.727	pX123dH	
Long filament length-WL	12.46 (0.01-23.46)	13.254	-0.097	4.874	pX123dH	
Long filament length-CS	72.45 (61.71-85.38)	13.388	-0.113	5.510	pX119bX	
Long filament length-WL	85.13 (74.89-89.38)	37.831	-0.165	14.533	fito151a	
Petal claw–CS	2.01 (0.01-23.46)	15.139	-0.070	5.018	fito097b	
Petal claw–CL	8.01 (0.01-23.46)	13.419	-0.075	5.146	pX123dH	
###Petal claw-WL	10.46 (0.01-23.46)	12.774	-0.062	4.879	pX123dH	
Petal claw–CS	91.38 (78.89-100.29)	23.582	-0.092	8.970	fito151a	
Petal claw–CL	95.38 (78.89-100.29)	15.779	-0.082	6.592	pW246cX	
Petal claw–WL	89.38 (72.89-100.29)	18.244	-0.081	8.260	fito151a	
###Stem length-CS	23.46 (10.01-35.52)	12.195	-1.491	4.791	pX123dH	
Stem length–WL	23.46 (10.01-35.52)	13.966	-1.253	4.370	pX123dH	
Stem length-CL	89.38 (72.89-100.29)	13.080	-1.332	5.504	fito151a	
Days to flowering–WL	61.57 (53.24-72.45)	13.934	-1.438	5.047	fito100b	
Collection interval-CS	37.31 (23.46-48.43)	15.106	0.490	7.626	pW130cX	
Collection interval-CL	25.46 (22.46-48.74)	14.275	0.489	8.919	pX123dH	
Herkogamy–WL	34.96 (22.46-37.31)	13.421	-0.109	4.674	BRMS016	
Stamen exsertion-WL	22.46 (10.01-35.52)	14.400	-0.060	5.565	pX123dH	
Stamen exsertion–WL	93.38 (85.13-100.29)	21.824	-0.082	11.276	pW246cX	
Pistil exsertion-WL	36.64 (22.46–48.43)	17.156	-0.106	6.684	pW188cE	
Chromosome 10						
Ovary length–CL	72.54 (61.1–90.55)	16.635	0.119	6.517	pW120aX	
Flowers aborted–CS	51.25 (42.79–51.83)	18.311	0.491	9.354	pW256aE	
Flowers aborted-WL	51.25 (44.79–51.83)	19.488	0.514	10.862	pW256aE	
Stem length–WL	50.79 (20.94–59.1)	14.568	-1.350	4.743	pW255aE	WL/CL^{\dagger}
Days to flowering–CL	70.54 (52.39-84.55)	15.355	-1.552	7.304	fito520a	
Days to flowering–WL	51.83 (38.94–53.1)	32.071	-2.127	12.489	pW174aX	
Collection interval–CS	16.01 (0.01–38.94)	17.460	0.586	10.471	pX139cH	
Collection interval–CL	20.94 (0.01-42.79)	12.981	0.449	7.347	FLC1aE	
Collection interval-WL	22.94 (2.01-40.94)	28.733	0.539	16.509	FLC1aE	
Herkogamy–CS	70.54 (61.1-88.55)	14.427	0.085	5.521	fito520a	
Herkogamy–WL	72.54 (62.04–94.55)	14.833	0.087	4.835	pW120aX	

Abbreviations: CL, cool temperature long photoperiod; CS cool temperature short photoperiod; WL, warm temperature long photoperiod.

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