Genome-wide estimation of heritability and its functional components for flowering, defense, ionomics and developmental traits in a geographically diverse population of *Arabidopsis thaliana*

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Genome-wide estimation of heritability and its functional components for flowering, defense, ionomics and developmental traits in a geographically diverse population of

Arabidopsis thaliana

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Abstract

Narrow-sense heritability (portion of the total phenotypic variation due to additive genetic effect, h^2) is a critical parameter in plant breeding and genetics, but its estimation is difficult for populations with unknown pedigree information. This study applied a marker-based linear mixed model (LMM) analysis to estimate narrow-sense heritability and its seven functional components corresponding to SNPs in coding and noncoding regions for each of 107 flowering, defense, ionomics and developmental traits in an *Arabidopsis* (*Arabidopsis thaliana*) population of 199 inbred lines with unknown genetic relatedness. Genetic relationship matrix (GRM) based on 214,051 SNPs and component GRMs based on seven subsets of SNPs were computed for LMM estimation of h^2 and functional components contributing to h^2 , respectively. The h^2 estimates for flowering traits were higher than those for defense, ionomics and developmental traits, supporting a general view that the fitness-related traits have lower heritabilities than other traits. The function component due to SNPs in coding (exon) regions was the least contributor to h^2 . Our LMM analysis provides an opportunity to gain a comprehensive view on heritability and its functional components for populations with unknown structure but with genome-wide DNA markers.

Keywords: heritability, additive genetic variance, *Arabidopsis*, statistical genomics

Introduction

Since Fisher (1930) proposed Fundamental Theorem of Natural Selection (i.e., "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time."), it has been generally accepted that the fitness-associated traits have lower heritabilities than those being less associated with fitness. Empirical support for this view has come from several surveys on heritabilities estimated for fitness-related and other traits using classic quantitative genetic methods (Falconer and Mackay 1996; Lynch and Walsh 1998; Mousseau and Roff 1987; Visscher et al. 2008). Recent intensive efforts on genome-wide association studies (GWAS) have enabled identification of numerous DNA markers (particularly single nucleotide polymorphisms, SNPs) as causal variants of quantitative traits in plant and animal species or complex diseases in humans. Quite often, however, these GWAS-identified causal variants collectively account for only a small amount of the total (additive) genetic variation, a phenomenon known as 'missing heritability' (Visscher et al. 2008). This phenomenon has been recently discussed and debated in the literature (Maher 2008; Manolio et al. 2009; Zaitlen and Kraft 2012; Zuk et al. 2012).

The traditional quantitative genetic approach to estimating the heritability is based on the genetic relatedness that is known from a mating design or inferred from a general pedigree (Kruuk et al. 2008; Thomas 2005). Such information may be readily available in laboratory animals or controlled experimental populations but it is generally unknown in unmanaged or natural populations. Since Ritland (1996), use of DNA markers has been made to infer genetic relatedness between pairs of individuals, relying on the fact that related individuals tend to share more marker alleles than unrelated individuals in a population. Thus, just like the classic method

of estimating the heritability based on the regression of phenotypic similarity on the genetic relatedness inferred from the pedigree information (Falconer and Mackay 1996; Lynch and Walsh 1998), a more generalized version of the regression under a linear mixed model (LMM) or a Bayesian framework estimates heritability and other quantitative genetic parameters with the unknown pedigree-based relationship being replaced by the marker-based relationship in the mixed-model equations (Hu and Yang 2014; Xu and Hu 2010; Yang et al. 2010).

Recent advances in genomics have raised the possibility that heritability can be further dissected by estimating individual components due to functional categories of SNPs across the genome (Gusev et al. 2014). The empirical distribution of GWAS hits in humans suggests that 11% of causal variants lie within coding regions and 57% are in the noncoding regions known as DNaseI hypersensitivity sites (DHSs) spanning 42% of the genome (Hindorff et al. 2009). Gusev et al. (2014) took this idea further by partitioning heritability into components due to different functional groups of SNPs in coding and noncoding regions. Such partitioning was carried out for 11 human disease traits; on average, genotyped SNPs in the DHS regions accounted for nearly 40% of heritability while imputed SNPs in the same regions accounted for the doubled amount at 79% of heritability for individual traits. In contrast, coding SNP variants contributed only <10% to heritability despite the highest GWAS hits. Similar analysis should be possible in plant and animal species as well, because genotyped or imputed sequence variants for a large number of individuals are now becoming increasingly available.

Model plant *Arabidopsis* (*Arabidopsis thaliana*) is a widely distributed, predominantly self-pollinated species with considerable genetic variation for many traits of adaptive or fitness importance (Koornneef et al. 2004). A recent comprehensive GWAS study on 107 flowering,

defense, ionomics and developmental traits by Atwell et al. (2010) showed a markedly different pattern of genetic variation from those of human GWAS studies: many common SNP alleles of major effect were statistically declared, but they may still be false positives because confounding may arise from complex genetics and population structure inherent in the study population consisting of a world-wide collection of *Arabidopsis* ecotypes or inbred lines. Atwell et al. (2010, Supplementary Table 7) did estimate broad-sense heritability for the 107 traits (reproduced in Table 1 of the present study), but the estimates for 32 of the 107 traits were not made due to lack of replicated measurements or use of a less flexible statistical method (i.e., traditional analysis of variance). More importantly, broad-sense heritability does not distinguish between additive vs. non-additive genetic variances. Furthermore, just like in human studies (Finucane et al. 2015; Gusev et al. 2014), there is a need for partitioning the narrow-sense heritability (due to additive genetic variation) into components by different functional groups of SNP variants across the genome. The objectives of the present study were (i) to investigate patterns of genome-wide estimates of narrow-sense heritability for different groups of traits with varying degrees of relation to fitness, and (ii) partition the narrow-sense heritability into components due different functional groups of SNP markers by gene annotation.

Materials and methods

The Arabidopsis data

The phenotypic and genotypic data used in this study were taken from the Arabidopsis thaliana polymorphism database (AtPolyDB) as deposited at the github repository of the Gregor Mendel Institute (<https://github.com/Gregor-Mendel-Institute/atpolydb>). While the data set was described in detail elsewhere (Atwell et al. 2010; Horton et al. 2012), we recapture its essential details here. The data set is a world-wide collection of 199 ecotypes or inbred lines of *A. thaliana* from 29 countries, now with the geographic (latitude and longitude) information being added (Table S1). Five countries that were represented most frequently in this collection are Sweden (49), Germany (30), Czech Republic (24), United States (16) and United Kingdom (12). All the 199 ecotypes or inbred lines in the collection were genotyped by using a custom Affymetrix 250K SNP-tiling array (AtSNPtile1) with a total of 248,584 possible SNPs (Kim et al. 2007). Following the same data quality control protocol as described in Horton et al. (2012), we retained a list of 214,051 SNPs for each of the 199 inbred lines for subsequent analyses.

According to Atwell et al. (2010), the inbred lines were phenotyped for a total of 107 traits belonging to four broadly defined groups (Table 1): (i) 23 flowering-related traits assessed under different controlled environmental conditions; (ii) 23 defense-related traits with a wide range of responses to pest infestation, from recognition of specific bacterial strains to trichome density; (iii) 18 ionomics traits measured in element concentrations using inductively coupled plasma mass spectroscopy; and (iv) 43 developmental traits including measurements at different plant growth stages such as dormancy and plant senescence. The trait evaluation was done

through different common garden experiments as detailed in Supplementary tables 2-5 of Atwell et al. (2010). As the phenotypic data were assembled from different studies for different traits and with different requirements for sample sizes, the actual sample sizes varied from 76 to 194 inbred lines, depending on the traits.

Functional annotations

The list of 214,501 SNPs described above were annotated based on their physical locations at the Arabidopsis genome by using SnpEff 4.1, an open-source, platform-independent free software for rapid genome-wide categorization of SNP variants (Cingolani et al. 2012). We (Peng et al. 2015, 2016) recently used the same procedure to annotate flowering-related genes in Arabidopsis and cereal crop plants. To run SnpEff, an input variant file was first prepared using the sequencing information available from the Arabidopsis Information Resource (TAIR10) (Berardini et al. 2015). The genomic information including the gene names and functional groups was extracted from the TAIR10 database and saved in the annotation format GFF (version 3) for the SnpEff analysis. The SnpEff then loaded the compressed input file and built a data structure known as “interval forest” for an efficient interval search. The SnpEff analysis allowed each SNP variant to query the data structures to detect intersecting genomic functional annotations. Such search led to the assignment of all SNP variants into distinct functional groups. A total of 34 distinct functional groups were identified according to the TAIR10 detailed annotations, but they were consolidated into seven groups (Table 2) because many TAIR10 groups had too few SNPs to construct a reliable genetic relationship matrix (GRM) for the LMM

analysis (see below for detailed description of the LMM analysis). Our consolidated groups were determined similarly as those by Gusev et al. (2014).

Marker-based estimation of heritability and its functional components

For each trait, a vector of phenotypic values ($\mathbf{y}$) for n (< 199) inbred lines each with an array of $m = 214,051$ diallelic SNP markers were analyzed using the following LMM model (Hu and Yang 2014; Yang et al. 2010),

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{W}\mathbf{u} + \mathbf{e} \quad . \quad (1)$$

In eq. (1), μ is the overall mean with $\mathbf{1}$ being a vector of n ones; $\mathbf{W}$ is an $n \times m$ standardized genotype matrix with its il th element being $w_{il} = (z_{il} - \hat{p}_l) / \sqrt{\hat{p}_l(1 - \hat{p}_l)}$, the original indicator variable z_{il} being 1 for the reference homozygote and 0 for the alternative homozygote, and $\hat{p}_l$ being the estimated frequency of the reference homozygote at the l th locus; $\mathbf{u}$ is a vector of m random SNP effects that are taken from a standard multivariate normal distribution

$\mathbf{u} \sim N(\mathbf{0}, \mathbf{I}_m \sigma_u^2)$; and $\mathbf{e}$ is a vector of n residual effects taken from a multivariate normal

distribution $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}_n \sigma_e^2)$. An alternative and equivalent form of model (1) is as follows,

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{a} + \mathbf{e} , \quad (2)$$

where $\mathbf{a} = \mathbf{W}\mathbf{u}$ is a $n \times 1$ vector of genome-wide additive genetic effects that are taken from a multivariate normal distribution, $\mathbf{a} \sim N(\mathbf{0}, \mathbf{G}\sigma_a^2)$ with the GRM $\mathbf{G}$ being estimated by

$\hat{\mathbf{G}} = \mathbf{W}\mathbf{W}'/m$ and additive genetic variance being given by $\sigma_a^2 = m\sigma_u^2$. Since there was no

pedigree information on the inbred lines, we used genome-wide SNP markers to estimate the

GRM for the LMM analysis. Thus, the estimated GRM would consist of the realized kinship values averaged over all loci in the entire genome for all pairs of inbred lines. With the high marker density, the realized kinship values would adequately comply with the infinitesimal model of genetic effects implicit in the LMM equation (Xu and Hu 2010).

For convenience, data transformation to each phenotypic value was made by dividing each mean-corrected phenotypic value by its standard deviation, i.e.,

$$y'_i = (y_i - \mu) / \sigma_p = a_i / \sigma_p + e_i / \sigma_p = a'_i + e'_i. \quad (3)$$

Obviously, the narrow-sense heritability was directly estimated as the additive genetic variance on the transformed data $[\sigma_{a'}^2 = \sigma_a^2 / \sigma_p^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2) = h^2]$.

The LMM model in eq. (1) and eq. (2) was for a single additive genetic variance due to the cumulative effects of all SNPs across the Arabidopsis genome. Following Gusev et al. (2014), this analysis was extended to partition the total additive genetic variance (and thus the narrow-sense heritability) into components due to the cumulative effects of SNPs belonging to different functional groups across the genome. With this partitioning, all variance components would be able to compete for the total additive genetic variance due to linkage disequilibria (LDs) of SNPs. For the seven functional groups identified in Table 2, we analyzed the phenotypic values for each trait as follows,

$$\mathbf{y} = \mathbf{1}\mu + \sum_{t=1}^7 \mathbf{W}_t \mathbf{u}_t + \mathbf{e} = \mathbf{1}\mu + \sum_{t=1}^7 \mathbf{a}_t + \mathbf{e}, \quad (4)$$

where $\mathbf{W}_t$, $\mathbf{u}_t$, and $\mathbf{a}_t$ are defined in the same way as $\mathbf{W}$, $\mathbf{u}$ and $\mathbf{a}$ but with the subscript t in each matrix indexing for the t th functional group. Consequently, the total additive genetic variance would be partitioned as follows,

$$\text{Var}(\mathbf{a}) = \mathbf{G}\sigma_a^2 = \sum_{t=1}^7 \mathbf{G}_t \sigma_{a(t)}^2 = \sum_{t=1}^7 (\mathbf{W}_t \mathbf{W}_t' / m_t) (m_t \sigma_{u(t)}^2) \quad (5)$$

where m_t is the number of SNPs belonging to the t th functional group. Just like the GRM for all SNP markers ($\mathbf{G}$) described above, the GRM for the t th functional group ($\mathbf{G}_t$) was not obtainable directly due to lack of pedigree information on the inbred lines, but it was estimated using genome-wide SNP markers belonging to the t th functional group. Separate realized kinship matrices for individual functional groups would provide an opportunity for heritability enrichment when the distribution of genome-wide marker effects for a given trait is deviated from the infinitesimal model (Gusev et al. 2014; Xu and Hu 2010). Since the phenotypic values were normalized, each component would estimate the heritability due to that component,

$$\sigma_{a(t)}^2 = \frac{\sigma_{a(t)}^2}{\sigma_p^2} = \frac{\sigma_{a(t)}^2}{\sum_{t=1}^7 \sigma_{a(t)}^2 + \sigma_e^2} = h_t^2 \quad (6)$$

Adjusting for geographic effects

Because strong population structure was observed in this Arabidopsis world-wide collection in previous studies (e.g., Atwell et al. 2010; Nordborg et al. 2005), it may be adjusted through the use of ‘Q+K model’ implemented in the LMM analysis (Yu et al. 2006) to help

control the false-positive rate and to minimize the bias in heritability estimates. For the data set used in our study, Atwell et al. (2010) grouped 199 inbred lines into five clusters using UPGMA clustering method based on the matrix of the realized kinship values. However, four of the five groups had a limited number of inbred lines ranging from 2 to 18 per group whereas the fifth group was very large with 166 inbred lines within the group. Obviously, the large cluster would consist of many inbred lines that are geographically non-contiguous. On the other hand, *Arabidopsis thaliana* is a long-day plant and thus it requires both vernalization and long photoperiod to stimulate flowering. These biological attributes indicate that geographic variation particularly latitudinal variation would play an important role in structuring and organizing genetic variation of this *Arabidopsis* population. Therefore, we subsequently used geographic variables to directly adjust for the population structure.

Adjustment for geographic effects was carried out by extending the LMM model in eq. (1) or eq. (2) to include two covariates, latitude and longitude of the location where each inbred line was originally sampled,

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{X}_1\beta_1 + \mathbf{X}_2\beta_2 + \mathbf{W}\mathbf{u} + \mathbf{e} = \mathbf{1}\mu + \mathbf{X}_1\beta_1 + \mathbf{X}_2\beta_2 + \mathbf{a} + \mathbf{e}, \quad (7)$$

where $\mathbf{X}_1$ and $\mathbf{X}_2$ are the vectors of n latitude and longitude values for inbred lines and β_1 and β_2 are the effects of these two geographic covariates. Similar adjustment for geographic effects was made in the partitioning of the total additive genetic variance into components due to the seven functional groups. The total phenotypic variance was used for calculating heritability and its functional components as such calculation would allow us to assess how adjustment for geographic effects would influence the heritability and its components.

Implementing the analyses

The LMM analysis was implemented using PROC MIXED of the SAS system (Littell et al. 2006). As the number of phenotypic records available for the analyses varied from trait to trait, the GRM for the LMM analysis were based on those inbred lines ($n < 199$) with phenotypic records for a given trait.

We used two PROC MIXED options to help improve the convergence when the convergence became difficult in the LMM analyses of individual traits. First, use of the SCORING=100 option was made to allow for computing covariance components based on the Fisher scoring algorithm with up to 100 iterations instead of the default Newton-Raphson algorithm. This option was used because the Fisher scoring algorithm is less sensitive to choice of initial values than Newton-Raphson (Jennrich and Sampson 1976). Second, use of the CONVH=1e-6 option was made to relax the convergence criterion from the default value of 10^{-8} to a more tolerate value of 10^{-6} , thereby achieving the convergence for all traits even though only a very few cases where the REML procedure would otherwise fail to converge at the default tolerate criterion.

Results

Estimates of heritability

Estimates of heritability for 107 flowering, defense, ionomics and developmental traits were made using the LMM analysis with the GRM being calculated from all SNPs (Figure 1, Table S2). The LMM analysis without adjustment for geographic effects could not give the heritability estimates for 12 traits, two flowering traits (traits 2 and 6), two defense traits (traits 24 and 41) and eight developmental traits (traits 65, 67, 69, 86, 89, 93, 94 and 103), due to the failure of the corresponding likelihood functions to converge. The convergence was achieved after geographic effects were adjusted for these traits. Such unavailability of heritability estimates would differ from the cases of zero heritability estimates as for three developmental traits (traits 70, 71 and 82) where the convergence was indeed achieved.

The results in Figure 1 showed two features. First, in addition to improved convergence as described above, the geographic adjustment helped reduce the confounding effect due to the variation of geographic origins as the heritability estimates for all four groups of traits with the adjustment were generally slightly or moderately smaller than those without the adjustment. Second, on average, flowering traits had higher heritability estimates than defense, ionomics and developmental traits did, even though the latter three trait groups had much wider ranges of the estimates regardless of the geographic adjustment. For example, with the adjustment, the heritability estimates for flowering traits ranged from 0.3593 for trait 22 (FT diameter field) to 0.8136 for trait 9 (FLC) but those for other groups of traits had the range of 0 to 0.999.

It is also evident from Table S2 that the heritability estimates for flowering traits were estimated with a greater degree of precision, on average, as indicated by smaller standard errors (SEs) of the estimates, than the other three groups of traits. The SEs of heritability estimates with no geographic adjustment ranged from 0.064 to 0.183 with the average of 0.107 for flowering traits, from 0.118 to 0.288 with the average of 0.191 for defense-related traits, from 0.174 to 0.283 with the average of 0.249 for ionomics traits, and from 0.089 to 0.280 with the average of 0.176 for developmental traits. Similar ranges of SEs were observed for adjusted data. Since these traits were assessed in the controlled conditions of common garden experiments, measuring errors alone may not be enough to account for observed different levels of precision in heritability estimates for different trait groups. Instead, the difference in sample sizes is likely to be a major cause of differing precisions in heritability estimates in the trait groups. The sample sizes varied from 119 to 194 with the average of 165.1 for flowering traits, from 76 to 175 for defense traits with the average of 125.9, and from 83 to 177 with the average of 138.9 for developmental traits. All ionomics traits were measured with the same 93 inbred lines. Considering all 107 traits in different trait groups, SEs of heritability estimates increased with reduced sample sizes with a moderate, negative correlation of -0.52.

Functional components of heritability

For each trait, partitioning of heritability into seven functional classes of SNP variants in different genomic regions showed that up to four nonzero functional components would contribute to the heritability (h^2) when the LMM analysis was carried out without adjustment for

geographic effects (Figure 2) and with the adjustment (Figure 3). In general, one or two functional components were the major contributors while the rest were either zero or minor contributors to h^2 . Because of the large sampling variability (standard errors) of individual components (see Table S3) in comparison to the standard errors of the heritability (see Table S2), the sums of all components sometimes exceeded 1.0, the unbound limit of h^2 .

Some functional classes of SNPs were more frequent contributors to h^2 than others and such across-functional-class distributions varied among four groups of traits. As shown in Table 3, the more frequent contributors were 5' UTR, Intron, 3' UTR and downstream sequence for flowering and defense-related traits; 5' UTR and intergenic for ionomics traits; 5' UTR, 3' UTR, downstream sequence and intergenic for developmental traits. Geographic adjustment generally made the individual components smaller but there was a similar frequency distribution of functional components contributing to h^2 with a couple of noticeable changes in the distribution patterns. First, with the adjustment for geographic effects, some traits showed a change in the relative importance of individual functional components. For example, for the flowering trait LD (trait 1), there were three non-zero functional components for SNPs in 5' UTR, intron and 3' UTR regions without the adjustment but only two components (5' UTR and 3' UTR) were left after the adjustment. Second, the SNP variants within the exon regions contributed to h^2 in four of 23 flowering traits without the adjustment but in none of the 23 traits with the adjustment.

Geographic relationships

Breeding values of inbred lines unadjusted vs. adjusted for geographic effects were correlated with their latitudes and longitudes (Figures 4 and 5). Flowering traits displayed a different correlation pattern from those of other three trait groups. The correlations of breeding values with latitude positive and moderate for all flowering traits except for FT diameter field, but the correlations with longitude were negative but only marginal. On the other hand, the correlations for the other three groups of traits were of mixed negative and positive signs with averaged correlations across the traits being always close to zero. As expected, the adjustment for geographic effects led to a substantial reduction in the magnitude of correlations; most traits had their correlations reduced by more than 50% after the adjustment.

Discussion

In this study, we applied the marker-based LMM analysis to estimate narrow-sense heritability (h^2) and its seven functional components for each of 107 flowering, defense, ionomics and developmental traits in an *Arabidopsis* population consisting of a world-wide collection of 199 inbred lines with unknown genetic relatedness. The h^2 estimates varied greatly among the traits with the whole range of 0 to 1 being covered, but with the averages being slightly or moderately smaller with geographic adjustment than without the adjustment for all four groups of traits. A standout result was that the h^2 estimates for flowering were, on average, higher than those for defense, ionomics and developmental traits regardless of whether or not geographic effects were adjusted. This is certainly consistent with the general expectation derived from

Fisher's classic fundamental theorem: fitness-related traits would have lower heritabilities than other traits (Falconer and Mackay 1996; Lynch and Walsh 1998; Mousseau and Roff 1987; Visscher et al. 2008), as defense and ionomics traits analyzed in our study are essentially fitness-related traits reflective of plant response to pest attack and mineral nutrient deficiency, respectively.

Our h^2 estimates are generally lower than their broad-sense counterparts (H^2) as given in Atwell et al. (2010), suggesting the presence of non-additive genetic variances in these traits. Since H^2 was estimated without no adjustment for geographic effects, the comparison was directly made with its h^2 counterpart that was estimated based on the data without the adjustment. Inspecting estimates of H^2 in Table 1 and estimates of h^2 in Figure 1 and Table S2, the extent of non-additive genetic variances as implied in the difference between H^2 and h^2 varies among traits. For example, the developmental traits contain those with the substantial amount of non-additive variation [$(H^2 - h^2) \geq 0.7$ for four traits] and those with little non-additive variation [$(H^2 - h^2) \leq 0.1$ for nine traits]. Since this Arabidopsis population consists of inbred lines only, the non-additive variation revealed is most likely due to the presence of epistatic interactions between additive effects at different causal SNP variants. As noted by Atwell et al. (2010), H^2 was not estimated for 32 out of 107 traits presumably because replicated measurements required by the usual analysis of variance used in their study were not available for these traits. In contrast, our LMM analysis required no such data structure and thus it offered a much greater flexibility of estimating h^2 for all traits except for only a few that failed to converge.

Like in many other common garden experiments (de Villemereuil et al. 2016), the population structure was observed in this Arabidopsis world-wide collection (e.g., Atwell et al.

2010; Nordborg et al. 2005). The effect of population structure needs to be adjusted in order to minimize the bias in heritability estimates. However, we did not use the usual ‘Q+K model’ approach (Yu et al. 2006) to such adjustment because of highly skewed cluster groups (Atwell et al. 2010). Instead, our geography-based adjustment was based on some important biological considerations of *Arabidopsis* plant (e.g., long-day plant and photoperiod sensitivity). Our adjustment for geographic effects (i.e., using longitude and latitude as covariates in the LMM analysis) improved the convergence of likelihood functions to the data as twelve traits (two flowering traits, two defense traits and eight developmental traits) that failed to converge for unadjusted data were able to converge with valid estimates of h^2 for adjusted data (Table S2). Most traits showed a small amount of change in h^2 estimates due to adjustment for geographic effects. However, for two defense-related traits, *AvrRpm1* and *AvrB*, the change due to the adjustment was substantial with the h^2 estimates being reduced from $h^2 = 0.99$ for unadjusted data to $h^2 = 0.57$ for adjusted data. Interestingly, the previous GWAS study by Atwell et al. (2010) found a very strong association in *AvrRpm1* that allowed for direct identification of a candidate gene, *RESISTANCE TO P. SYRINGAE PV MACULICOLA 1 (RPM1)*. At least part of this strong association may be geographically dependent for some defense traits. For the majority of the traits, however, the geographic adjustment had negligible impact on heritability estimates. Thus, our study would lend a support for previous GWAS studies based on unadjusted data for most (if not all) traits (e.g., Atwell et al. 2010).

In the presence of population structure, heritability needs to be adjusted. One possible adjustment can be made according to eq. (15.1) of Falconer and Mackay (1996),

$$h_{adj}^2 = \frac{h^2(1 - F_{ST})}{1 - h^2 F_{ST}},$$

where F_{ST} is the statistic to measure the population differentiation as devised by Wright (1951). This adjustment is applicable only to the traits with pure additive genetic effects and no selection. A simple numerical analysis of this equation (Figure 6) demonstrates that the heritability is reduced with increased population differentiation and that the marked reduction occurs only when there is a strong population structure ($F_{ST} > 0.2$). A preliminary estimate of F_{ST} of 0.027 based on all 214,051 SNP markers for this Arabidopsis meta-population (unpublished) is similar to those for other organisms including maize ($F_{ST} = 0.047 - 0.073$) (Yu et al. 2006), human ($F_{ST} = 0.013 - 0.145$) (Marchini et al. 2004) and a conifer tree ($F_{ST} = 0.017$) (Yang et al. 1996). It appears that population differentiation is generally small ($F_{ST} < 0.2$) for a variety of organisms. Thus, possible downward biased estimation of heritability due to the presence of population structure is likely to be small or negligible.

Our partitioning of heritability into components of functional groups for SNPs in coding and noncoding genomic regions contributes to further understanding of the problem with ‘missing heritability’ (i.e., numerous SNPs identified have collectively accounted for only a small amount of additive genetic variation) as shown in many previous GWAS studies. Several of these studies (Hu and Yang 2014; Yang et al. 2010; Zaitlen and Kraft 2012; Zuk et al. 2012) have also applied the marker-based LMM analysis to allow for uncovering a substantial amount of hidden (rather than missing) heritability. The LMM analysis or its equivalence is effective because it leverages the entire polygenic architecture and accounts for widespread linkage disequilibrium in the genome. However, this overall enrichment did not distinguish the

contributions to the trait heritability by individual functional groups. More recently, further partitioning of the heritability into functional components has been tried in humans and livestock species (Gusev et al. 2014; MacLeod et al. 2016), but the number of traits examined by these studies are not large enough for uncovering any general pattern. Our attempt is probably the first for plant species and more importantly its inclusion of 107 flowering, defense, ionomics and developmental traits reveals some interesting similarities and differences among four trait groups (Figures 2 and 3, Table S3). Perhaps one of the most revealing features from our study is that the component due to SNPs in exon (coding) regions is the least contributor to heritability judging from its low frequencies of nonzero components occurred across all four groups of traits (Table 3) while the components due to SNPs in 5' UTR, 3' UTR and downstream sequence regions all contribute more to heritability. This is certainly consistent with the finding of many GWAS studies that causal SNP variants are often located in noncoding regions due to events of noncoding RNA, DNA methylation, alternative splicing and unannotated transcripts (Edwards et al. 2013; Mudge et al. 2013). It is well known that identification of causal SNP variants as in GWAS studies is only the very first step toward their functional characterization individually or collectively. The LMM analysis in our study and similar analyses in other studies would help narrow down the characterization to a much smaller subset of SNPs based on the relative contributions to heritability by individual function groups.

Our marker-based LMM analysis provides an opportunity to gain a comprehensive view on heritabilities and their functional components for a wide range of traits in plant natural populations. In the past, such view is difficult to achieve because estimation of heritability or other genetic parameters for quantitative traits with varying degrees of adaptive significance has

been challenging for natural populations where genetic relatedness between individuals required for such estimation is unknown. Some applications of DNA markers for inferring the genetic relatedness have been made (Kruuk et al. 2008; Ritland 1996; Thomas 2005), but their usefulness is often constrained by a limited number of DNA markers. Additionally, only very few traits have been available for such investigations. Our study is advantageous in three ways. First, the heritability estimates should be more reliable because the GRM required for the LMM estimation was based on >210K SNP markers across the Arabidopsis genome. Second, more insights into genetic control of quantitative traits with varying degrees of adaptive significance would be gained from comparison of the heritability estimates among and within the four trait groups. Such comparison was previously possible only from across-study surveys and meta-data analyses (e.g., Mousseau and Roff 1987). Thus, it eliminates some deficiencies from the previous attempts including (i) reliance on the use of genetic relatedness inferred from designed experiments or a general pedigree for estimation of heritability and other genetic parameters, (ii) no account for Mendelian sampling from pedigree-based analysis and (iii) heterogeneity of data sources for different traits by different studies. Third, to the best of our knowledge, our study is a first effort to dissect the heritability into functional components for a wide array of traits in natural populations, thereby paving the way towards molecular characterization of genome-wide causal variants in coding and noncoding regions controlling complex traits of fitness or adaptive significance.

There are some limitations of the current study that require further research. The LMM analysis along with explicit geographic adjustment should have removed much of the confounding in the highly structured Arabidopsis population used in our study. However, it is

expected that some confounding certainly remains. Future studies can investigate the following two approaches to further correction of the confounding. First, in addition to our current geographic adjustment that relies on the linear relationship between breeding values and geographic origins of individual inbred lines, the confounding may be further reduced by modeling such relationship using nonlinear covariance functions such as the commonly used spatial covariance functions in geostatistics, Exponential, Gaussian, Power and Spherical (Cressie 1993; Schabenberger and Gotway 2005). Second, climatic and adaptive variables may be developed and included in future studies to account for additional variation left in the residual variance. Adding these new exogenous variables should also help interpret heritability estimates of different traits with differing responses to environmental conditions. Another important limitation with the present and previous studies (e.g., Atwell et al. 2010) is the small sample size relative to the sample sizes typically used in humans and livestock species (Gusev et al. 2014; MacLeod et al. 2016). This problem would be even more acute with our estimation of functional components of narrow-sense heritability as up to seven genetic variance components need to be estimated simultaneously. In general, the sample size issue would be less severe in the inbred *Arabidopsis* population than in outbred human and livestock populations due to less chance of extremely rare, deleterious alleles. Additionally, repeated patterns of heritability or additive genetic variation detected from a large array of traits within and among the four trait groups suggest that the patterns are probably true despite the limited sample size. With genotyped SNPs being now available for over 1,000 inbred lines (Alonso-Blanco et al. 2016) and phenotyping the 107 traits for the same set of inbred lines presumably becoming available in the near future, the marker-based LMM analysis will be more powerful and will provide more reliable estimates of heritability and its functional components for all the traits.

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Table 1. Atwell et al.'s (2010) estimates of broad-sense heritability (H^2) for 107 flowering, defense, ionomics and developmental traits in *Arabidopsis thaliana*.

Trait ID	Trait name	H^2	Trait ID	Trait name	H^2	Trait ID	Trait name	H^2
Flowering traits (ID 1-23)			36	At2	0.69	71	Chlorosis 16	NA
1	LD	0.99	37	As2	0.68	72	Chlorosis 22	NA
2	LDV	0.94	38	At1 CFU2	0.51	73	Anthocyanin 10	NA
3	SD	1.00	39	As CFU2	0.54	74	Anthocyanin 16	NA
4	SDV	0.94	40	Bs CFU2	0.62	75	Anthocyanin 22	NA
5	0W	0.99	41	At2 CFU2	0.66	76	Seed dormancy	0.99
6	2W	0.99	42	As2 CFU2	0.60	77	Germ 10	NA
7	4W	0.99	43	Trichome avg C	0.88	78	Germ 16	NA
8	8W	0.96	44	Trichome avg JA	0.88	79	Germ 22	NA
9	FLC	NA	45	Bacterial titer	0.66	80	Seedling growth	0.74
10	FRI	NA	46	Aphid number	0.42	81	Vern growth After vern	0.86
11	FT10	1.00	Ionomics traits (ID 47-64)			82	growth	0.78
12	FT16	0.99	47	Lithium	0.74	83	Secondary dorm	0.91
13	FT22	0.99	48	Boron	0.89	84	Germ in dark	0.91
14	LN10	0.98	49	Sodium	0.96	85	DSDS50	0.95
15	LN16	0.98	50	Magnesium	0.93	86	Seed bank 133- 91	0.79
16	LN22	0.99	51	Phosphorus	0.90	87	Storage 7 days	0.95
17	8W GH FT	1.00	52	Sulfur	0.86	88	Storage 28 days	0.92
18	8W GH LN	1.00	53	Potassium	0.88	89	Storage 56 days	0.94
19	0W GH FT	1.00	54	Calcium	0.86	90	Hypocotyl length	0.97
20	0W GH LN	1.00	55	Manganese	0.82	91	Width 10	NA
21	FT Field	0.91	56	Iron	0.69	92	Width 16	NA
22	FT dm	0.60	57	Colbolt	0.81	93	Width 22	NA
23	field	0.60	58	Nickel	0.60	94	Leaf serr 10	NA
24	FT GH	0.99	59	Copper	0.63	95	Leaf serr 16	NA
Defense traits (ID 24-46)			60	Zinc	0.91	96	Leaf serr 22	NA
24	AvrPphB	NA	61	Arsenic	0.59	97	Leaf roll 10	NA
25	AvrRpm1	NA	62	Selenium	0.77	98	Leaf roll 16	NA
26	AvrB	NA	63	Molybdenum	0.89	99	Leaf roll 22	NA
27	AvrRpt2	NA	64	Cadmium	0.84	100	Rosette erect 22	NA
28	Emco5	NA	Developmental traits (ID 65-107)			101	Silique length 16	0.97
29	Emwa1	NA	65	LES	NA	102	Silique length 22	0.99
30	Emoy2	NA	66	YEL	NA	103	FT duration GH	0.89
31	Hiks1	NA						

32	Noco2	NA	67	LY	NA	104	LC duration GH	0.96
33	At1	0.69	68	FW	0.97	105	LFS GH	0.97
34	As	0.66	69	DW	0.92	106	MT GH	0.84
35	Bs	0.64	70	Chlorosis 10	NA	107	RP GH	0.89

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Table 2. Distributions of 214,051 SNPs over seven functional groups at five chromosomes of *Arabidopsis thaliana* (AT1 to AT5))

Functional group*	AT1	AT2	AT3	AT4	AT5	Total
Promoter	6,192	3,098	4,980	4,199	6,121	24,590
5' UTR	1,368	688	1,081	840	1,327	5,304
Exon	21,617	11,498	17,144	14,525	20,992	85,776
Intron	8,318	3,701	6,675	5,806	8,846	33,346
3' UTR	2,173	1,045	1,638	1,478	2,134	8,468
Downstream Seq	5,709	2,923	4,880	4,100	5,951	23,563
Intergenic	6,624	5,509	7,017	6,021	7,833	33,004
Total	52,001	28,462	43,415	36,969	53,204	214,051

* Promoter: SNPs located within the 1kb upstream sequence of a gene; 5 UTR: SNPs located within five prime untranslated region of a gene; Exon: SNPs located in coding DNA sequences (CDS) of a gene after removal of introns by RNA splicing; Intron: SNPs located in nucleotide sequences within a gene that are removed by RNA splicing; 3 UTR: SNPs located within three prime untranslated regions of a gene; Downstream-Seq: SNPs located within the 1kb downstream sequence of a gene; and Intergenic: SNPs located at least 1kb away from any protein-coding gene.

Table 3. Frequency distributions of functional components of narrow-sense heritability across 23 flowering traits, 23 defense traits, 18 ionomics traits and 43 developmental traits unadjusted and adjusted for geographic effects.

Functional group*	Flowering		Defense		Ionomics		Development	
	Unadj	Adj	Unadj	Adj	Unadj	Adj	Unadj	Adj
Promoter	2	2	2	1	2	3	6	6
5' UTR	8	10	10	10	9	8	14	15
Exon	4	0	2	4	3	3	7	6
Intron	12	9	9	8	3	2	5	8
3' UTR	17	18	6	6	3	3	14	17
Downstream								
Seq	7	11	5	6	3	2	14	12
Intergenic	5	6	2	3	9	7	13	12
Total	23	23	23	23	18	18	43	43

*See Table 2 for detailed descriptions.

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Figure captions

Figure 1. Estimates of narrow-sense heritability for 107 flowering, defense, ionomoics and developmental traits unadjusted (blue) and adjusted (orange) for geographic effects. Trait IDs (1-107) and names are given in Table 1.

Figure 2. Estimates of seven functional components of narrow-sense heritability for 107 flowering, defense, ionomoics and developmental traits unadjusted for geographic effects. Trait IDs (1-107) and names are given in Table 1. The seven functional components (promoter, 5' UTR, Exon, intron, 3'UTR, Downstream-Seq and intergenic) are described in footnotes of Table 2.

Figure 3. Estimates of seven functional components of narrow-sense heritability for 107 flowering, defense, ionomoics and developmental traits adjusted for geographic effects. Trait IDs (1-107) and names are given in Table 1. The seven functional components (promoter, 5' UTR, Exon, intron, 3'UTR, Downstream-Seq and intergenic) are described in footnotes of Table 2.

Figure 4. Correlations between breeding values and latitudes of inbred lines for 107 flowering, defense, ionomoics and developmental traits unadjusted (blue) and adjusted (orange) for geographic effects. Traits 1-107 are identified in consecutive order from the left to right of the chart. Trait IDs (1-107) and names are given in Table 1.

Figure 5. Correlations between breeding values and longitudes of inbred lines for 107 flowering, defense, ionomoics and developmental traits unadjusted (blue) and adjusted (orange) for geographic effects. Traits 1-107 are identified in consecutive order from the left to right of the chart. Trait IDs (1-107) and names are given in Table 1.

Figure 6. Relationship between heritability (h^2) and population differentiation (F_{ST}).

Table S1. Geographical origins of a world-wide collection of 199 *Arabidopsis* inbred lines.

ID	name	country	sitename	latitude	longitude
5837	Bor-1	CZE	Bor	49.40	16.23
6008	Duk	CZE	Duk	49.10	16.20
6009	Eden-1	SWE	Eden	62.88	18.18
6016	Eds-1	SWE	Eds	62.90	18.40
6040	Kni-1	SWE	Kni1	55.66	13.40
6042	Lom1-1	SWE	Lom1	56.09	13.90
6043	L04304	SWE	LWE3	62.80	18.08
6046	L04604	SWE	LWE6	62.80	18.08
6064	Nyl-2	SWE	Nyl	62.95	18.28
6074	B°a5-1	SWE	B°a5-1	56.46	16.13
6243	Tottarp-2	SWE	Tottarp	56.27	13.90
6709	Bg-2	USA	BG	47.65	-122.31
6897	Ag-0	FRA	Ag	45.00	1.30
6898	An-1	BEL	An	51.22	4.40
6899	Bay-0	GER	Bayreuth	49.00	11.00
6900	Bil-5	SWE	Bil	63.32	18.48
6901	Bil-7	SWE	Bil	63.32	18.48
6903	Bor-4	CZE	Bor	49.40	16.23
6904	Br-0	CZE	Br	49.20	16.62
6905	Bur-0	IRL	Bur	54.10	-6.20
6906	C24	POR	Co	40.21	-8.43
6907	CIBC-17	UK	CIBC	51.41	-0.64
6908	CIBC-5	UK	CIBC	51.41	-0.64
6909	Col-0	USA	Col	38.30	-92.30
6910	Ct-1	ITA	Ct	37.30	15.00
6911	Cvi-0	CPV	Cvi	15.11	-23.62
6913	Eden-2	SWE	Eden	62.88	18.18
6914	Edi-0	UK	Edi	55.95	-3.16
6915	Ei-2	GER	Eifel	50.30	6.30
6916	Est-1	RUS	Est	58.30	25.30
6917	F917rt	SWE	FWE7	63.02	18.32
6918	F91885	SWE	FWE8	63.02	18.32
6919	Ga-0	GER	Gabelstein	50.30	8.00
6920	Got-22	GER	Goettingen	51.53	9.94
6921	Got-7	GER	Goettingen	51.53	9.94
6922	Gu-0	GER	Glueckingen	50.30	8.00
6923	HR-10	UK	HR	51.41	-0.64
6924	HR-5	UK	HR	51.41	-0.64
6926	Kin-0	USA	Kin	44.46	-85.37
6927	KNO-10	USA	Knox	41.28	-86.62
6928	KNO-18	USA	Knox	41.28	-86.62
6929	Kondara	TJK	Kondara	38.48	68.49
6930	Kz-1	KAZ	KZ	49.50	73.10
6931	Kz-9	KAZ	KZ	49.50	73.10

6932	Ler-1	GER	Ler	47.98	10.87
6933	LL-0	ESP	LI	41.59	2.49
6936	Lz-0	FRA	Lz	46.00	3.30
6937	Mrk-0	GER	Markt/Baden	49.00	9.30
6939	Mt-0	LIB	Mt	32.34	22.46
6940	Mz-0	GER	Merzhausen/Ts.	50.30	8.30
6942	Nd-1	GER	Niederzenz	50.00	10.00
6943	NFA-10	UK	NFA	51.41	-0.64
6944	NFA-8	UK	NFA	51.41	-0.64
6945	Nok-3	NED	Nok	52.24	4.45
6946	Oy-0	NOR	Oy	60.39	6.19
6951	Pu2-23	CZE	Pu2	49.42	16.36
6956	Pu2-7	CZE	Pu2	49.42	16.36
6957	Pu2-8	CZE	Pu2	49.42	16.36
6958	Ra-0	FRA	Ra	46.00	3.30
6959	Rennes-1	FRA	REN	48.50	-1.41
6960	Rennes-11	FRA	REN	48.50	-1.41
6961	Se-0	ESP	Se	38.33	-3.53
6962	Shahdara	TJK	Sha	38.35	68.48
6963	Sorbo	TJK	Sorbo	38.35	68.48
6964	Spr1-2	SWE	Spr1	56.32	16.04
6965	Spr1-6	SWE	Spr1	56.32	16.04
6966	Sq-1	UK	SQ	51.41	-0.64
6967	Sq-8	UK	SQ	51.41	-0.64
6968	Tamm-2	FIN	Tamm	60.00	23.50
6969	Tamm-27	FIN	Tamm	60.00	23.50
6970	Ts-1	ESP	Ts	41.72	2.93
6971	Ts-5	ESP	Ts	41.72	2.93
6972	Tsu-1	JPN	Tsu	34.43	136.31
6973	UII2-3	SWE	UII2	56.06	13.97
6974	UII2-5	SWE	UII2	56.06	13.97
6975	Uod-1	AUT	Uod	48.30	14.45
6976	Uod-7	AUT	Uod	48.30	14.45
6977	Van-0	CAN	Van	49.30	-123.00
6978	Wa-1	POL	Wa	52.30	21.00
6979	Wei-0	SUI	Wei	47.25	8.26
6980	Ws-0.1	RUS	Ws	52.30	30.00
6981	Ws-2	RUS	Ws	52.30	30.00
6982	Wt-5	GER	Wietze	52.30	9.30
6983	Yo-0	USA	Yo	37.45	-119.35
6984	Zdr-1	CZE	Zdr	49.39	16.25
6985	Zdr-6	CZE	Zdr	49.39	16.25
6988	Alc-0	ESP	Alc	40.49	-3.36
7000	Aa-0	GER	Aua/Rhon	50.92	9.57
7014	Ba-1	UK	Black Mount (Ba)	56.55	-4.80
7033	Buckhorn Pass	USA	Buckhorn Pass	41.36	-122.76
7062	Ca-0	GER	Camberg/Taunus	50.30	8.27

7064	Cnt-1	UK	Canterbury (Sullivan garden)	51.30	1.10
7081	Co	POR	Co	40.21	-8.43
7094	Da-0	GER	Darmstadt	49.87	8.65
7123	Ep-0	GER	Eppenheim/Taunus	50.17	8.39
7147	Gie-0	GER	Gieben	50.58	8.68
7163	Ha-0	GER	Hannover	52.37	9.74
7231	Li-7	GER	Limburg	50.38	8.07
7255	Mh-0	POL	Muhlen	50.95	20.50
7275	No-0	GER	Halle	51.06	13.30
7282	Or-0	GER	Oranienstein	50.38	8.01
7296	Petergof	RUS	Petergof	59.00	29.00
7306	Pog-0	CAN	Pog	49.27	-123.21
7323	Rubezhnoe-1	UKR	Rubezhnoe	49.00	38.28
7346	Sten-0	GER	Stendal	52.61	11.86
7418	Zu-1	SUI	Zu	47.37	8.55
7424	Jl-3	CZE	Br	49.20	16.62
7438	N13	RUS	Konchezero	61.36	34.15
7460	Da(1)-12	CZE	Unknown - Czech Republic	49.82	15.47
7461	H55	CZE	Relichova	49.00	15.00
7477	WAR	USA	Lincoln Woods State Park	41.73	-71.28
7514	RRS-7	USA	RRS	41.56	-86.43
7515	RRS-10	USA	RRS	41.56	-86.43
7516	V516592	SWE	VWE65	55.58	14.33
7517	V517830	SWE	VWE78	55.58	14.33
7518	B°a1-2	SWE	B°a1-2	56.14	15.78
7519	B°a4-1	SWE	B°a4-1	56.14	15.78
7520	Lp2-2	CZE	Lp2	49.38	16.81
7521	Lp2-6	CZE	Lp2	49.38	16.81
7522	Mr-0	ITA	Mr	44.15	9.65
7523	Pna-17	USA	PNA	42.09	-86.33
7524	Rmx-A02	USA	RMX	42.04	-86.51
7525	Rmx-A180	USA	RMX	42.04	-86.51
7526	Pna-10	USA	PNA	42.09	-86.33
8213	Pro-0	ESP	Pro	43.25	-6.00
8214	Gy-0	FRA	Gy	49.00	2.00
8215	Fei-0	POR	Fei	40.50	-8.32
8222	Lis-2	SWE	Lis	56.03	14.78
8230	Algutsum	SWE	Algutsum	56.68	16.50
8231	Br31657	SWE	BrE1657Nor	56.30	16.00
8233	Dem-4	USA	Dem	41.19	-87.19
8235	Hod	CZE	Hodonin	48.80	17.10
8236	HSm	CZE	Horni Smrcne	49.33	15.76
8237	K23794100 0	SWE	KWE794100	55.80	13.10
8239	PHW-3	GER	Koeln	51.00	7.00
8240	Kulturen-1	SWE	Kulturen	55.71	13.20
8241	Liarum	SWE	Liarum	55.95	13.82
8242	Lill038n	SWE	Lill03	56.15	15.79

8243	PHW-2	ITA	Florence	43.77	11.25
8245	Seattle-0	USA	Seattle	47.00	-122.20
8247	San-2	SWE	Sand2Amas	56.07	13.74
8249	Vimmerby	SWE	Vimmerby	57.70	15.80
8254	Ang-0	BEL	Ang	50.30	5.30
8256	B256rt	SWE	BWE	56.40	12.90
8258	B25867	SWE	BWE	56.40	12.90
8259	B25967	SWE	BWE	56.40	12.90
8264	Bla-1	ESP	Bla	41.68	2.80
8265	Blh-1	CZE	Blh	48.30	19.85
8266	Boo2-1	SWE	Boo2	55.86	13.51
8270	Bs-1	SUI	Bs	47.50	7.50
8271	Bu-0	GER	Burghaun/Rhon	50.50	9.50
8274	Can-0	ESP	Can	29.21	-13.48
8275	Cen-0	FRA	Cen	49.00	0.50
8283	Dra3-1	SWE	Dra3	55.76	14.12
8284	Drall-1	CZE	Drall	49.41	16.28
8285	Drall-1	CZE	Drall	49.41	16.28
8290	En-1	GER	Enkheim/Frankfurt	50.00	8.50
8296	Gd-1	GER	Gudow	53.50	10.50
8297	Ge-0	SUI	Ge	46.50	6.08
8300	Gr-1	AUT	Graz	47.00	15.50
8306	Hov4-1	SWE	Hovdala	56.10	13.74
8310	Hs-0	GER	Hannover/Stroehe	52.24	9.44
8311	In-0	AUT	In	47.50	11.50
8312	Is-0	GER	Isenburg/Neuwied	50.50	7.50
8313	Jm-0	CZE	Jm	49.00	15.00
8314	Ka-0	AUT	Ka	47.00	14.00
8323	Lc-0	UK	Lc	57.00	-4.00
8325	Lip-0	POL	Lip	50.00	19.30
8326	Lis-1	SWE	Lis	56.03	14.78
8329	Lm-2	FRA	Lm	48.00	0.50
8334	Lu-1	SWE	Lund	55.71	13.20
8335	Lund	SWE	Lund	55.71	13.20
8337	Mir-0	ITA	Mir	44.00	12.37
8343	Na-1	FRA	Na	47.50	1.50
8351	Ost-0	SWE	Ost	60.25	18.37
8353	Pa-1	ITA	Pa	38.07	13.22
8354	Per-1	RUS	Per	58.00	56.32
8357	Pla-0	ESP	Pla	41.50	2.25
8365	Rak-2	CZE	Rak	49.00	16.00
8366	Rd-0	GER	Rodenbach/Dill	50.50	8.50
8369	Rev-1	SWE	Rev1	55.69	13.45
8374	Rsch-4	RUS	Rsch	56.30	34.00
8376	Sanna-2	SWE	San	62.69	18.00
8378	Sap-0	CZE	Sap	49.49	14.24
8387	St-0	SWE	St	59.00	18.00

8388	Stw-0	RUS	Stw	52.00	36.00
8389	Ta-0	CZE	Ta	49.50	14.50
8395	Tu-0	ITA	Tu	45.00	7.50
8411	Rd-0	GER	Rodenbach/Dill	50.50	8.50
8412	Sav-0	CZE	Slavice	49.18	15.88
8420	Kelsterbach-4	GER	Kelsterbach	50.07	8.53
8422	Fj22525	SWE	FjE25	56.06	14.29
8423	Hov2-1	SWE	Hov2	56.10	13.74
8424	Kas-2	IND	Kas	35.00	77.00
8426	Ull1-1	SWE	Ull1	56.06	13.97
8430	Lisse	NED	Lisse	52.25	4.57
9057	VinslWil	SWE	VinslWil	56.10	13.92
9058	V058847n S	SWE	VWE8847n S	57.75	16.63
100000	Wil-1	LTU	Wil	54.68	25.32

Draft

Table S2. Genome-wide estimation of narrow-sense heritabilities for 107 flowering, defense, ionomoi

Trait ID	Trait Group	Trait name	Unadjusted heritability	Standard Error	Corr(obs,	Corr(BV, la
1	Flowering	LD	0.5848	0.06419	1	0.44225
2	Flowering	LDV				
3	Flowering	SD	0.6634	0.07394	1	0.45391
4	Flowering	SDV	0.7152	0.09849	0.99981	0.56841
5	Flowering	0W	0.7629	0.09252	1	0.21074
6	Flowering	2W				
7	Flowering	4W	0.6449	0.08397	1	0.49471
8	Flowering	8W	0.7088	0.09955	0.99982	0.31929
9	Flowering	FLC	0.8121	0.1142	0.99919	0.09397
10	Flowering	FRI	0.6573	0.1831	0.97407	0.19618
11	Flowering	FT10	0.7246	0.1129	0.9961	0.5193
12	Flowering	FT16	0.6382	0.08371	0.99935	0.36162
13	Flowering	FT22	0.613	0.0742	0.99996	0.3512
14	Flowering	LN10	0.6697	0.1294	0.98987	0.5305
15	Flowering	LN16	0.8019	0.08572	1	0.2219
16	Flowering	LN22	0.6433	0.09767	0.99754	0.3329
17	Flowering	8W GH FT	0.712	0.1178	0.99599	0.28869
18	Flowering	8W GH LN	0.5504	0.1512	0.97087	0.47019
19	Flowering	0W GH FT	0.5462	0.09439	0.99564	0.41998
20	Flowering	0W GH LN	0.6629	0.1716	0.98162	0.0293
21	Flowering	FT Field	0.659	0.06965	1	0.52619
22	Flowering	FT dm field	0.4137	0.1653	0.91544	-0.41581
23	Flowering	FT GH	0.7178	0.07903	1	0.2496
			0.66200476			
24	Defense-related	AvrPphB				
25	Defense-related	AvrRpm1	0.999	0	1	0.21274
26	Defense-related	AvrB	0.999	0	1	0.19928
27	Defense-related	AvrRpt2	0.999	0	1	0.13475
28	Defense-related	Emco5	0.999	0	1	-0.01956
29	Defense-related	Emwa1	0.5969	0.2809	0.96942	0.22694
30	Defense-related	Emoy2	0.999	0	1	0.0849
31	Defense-related	Hiks1	0.999	0	1	-0.01987
32	Defense-related	Noco2	0.3696	0.2877	0.92561	0.25412
33	Defense-related	At1	0.5134	0.2025	0.95524	-0.12793
34	Defense-related	As	0.3581	0.2	0.93453	-0.09464
35	Defense-related	Bs	0.1233	0.1604	0.84526	-0.21695
36	Defense-related	At2	0.7261	0.1913	0.98111	0.05875
37	Defense-related	As2	0.2027	0.1782	0.86985	0.14859
38	Defense-related	At1 CFU2	0.1137	0.1576	0.82767	-0.32302
39	Defense-related	As CFU2	0.002596	0.1179	0.74412	0.26015
40	Defense-related	Bs CFU2	0.3207	0.1933	0.90122	0.17835

41	Defense-related	At2 CFU2				
42	Defense-related	As2 CFU2	0.1094	0.1562	0.79231	-0.19237
43	Defense-related	Trichome avg C	0.9292	0.172	0.99929	0.1749
44	Defense-related	Trichome avg JA	0.8464	0.1702	0.99808	0.14138
45	Defense-related	Bacterial titer	0.784	0.2023	0.99199	-0.34195
46	Defense-related	Aphid number	0.03765	0.1998	0.75262	-0.47909
			0.57274981			
47	Ionomics	Lithium	0.3891	0.2628	0.91307	-0.39317
48	Ionomics	Boron	0.5971	0.2386	0.969	-0.54006
49	Ionomics	Sodium	0.4864	0.271	0.94755	-0.03548
50	Ionomics	Magnesium	0.8305	0.1742	0.99735	-0.23829
51	Ionomics	Phosphorus	0.631	0.2428	0.97316	0.33786
52	Ionomics	Sulfur	0.4916	0.2828	0.96069	0.27234
53	Ionomics	Potassium	0.9408	0.2265	0.99512	-0.00814
54	Ionomics	Calcium	0.5406	0.2612	0.95663	-0.27624
55	Ionomics	Manganese	0.4806	0.2747	0.94907	0.2425
56	Ionomics	Iron	0.3647	0.2739	0.93159	0.40473
57	Ionomics	Colbolt	0.2476	0.2592	0.90623	0.10788
58	Ionomics	Nickel	0.3502	0.2665	0.90735	0.43567
59	Ionomics	Copper	0.1278	0.2314	0.86208	0.21105
60	Ionomics	Zinc	0.999	0	1	-0.12084
61	Ionomics	Arsenic	0.2671	0.2477	0.83642	0.36635
62	Ionomics	Selenium	0.7097	0.2622	0.98124	0.29283
63	Ionomics	Molybdenum	0.999	0	0.99975	0.03103
64	Ionomics	Cadmium	0.9976	0.2164	0.9971	0.05271
			0.58057778			
65	Developmental	LES				
66	Developmental	YEL	0.61	0.08898	1	-0.16359
67	Developmental	LY				
68	Developmental	FW	0.7033	0.2029	0.98746	-0.43575
69	Developmental	DW				
70	Developmental	Chlorosis 10	1.00E-08	0	0.80002	0.20431
71	Developmental	Chlorosis 16	1.00E-08	0	0.79635	0.01402
72	Developmental	Chlorosis 22	0.3115	0.1872	0.87703	0.21769
73	Developmental	Anthocyanin 10	0.7317	0.1855	0.98139	-0.22359
74	Developmental	Anthocyanin 16	0.3349	0.1936	0.90559	0.09369
75	Developmental	Anthocyanin 22	0.324	0.1891	0.88801	0.29889
76	Developmental	Seed dormancy	0.8484	0.1554	0.99994	-0.36457
77	Developmental	Germ 10	0.3305	0.1937	0.91213	0.08807
78	Developmental	Germ 16	0.6115	0.1972	0.96898	0.22687
79	Developmental	Germ 22	0.2862	0.1908	0.91606	-0.04187
80	Developmental	Seedling growth	0.266	0.2803	0.9174	0.35103
81	Developmental	Vern growth	0.06977	0.1996	0.85502	0.14122
82	Developmental	After vern growth	1.00E-08	0	0.7812	-0.13932

83	Developmental	Secondary dorm	0.8793	0.17	0.99903	0.33227
84	Developmental	Germ in dark	0.9242	0.1859	0.99857	-0.16713
85	Developmental	DSDS50	0.7949	0.1254	1	-0.40616
86	Developmental	Seed bank 133-91				
87	Developmental	Storage 7 days	0.7722	0.1046	1	0.42971
88	Developmental	Storage 28 days	0.8331	0.1128	1	0.32723
89	Developmental	Storage 56 days				
90	Developmental	Hypocotyl length	0.9771	0.1869	0.99936	-0.12707
91	Developmental	Width 10	0.6255	0.1898	0.96914	-0.30857
92	Developmental	Width 16	0.7743	0.1774	0.9854	-0.16016
93	Developmental	Width 22				
94	Developmental	Leaf serr 10				
95	Developmental	Leaf serr 16	0.561	0.197	0.96057	-0.09342
96	Developmental	Leaf serr 22	0.9191	0.1648	0.99393	-0.07399
97	Developmental	Leaf roll 10	0.999	0	0.99776	-0.27603
98	Developmental	Leaf roll 16	0.3944	0.1924	0.91407	-0.25769
99	Developmental	Leaf roll 22	0.3063	0.1937	0.92332	0.02477
100	Developmental	Rosette erect 22	0.5142	0.1862	0.94733	-0.10853
101	Developmental	Silique length 16	0.7452	0.2456	0.98456	-0.3788
102	Developmental	Silique length 22	0.9961	0.1453	1	-0.52789
103	Developmental	FT duration GH				
104	Developmental	LC duration GH	0.9064	0.1061	1	-0.03912
105	Developmental	LFS GH	0.8981	0.1048	1	-0.02945
106	Developmental	MT GH	0.5594	0.1987	0.95995	0.18534
107	Developmental	RP GH	0.1776	0.1933	0.84257	0.01922
			0.57100486			

traits and developmental traits in a world-wide collection of 199 Arabidopsis inbred lines.

	Adjusted				
Corr(BV, la	Heritability	Standard	Corr(obs,p	Corr(BV, la	Corr(BV, long.)
0.09685	0.5707	0.06302	0.98574	0.29127	0.00854
	0.5959	0.09489	0.95234	0.24172	0.04742
-0.10411	0.6287	0.07051	0.97947	0.26674	-0.13879
-0.05023	0.6287	0.07051	0.97947	0.26674	-0.13879
-0.11153	0.7693	0.09399	0.99719	0.14039	-0.14711
	0.6034	0.06991	0.98656	0.23493	-0.10545
-0.04495	0.6034	0.06991	0.98656	0.23493	-0.10545
-0.16496	0.6848	0.1037	0.99181	0.19641	-0.20447
0.04994	0.8136	0.1164	0.99535	0.07621	-0.0352
-0.06609	0.7292	0.1802	0.96606	0.12214	0.09284
0.16721	0.6216	0.1118	0.95444	0.25209	0.17911
0.04698	0.6336	0.08439	0.99029	0.24704	-0.05594
-0.02875	0.5967	0.07209	0.9882	0.22151	0.00006
0.17021	0.5735	0.1282	0.94977	0.23758	0.12103
0.00794	0.7974	0.08573	0.99268	0.14613	-0.10413
-0.03182	0.6215	0.09847	0.98417	0.16796	-0.063
-0.13888	0.6769	0.1222	0.98518	0.14236	-0.19467
-0.14679	0.3979	0.1434	0.8998	0.10381	-0.2292
0.03747	0.523	0.09443	0.97664	0.24105	-0.09797
-0.1687	0.6713	0.1775	0.97365	-0.0794	-0.22081
0.02752	0.604	0.0642	0.96728	0.29415	-0.03165
-0.3502	0.3591	0.1667	0.91366	-0.23969	-0.1983
0.00671	0.7148	0.07918	0.9928	0.15272	-0.0856
	0.626913				
	0.999	0	0.97927	0.0671	-0.11295
0.32534	0.5673	0.2761	0.94753	0.01668	0.1415
0.32127	0.5659	0.278	0.95571	0.03929	0.14785
0.25316	0.999	0	0.93155	-0.00633	-0.11131
-0.01243	0.999	0	0.99167	0.07919	0.08845
0.24275	0.6127	0.2918	0.96405	0.07718	0.23624
-0.00988	0.999	0	0.98067	0.06884	0.18038
0.10754	0.999	0	0.99498	0.08026	0.12939
0.29166	0.3427	0.2978	0.89657	-0.04052	0.15417
-0.05855	0.529	0.212	0.95755	-0.09157	-0.0577
-0.01126	0.4943	0.2163	0.93002	-0.1528	0.10012
-0.21997	0.1292	0.1798	0.86778	-0.08378	-0.05023
0.00448	0.7538	0.197	0.97877	-0.01282	-0.0695
0.00179	0.2178	0.1953	0.87419	0.01087	-0.01979
-0.08412	0.1316	0.1808	0.84673	-0.27793	-0.12058
-0.17654	1.00E-08	0	0.72128	-0.12063	-0.20509
0.18382	0.3814	0.2091	0.91308	0.19146	0.05069

	0.1288	0.1799	0.80815	-0.0425	0.22491
-0.32023	0.1346	0.1774	0.79002	-0.03389	0.13978
0.05269	0.9397	0.1756	0.98858	0.03348	-0.02537
0.11325	0.849	0.1721	0.97737	0.02543	-0.07878
-0.06567	0.7537	0.2028	0.96455	-0.1041	-0.09201
-0.59957	1.00E-08	0	0.79167	0.09476	-0.00719
	0.54463				
-0.21891	0.345	0.2704	0.89878	-0.21202	0.03827
-0.29341	0.3669	0.2325	0.90492	-0.22437	0.01196
-0.21498	0.5809	0.2799	0.92546	-0.20394	-0.28659
-0.31848	0.8267	0.1758	0.97697	-0.20911	-0.10658
0.27078	0.5926	0.249	0.9562	0.17328	0.04427
0.16305	0.4383	0.2934	0.94741	0.05212	-0.00897
-0.22419	0.9573	0.2315	0.98584	0.04548	-0.06636
-0.31135	0.5143	0.2719	0.95744	-0.17817	-0.12939
0.27172	0.4463	0.2894	0.9538	0.14111	0.168
0.09828	0.2206	0.2657	0.89798	0.05619	-0.087
0.14886	0.3315	0.294	0.91894	0.06979	-0.02908
-0.01813	0.2097	0.2559	0.86747	0.10625	-0.11256
-0.28914	1.00E-08	0	0.86425	0.16856	-0.18201
-0.07657	0.999	0	0.97927	0.0671	-0.11295
0.58546	0.07464	0.218	0.82955	0.16154	0.37839
0.2294	0.6669	0.2735	0.97495	0.11392	0.1082
-0.1723	0.999	0	0.99893	0.04467	-0.19905
0.23989	0.999	0	0.97553	0.02983	0.02016
	0.531591				
	0.8058	0.1188	0.94785	0.14124	-0.04233
0.3707	0.573	0.08448	0.95906	-0.06619	0.14607
	0.7235	0.1067	0.94375	0.08707	0.04918
-0.06188	0.6459	0.2057	0.96385	-0.20789	-0.09674
	0.6349	0.2455	0.96751	-0.16283	-0.08555
-0.10897	1.00E-08	0	0.79347	-0.04659	-0.18575
0.06655	0.00602	0.08884	0.79362	-0.04599	-0.13716
0.47478	0.2414	0.1811	0.84059	-0.0352	0.00436
0.05155	0.6096	0.1889	0.92912	0.02767	-0.05094
0.05652	0.4255	0.2084	0.90936	0.05214	-0.13709
-0.07095	0.2791	0.1934	0.87956	0.10293	-0.14602
0.15102	0.7876	0.1455	0.93771	-0.06852	0.03756
0.13692	0.3507	0.206	0.91064	-0.0278	0.09925
0.13582	0.6558	0.1997	0.95725	0.028	-0.06436
-0.16731	0.3286	0.2074	0.92971	0.0015	-0.09227
0.2834	0.06561	0.2525	0.89029	0.14835	0.04164
-0.21237	0.08541	0.2326	0.85108	0.00041	0.04499
-0.30496	1.00E-08	0	0.77054	-0.09652	0.07038

0.36447	0.848	0.1732	0.97435	0.13944	0.17777
-0.24244	0.9408	0.1912	0.99483	-0.07576	-0.17471
0.02789	0.7601	0.1044	0.95701	-0.20988	-0.10322
	0.7601	0.1044	0.95701	-0.20988	-0.10322
0.20441	0.7625	0.1043	0.98179	0.25261	0.12394
-0.00827	0.8249	0.1128	0.9817	0.19591	0.07544
	0.8589	0.1174	0.98146	0.1552	-0.0056
-0.12726	0.9778	0.1863	0.97365	0.088	-0.15241
0.00915	0.7339	0.1744	0.92413	0.02467	-0.07908
-0.02838	0.7339	0.1744	0.92413	0.02467	-0.07908
	0.9134	0.1804	0.96334	-0.10732	0.09992
	0.5164	0.1928	0.94778	-0.12866	0.12919
0.13162	0.6191	0.2034	0.95898	-0.09457	0.18688
0.00885	0.9566	0.1663	0.98741	-0.02591	0.12285
-0.12666	0.999	0	0.98873	-0.20861	-0.21615
-0.28249	0.3631	0.1976	0.91031	-0.07663	-0.0737
0.13305	0.3531	0.2096	0.92604	-0.05536	0.10265
-0.15454	0.5174	0.1909	0.92634	0.07435	-0.13921
0.13147	0.5405	0.2455	0.90519	-0.01607	0.01961
-0.09583	0.8999	0.1331	0.90397	-0.11643	-0.0464
	0.1947	0.212	0.81456	-0.19032	-0.1591
-0.04636	0.9146	0.1078	0.99785	-0.08354	-0.10343
-0.05239	0.8949	0.1051	0.9924	-0.11438	-0.15839
0.27686	0.5437	0.2083	0.96124	0.11537	0.21512
0.13963	0.1857	0.2106	0.83287	-0.06193	-0.02484
	0.577475				

Table S3. Genome-wide estimation of seven functional components of narrow-sense heritability

Trait ID	Trait Group	Trait name	Unadjusted		vg3	vg4	vg5	vg6
			vg1	vg2				
1	Flowering	LD	0	0.1749	0	0.1129	0.2943	0
2	Flowering	LDV	0.1888	0	0	0	0	0.4828
3	Flowering	SD	0	0	0	0	0.655	0
4	Flowering	SDV	0	0	0	0.4697	0.2246	0
5	Flowering	0W	0	0.1463	0	0	0.4336	0.1819
6	Flowering	2W	0	0.0106	0	0.2301	0.3818	0
7	Flowering	4W	0	0.0519	0	0.208	0.374	0
8	Flowering	8W	0	0.5861	0	0	0.0338	0
9	Flowering	FLC	0	0	0	0.026	0.5145	0.2265
10	Flowering	FRI	0	0.0277	0	0	0.636	0
11	Flowering	FT10	0	0	0.4772	0	0	0.2387
12	Flowering	FT16	0	0.09	0	0.1104	0.4186	0
13	Flowering	FT22	0	0	0	0.3629	0.1532	0.0738
14	Flowering	LN10	0	0	0.1179	0.2291	0	0.3092
15	Flowering	LN16	0	0	0	0.3354	0.3376	0.0941
16	Flowering	LN22	0	0	0	0.4055	0.2155	0
17	Flowering	8W GH FT	0	0.1372	0	0.5581	0	0
18	Flowering	8W GH LN	0	0	0.5432	0	0	0
19	Flowering	0W GH FT	0	0	0	0	0.5269	0
20	Flowering	0W GH LN	0	0	0	0	0.1318	0
21	Flowering	FT Field	0	0	0.4951	0.1613	0	0
22	Flowering	FT dm field	0.2102	0	0	0	0.1926	0
23	Flowering	FT GH	0	0	0	0	0.6584	0
24	Defense-re	AvrPphB	0	0	0	0	0.898	0
25	Defense-re	AvrRpm1	0	0.1534	0	0.999	0	0
26	Defense-re	AvrB	0	0	0	0.9988	0	0
27	Defense-re	AvrRpt2	0	0	0.567	0.0047	0.621	0
28	Defense-re	Emco5	0	0.999	0	0.0699	0	0
29	Defense-re	Emwa1	0	0	0	0.0242	0.5912	0
30	Defense-re	Emoy2	0	0	0	0.999	0.0925	0
31	Defense-re	Hiks1	0	0.1409	0.9948	0	0	0
32	Defense-re	Noco2	0	0	0	0.3966	0	0
33	Defense-re	At1	0	0.2398	0	0	0.2964	0
34	Defense-re	As	0	0	0	0	0.3606	0
35	Defense-re	Bs	0	0.1581	0	0	0	0
36	Defense-re	At2	0	0	0	0	0	0.781
37	Defense-re	As2	0	0.2657	0	0	0	0
38	Defense-re	At1 CFU2	0	0	0	0	0	0.144
39	Defense-re	As CFU2	0	0.0349	0	0	0	0
40	Defense-re	Bs CFU2	0	0	0	0.3092	0	0
41	Defense-re	At2 CFU2	0.0459	0.0123	0	0	0	0
42	Defense-re	As2 CFU2	0	0	0	0.1181	0	0
43	Defense-re	Trichome a	0	0.0848	0	0	0	0.2875

44	Defense-re	Trichome a	0.2433	0	0	0	0	0.6011
45	Defense-re	Bacterial ti	0	0.3877	0	0	0	0.392
46	Defense-re	Aphid num	0	0	0	0	0	0
47	Ionomics	Lithium	0	0.1085	0	0	0	0
48	Ionomics	Boron	0	0	0.5923	0	0	0
49	Ionomics	Sodium	0	0	0	0	0	0
50	Ionomics	Magnesium	0	0.1491	0	0	0	0
51	Ionomics	Phosphoru	0	0	0	0.0023	0	0
52	Ionomics	Sulfur	0	0.5256	0	0	0	0
53	Ionomics	Potassium	0.8335	0	0	0	0	0
54	Ionomics	Calcium	0	0	0	0	0	0.1358
55	Ionomics	Manganese	0	0.5436	0	0	0	0
56	Ionomics	Iron	0	0.3857	0	0.0383	0	0
57	Ionomics	Colbolt	0	0	0	0	0	0
58	Ionomics	Nickel	0	0	0	0.0063	0	0.3876
59	Ionomics	Copper	0	0.0924	0	0	0.0641	0
60	Ionomics	Zinc	0	0.999	0.2098	0	0	0.0072
61	Ionomics	Arsenic	0.2773	0	0	0	0	0
62	Ionomics	Selenium	0	0.6779	0	0	0	0
63	Ionomics	Molybdenu	0	0.0995	0.0711	0	0.999	0
64	Ionomics	Cadmium	0	0	0	0	0.9905	0
65	Developme	LES	0	0	0	0	0.8456	0
66	Developme	YEL	0	0.5906	0	0	0	0
67	Developme	LY	0	0	0	0	0.7693	0
68	Developme	FW	0.1334	0	0	0	0	0.28
69	Developme	DW	0.3338	0.0274	0	0	0	0.0746
70	Developme	Chlorosis 1	0	0	0	0	0	0
71	Developme	Chlorosis 1	0	0	0	0	0	0
72	Developme	Chlorosis 2	0	0.0057	0	0.3126	0	0
73	Developme	Anthocyan	0.4228	0.132	0	0	0	0.211
74	Developme	Anthocyan	0	0	0	0.3695	0	0
75	Developme	Anthocyan	0	0	0	0.2166	0.0886	0
76	Developme	Seed dorm	0	0	0.8381	0	0	0
77	Developme	Germ 10	0	0.2245	0	0	0	0
78	Developme	Germ 16	0	0	0	0	0	0.6681
79	Developme	Germ 22	0	0	0	0	0	0.3972
80	Developme	Seedling gr	0	0	0	0	0	0
81	Developme	Vern growt	0	0	0	0	0	0
82	Developme	After vern g	0	0	0	0	0	0
83	Developme	Secondary	0	0	0	0	0	0.8807
84	Developme	Germ in da	0	0	0	0	0	0.9262
85	Developme	DSDS50	0	0	0	0	0.7643	0
86	Developme	Seed bank	0	0	0	0	0.1771	0.2617
87	Developme	Storage 7 d	0	0	0	0.4148	0.3493	0
88	Developme	Storage 28	0	0.035	0	0	0.7883	0
89	Developme	Storage 56	0	0	0	0	0.8613	0
90	Developme	Hypocotyl	0	0	0.2859	0	0.675	0

91	Developme	Width 10	0	0.0852	0	0	0	0
92	Developme	Width 16	0	0	0	0	0	0.789
93	Developme	Width 22	0.7972	0	0	0	0	0
94	Developme	Leaf serr 10	0.1113	0.1419	0.3369	0	0	0
95	Developme	Leaf serr 16	0	0	0.3323	0	0.1766	0
96	Developme	Leaf serr 22	0	0	0	0	0.5463	0.3491
97	Developme	Leaf roll 10	0.91	0.0725	0	0	0	0.1433
98	Developme	Leaf roll 16	0	0.3695	0	0	0	0
99	Developme	Leaf roll 22	0	0	0	0	0	0
100	Developme	Rosette ere	0	0.2867	0	0	0	0.2557
101	Developme	Silique leng	0	0	0.7416	0	0	0
102	Developme	Silique leng	0	0	0.9978	0	0	0
103	Developme	FT duration	0	0	0	0	0.0824	0
104	Developme	LC duration	0	0.2399	0.0322	0.0758	0.3985	0.1706
105	Developme	LFS GH	0	0	0	0	0.5674	0.0791
106	Developme	MT GH	0	0.3157	0	0	0	0
107	Developme	RP GH	0	0.1983	0	0	0	0

Draft

es for 107 flowering, defense, ionomoics and developmental traits in a world-wide collection of 1

vg7	ve	vg_se1	vg_se2	vg_se3	vg_se4	vg_se5	vg_se6	vg_se7
0	1.00E-08	0	0.3052	0	0.4205	0.3741	0	0
0	0.04732	0.623	0	0	0	0	0.6299	0
0	4.63E-06							
0	0.02996	0	0	0	0.5123	0.5093	0	0
0	1.00E-08	0	0.4666	0	0	0.5289	0.4605	0
0	1.00E-08	0	0.3635	0	0.5047	0.4467	0	0
0	0.008104	0	0.4855	0	0.6696	0.5929	0	0
0.076	0.02369	0	0.386	0	0	0.3947	0	0.2606
0.0323	0.04093	0	0	0	0.7203	0.601	0.7641	0.3768
0	0.3078	0	0.5109	0	0	0.5298	0	0
0	0.0863							
0	0.04044	0	0.3212	0	0.4455	0.3983	0	0
0	0.01746	0	0	0	0.4494	0.3618	0.388	0
0	0.1516	0	0	0.9505	0.7736	0	0.7314	0
0.0198	0.0131	0	0	0	0.6383	0.5212	0.6644	0.3307
0	0.0711	0	0	0	0.4571	0.4557	0	0
0	0.09668	0	0.4658	0	0.4744	0	0	0
0	0.2548	0	0	0.1462	0	0	0	0
0	0.08036	0	0	0	0	0.09195	0	0
0.5561	0.2038	0	0	0	0	0.4099	0	0.4594
0	1.00E-08	0	0	0.5103	0.5204	0	0	0
0	0.4626	0.5444	0	0	0	0.5212	0	0
0.0621	0.002372	0	0	0	0	0.2401	0	0.2352
0	1.00E-08	0	0	0	0	0.1346	0	0
0	1.00E-08	0	0.1758	0	0	0	0	0
0	0.1044							
0	1.00E-08	0	0	1.8502	1.9383	1.512	0	0
0	1.00E-08	0	0	0	0.1598	0	0	0
0	0.381	0	0	0	1.4122	1.419	0	0
0	1.00E-08	0	0	0	0	0.1755	0	0
0	1.00E-08	0	1.1216	1.1154	0	0	0	0
0	0.5951	0	0	0	0.2813	0	0	0
0	0.4823	0	0.5162	0	0	0.5214	0	0
0	0.656	0	0	0	0	0.1924	0	0
0	0.8439	0	0.1617	0	0	0	0	0
0	0.2736	0	0	0	0	0	0.1861	0
0	0.7358	0	0.1798	0	0	0	0	0
0	0.8576	0	0	0	0	0	0.1665	0
0	0.9652	0	0.1251	0	0	0	0	0
0	0.6852	0	0	0	0.1865	0	0	0
0	0.9421	0.4882	0.4609	0	0	0	0	0
0	0.8796	0	0	0	0.1531	0	0	0
0.5986	0.000018							

0	0.05676							
0	0.1587	0	0.8196	0	0	0	0.8433	0
0.0773	0.9213							
0.2975	0.5502	0	0.5221	0	0	0	0	0.5721
0	0.3223	0	0	0.2318	0	0	0	0
0.5691	0.4252							
0.7187	0.03915	1.1679	0.8244	0	0	0	0	0.8005
0.6677	0.279							
0.0102	0.5002	0	0.5499	0	0	0	0	0.5486
0.1117	0.136	0.8226	0	0	0	0	0	0.8426
0.422	0.4048	0	0	0	0	0	0.8022	0.832
0	0.47	0	0.2648	0	0	0	0	0
0	0.5894	0	1.0617	0	1.0702	0	0	0
0.3438	0.6616	0	0	0	0	0	0	0.2771
0	0.5906							
0	0.8451	0	0.9042	0	0	0.9056	0	0
0	1.00E-08	0	0	1.0325	0	0	0.972	0
0	0.6584	0.2491	0	0	0	0	0	0
0.075	0.2985	0	0.5676	0	0	0	0	0.5735
0	1.00E-08	0	1.0327	1.0172	0	0	0	0
0	0.1127	0	0	0	0	0.2086	0	0
0	1.00E-08	0	0	0	0	0.1233	0	0
0	1.00E-08	0	0.08614	0	0	0	0	0
0	1.00E-08	0	0	0	0	0.1122	0	0
0.3133	0.1654	1.4215	0	0	0	0	1.4676	0.7652
0.2474	0.2736	1.6799	0.9299	0	0	0	1.6619	0.8207
0	0.999	0	0	0	0	0	0	0
0	0.999	0	0	0	0	0	0	0
0	0.6514	0	0.5448	0	0.5615	0	0	0
0	0.2807	0.9707	0.5507	0	0	0	0.9376	0
0	0.6292	0	0	0	0.1907	0	0	0
0	0.6717	0	0	0	0.6814	0.6689	0	0
0	0.0133	0	0	0.1506	0	0	0	0
0.1775	0.6059	0	0.3262	0	0	0	0	0.3387
0	0.368	0	0	0	0	0	0.1946	0
0	0.6247	0	0	0	0	0	0.2013	0
0.3197	0.6831	0	0	0	0	0	0	0.2894
0.0918	0.9091	0	0	0	0	0	0	0.2072
0	0.999	0	0	0	0	0	0	0
0	0.03516	0	0	0	0	0	0.1681	0
0	0.04578	0	0	0	0	0	0.1812	0
0	0.01665	0	0	0	0	0.1217	0	0
0	0.5173	0	0	0	0	0.8579	0.9085	0
0	1.00E-08	0	0	0	0.7165	0.7168	0	0
0	1.00E-08	0	0.5494	0	0	0.5679	0	0
0	1.00E-08	0	0	0	0	0.1167	0	0
0	0.05303							

0.5998	0.319	0	0.3481	0	0	0	0	0.3996
0	0.2375	0	0	0	0	0	0.1753	0
0	0.2846	0.1884	0	0	0	0	0	0
0	0.376	0.9448	0.5527	1.0107	0	0	0	0
0.0576	0.4476							
0	0.1741	0	0	0	0	0.6197	0.6309	0
0.0383	1.00E-08	1.0039	0.5577	0	0	0	0.988	0.4481
0.0324	0.5709	0	0.3076	0	0	0	0	0.297
0.385	0.633	0	0	0	0	0	0	0.2021
0	0.4104	0	0.4787	0	0	0	0.5022	0
0	0.2715	0	0	0.2377	0	0	0	0
0	1.00E-08	0	0	0.1455	0	0	0	0
0.0972	0.8093							
0	1.00E-08							
0.2431	1.00E-08	0	0	0	0	0.5351	0.7538	0.3977
0.2694	0.3585							
0	0.7953	0	0.1891	0	0	0	0	0

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199 Arabidopsis inbred lines.

	Adjusted							
ve_se	vg1	vg2	vg3	vg4	vg5	vg6	vg7	ve
0	0	0.2795	0	0	0.291	0	0	0
0.04034	0	0.0989	0	0	0	0.4938	0	0.0495
	0	0	0	0	0.618	0	0	0
0.02772	0	0	0	0.3097	0.2626	0	0	0.068
0	0	0.1937	0	0	0.1402	0.4245	0	0
0	0	0.2906	0	0	0.3091	0	0.0075	0
0.02513	0	0.3588	0	0	0.2276	0	0	0.0052
0.03672	0	0.5176	0	0	0.0389	0	0.1206	0.0312
0.04361	0	0	0	0.0754	0.4834	0.1532	0.0907	0.0394
0.1181	0	0.1293	0	0	0.6047	0	0	0.2475
	0	0	0	0	0.1289	0.4863	0	0.1118
0.02761	0	0.1332	0	0.0749	0.3572	0.0471	0	0.0402
0.02214	0	0	0	0.2546	0.1188	0.2054	0	0.0087
0.075	0	0.1509	0	0.0744	0	0.3399	0	0.1723
0.03059	0.0099	0	0	0.3701	0.2484	0.1817	0	0
0.03902	0	0	0	0.3648	0.2353	0	0.0013	0.0751
0.05068	0	0.1763	0	0.491	0	0	0	0.1112
0.1016	0	0	0	0	0	0.3992	0	0.2907
0.04065	0	0	0	0	0.4625	0.0475	0	0.0808
0.1161	0	0	0	0	0.0888	0	0.6157	0.1935
0	0	0	0	0.2482	0	0.3527	0	0
0.1356	0.2483	0	0	0	0.1039	0	0	0.4909
0.02263	0	0	0	0	0.632	0	0.0783	0.0048
0	0	0	0	0	0.9039	0	0	0
0	0	0.1446	0	0.999	0	0	0	0
	0	0	0.121	0.999	0	0	0	0
0	0	0	0.999	0	0.147	0	0	0
0	0	0.999	0	0.0912	0	0	0	0
0.2044	0	0.0084	0	0	0.623	0	0	0.3776
0	0	0	0	0.8731	0.227	0	0	0
0	0	0.1583	0.999	0	0	0	0	0
0.2495	0	0	0	0.3593	0	0	0	0.6126
0.1533	0	0.2225	0	0	0.3364	0	0	0.4749
0.171	0	0	0	0	0.3789	0.0966	0	0.5657
0.171	0	0.1617	0	0	0	0	0	0.8488
0.1221	0	0	0	0	0	0.8051	0	0.2623
0.1718	0	0.2732	0	0	0	0	0	0.7358
0.1779	0	0	0	0	0	0.1729	0	0.842
0.1595	0	0.0322	0	0	0	0	0	0.9484
0.1718	0	0	0	0.2793	0.0635	0	0.0451	0.6242
0.1683	0	0.1284	0	0	0	0	0.0229	0.8598
0.1693	0	0	0	0.1469	0	0	0	0.8391
	0	0.1106	0.1753	0	0	0.2927	0.3829	0.0154

	0.2916	0	0	0	0	0.5544	0	0.0555
0.1162	0	0	0	0	0	0.7667	0	0.1456
	0	0	0	0	0	0	0	0.9132
0.2347	0	0.124	0	0	0.0741	0	0.1549	0.5883
0.1696	0	0	0.3896	0	0	0	0	0.4218
	0	0	0	0	0	0	0.6621	0.356
0.08647	0.0776	0	0	0	0	0	0.7976	0.0296
	0	0	0	0.1145	0	0	0.5112	0.3076
0.2301	0	0.5231	0	0	0	0	0	0.5094
0.1244	0.8038	0	0	0	0	0	0.1577	0.1351
0.2136	0	0	0	0	0	0.1225	0.4116	0.4298
0.2094	0	0.5263	0	0	0	0	0	0.497
0.2342	0	0.3711	0	0	0	0	0	0.6051
0.2552	0	0	0	0	0	0	0.4124	0.6164
	0	0	0	0	0	0.248	0	0.6778
0.2443	0	0.0528	0	0	0	0	0	0.954
0	0	0.999	0	0.2187	0	0	0	0
0.2364	0.0913	0	0	0	0	0	0	0.779
0.1779	0	0.5327	0.1838	0	0	0	0	0.3286
0	0	0.1055	0.0835	0	0.999	0	0	0
0.08814	0	0	0	0	0.997	0	0	0.1104
0	0	0	0	0	0.8064	0	0	0
0	0	0.5665	0	0	0	0	0	0
0	0	0	0	0	0.7257	0	0	0
0.1309	0	0	0	0	0	0.3714	0.2968	0.1865
0.1734	0.318	0	0	0	0	0.188	0.1466	0.2921
0	0	0	0	0	0	0	0	0.999
0	0	0	0	0	0.0697	0	0	0.9424
0.166	0	0.1902	0	0.072	0	0	0	0.6547
0.1209	0.3775	0.1036	0	0	0.0973	0.056	0	0.346
0.1682	0	0	0	0.4541	0	0	0	0.5616
0.1675	0	0	0	0.2685	0	0	0	0.6997
0.03442	0	0	0.7827	0	0	0	0	0.0109
0.1735	0	0.3139	0	0	0	0	0.1073	0.5984
0.1418	0	0.1144	0	0	0	0.5907	0	0.335
0.1772	0	0	0	0	0	0.4293	0	0.6086
0.2725	0	0	0.0233	0	0	0	0.0627	0.8885
0.2325	0.098	0	0	0	0	0	0	0.895
0	0	0.0134	0	0	0	0	0	0.9891
0.06246	0.1497	0.0926	0	0.0017	0.1506	0.3223	0	0.0969
0.07133	0	0	0	0	0	0.9445	0	0.0444
0.03118	0	0	0	0	0.7132	0	0	0.0204
0.2223	0	0	0	0	0.1784	0	0.2738	0.4855
0	0	0	0	0.6194	0.1396	0	0	0
0	0	0	0	0	0.8163	0	0	0
0	0	0	0	0	0.8514	0	0	0
	0	0	0	0	0.964	0	0	0.0473

0.1376	0	0.2398	0	0	0	0	0.5456	0.2002
0.1101	0	0	0	0	0	0.7841	0	0.247
0.1227	0.8659	0	0	0	0.0549	0	0	0.1893
0.1392	0	0.3833	0.1178	0	0	0	0	0.4393
	0	0	0.4693	0	0.0855	0	0.0668	0.4129
0.08951	0	0	0	0	0.5147	0.4169	0	0.1541
0	0.9674	0	0	0	0	0.0675	0	0.0636
0.1642	0	0.3262	0	0.0367	0	0	0	0.5991
0.1782	0	0	0	0	0	0	0.4083	0.6232
0.1419	0	0.2028	0	0	0	0.3398	0	0.405
0.158	0	0	0.2534	0	0	0	0.3331	0.3233
0	0	0.2831	0.3266	0.3037	0	0	0	0.0034
	0	0	0	0	0.0816	0	0.117	0.8036
	0	0.2325	0	0.1341	0.3302	0.2261	0	0
0	0	0	0	0	0.5967	0	0.2895	0
	0	0.3441	0	0	0	0	0.212	0.3903
0.1923	0	0.2056	0	0	0	0	0	0.7963

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vg_se1	vg_se2	vg_se3	vg_se4	vg_se5	vg_se6	vg_se7	ve_se
0	0.2618	0	0	0.2615	0	0	0
0	0	0	0.4707	0.4699	0	0	0.04319
0	0.4845	0	0	0.5473	0.5126	0	0
0	0.3196	0	0	0.3328	0	0.1648	0
0	0.3927	0	0	0.3904	0	0	0.02327
0	0.3873	0	0	0.3988	0	0.2721	0.04472
0	0	0	0.7314	0.6074	0.7764	0.3933	0.04639
0	0.5196	0	0	0.535	0	0	0.1063
0	0	0	0	0.3814	0.3995	0	0.06257
0	0.3271	0	0.5243	0.4091	0.4308	0	0.03265
0	0	0	0.4365	0.3509	0.3823	0	0.021
0	0.4237	0	0.6103	0	0.5603	0	0.08076
0.6993	0	0	0.598	0.5171	0.6121	0	0
0	0	0	0.4892	0.4525	0	0.2362	0.04612
0	0.4669	0	0.4739	0	0	0	0.05778
0	0	0	0	0	0.1433	0	0.1106
0	0	0	0	0.3919	0.3912	0	0.04538
0	0	0	0	0.4203	0	0.4744	0.1189
0	0	0	0.3174	0	0.3027	0	0
0	0	0	0	0.2429	0	0.2397	0.02502
0	0	0	0	0.137	0	0	0
0	0.1764	0	0	0	0	0	0
0	0	0.1678	0	0	0	0	0
0	0	0	0	0.1761	0	0	0
0	0	0	0.1653	0	0	0	0
0	1.0297	0	0	1.0551	0	0	0.207
0	0	0	1.5053	1.4859	0	0	0
0	0.1825	0	0	0	0	0	0
0	0.5297	0	0	0.5374	0	0	0.1576
0	0	0	0	0.6221	0.6457	0	0.1795
0	0.1771	0	0	0	0	0	0.1812
0	0	0	0	0	0.191	0	0.1237
0	0.192	0	0	0	0	0	0.1794
0	0	0	0	0	0.1899	0	0.1918
0	0.1417	0	0	0	0	0	0.1684
0	0	0	0.7841	0.7196	0	0.3627	0.1809
0	0.2997	0	0	0	0	0.2968	0.1878
0	0	0	0.1737	0	0	0	0.1789

0	0	0	0	0	0.1998	0	0.1125
0	0	0	0	0	0	0	0.1354
0	0.9196	0	0	0.9705	0	0.5975	0.2424
0	0	0.2282	0	0	0	0	0.1884
0	0	0	0	0	0	0.2884	0.2144
0.7584	0	0	0	0	0	0.8278	0.08481
0	0	0	0.638	0	0	0.6997	0.1893
0	0.2806	0	0	0	0	0	0.2242
0.8701	0	0	0	0	0	0.8961	0.1271
0	0	0	0	0	0.8341	0.8613	0.2237
0	0.2775	0	0	0	0	0	0.2205
0	0.2684	0	0	0	0	0	0.234
0	0	0	0	0	0	0.3037	0.2652
0	0.2287	0	0	0	0	0	0.2566
0	0	0	0.178	0	0	0	0
0	1.0954	1.1101	0	0	0	0	0.1816
0	1.0723	1.0572	0	0	0	0	0
0	0	0	0	0.2112	0	0	0.08732
0	0	0	0	0.1189	0	0	0
0	0.08353	0	0	0	0	0	0
0	0	0	0	0.107	0	0	0
0	0	0	0	0	0.717	0.7435	0.1373
1.5767	0	0	0	0	1.6204	0.8011	0.1778
0	0	0	0	0	0	0	0
0	0	0	0	0.1557	0	0	0.1759
0	0.5261	0	0.5349	0	0	0	0.1642
0.9711	0.5536	0	0	0.6665	0.9201	0	0.136
0	0	0	0.2025	0	0	0	0.1678
0	0	0	0.1862	0	0	0	0.1731
0	0	0.1419	0	0	0	0	0.03122
0	0.3352	0	0	0	0	0.3359	0.1778
0	0.5245	0	0	0	0.5612	0	0.1381
0	0	0	0	0	0.2131	0	0.183
0	0	0.6171	0	0	0	0.6183	0.2757
0.2367	0	0	0	0	0	0	0.2507
0	0.199	0	0	0	0	0	0.2332
0	0	0	0	0	0.1859	0	0.0715
0	0	0	0	0.117	0	0	0.03231
0	0	0	0	0.5051	0	0.5361	0.2211
0	0	0	0.7207	0.7127	0	0	0
0	0	0	0	0.1116	0	0	0
0	0	0	0	0.1164	0	0	0
0	0	0	0	0.1829	0	0	0.05658

0	0.3452	0	0	0	0	0.3869	0.1104
0	0	0	0	0	0.182	0	0.1164
0.7068	0	0	0	0.6746	0	0	0.101
0	0.5417	0.5579	0	0	0	0	0.1498
0	0	0.943	0	0.7231	0	0.4777	0.1534
0	0	0	0	0.6331	0.6462	0	0.08752
0.915	0	0	0	0	0.9071	0	0.05866
0	0.5569	0	0.5629	0	0	0	0.1665
0	0	0	0	0	0	0.2138	0.1847
0	0.4822	0	0	0	0.5113	0	0.1449
0	0	0.7138	0	0	0	0.7495	0.186
0	0.8729	1.4911	1.4955	0	0	0	0.02684
0	0.5798	0	0.8542	0.7137	0.5567	0	0
0	0	0	0	0.2938	0	0.2658	0
0	0.3747	0	0	0	0	0.386	0.1613
0	0.2039	0	0	0	0	0	0.202

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