Overcompensation in Response to Herbivory in *Arabidopsis thaliana*: The Role of Glucose-6-Phosphate Dehydrogenase and the Oxidative Pentose-Phosphate Pathway

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ABSTRACT That some plants benefit from being eaten is counterintuitive, yet there is now considerable evidence demonstrating enhanced fitness following herbivory (*i.e.*, plants can overcompensate). Although there is evidence that genetic variation for compensation exists, little is known about the genetic mechanisms leading to enhanced growth and reproduction following herbivory. We took advantage of the compensatory variation in recombinant inbred lines of *Arabidopsis thaliana*, combined with microarray and QTL analyses to assess the molecular basis of overcompensation. We found three QTL explaining 11.4, 10.1, and 26.7% of the variation in fitness compensation, respectively, and 109 differentially expressed genes between clipped and unclipped plants of the overcompensating ecotype Columbia. From the QTL/microarray screen we uncovered one gene that plays a significant role in overcompensation: glucose-6-phosphate-1-dehydrogenase (*G6PDH1*). Knockout studies of Transfer-DNA (T-DNA) insertion lines and complementation studies of *G6PDH1* verify its role in compensation. *G6PDH1* is a key enzyme in the oxidative pentose-phosphate pathway that plays a central role in plant metabolism. We propose that plants capable of overcompensating reprogram their transcriptional activity by up-regulating defensive genes and genes involved in energy metabolism and by increasing DNA content (via endoreduplication) with the increase in DNA content feeding back on pathways involved in defense and metabolism through increased gene expression.

THE loss of plant tissue to herbivores is an important selective agent shaping plant phenotypes. Most studies of plant adaptation, to date, have focused on the evolution of structural or chemical defensive traits that reduce or prevent tissue damage by herbivores (Berenbaum *et al.* 1986; Mauricio *et al.* 1997; Agrawal 1998). However, herbivores may also select for traits that allow plants to maintain fitness in the face of tissue loss (Stowe *et al.* 2000). Plant genotypes that can compensate for tissues lost with little or no decrement in fitness relative to those that are undamaged represent such an example and are termed "tolerant" (see Stowe *et al.* 2000 for a review). Interest in tolerance was motivated by empirical studies demonstrating that herbivore damage, under certain circumstances, can increase, rather than decrease, plant reproductive success (a specialized case termed "overcompensation," *i.e.*, increased flower, fruit, and seed production following herbivory). Specifically, studies by Paige and Whitham (1987) showed that when mule deer and elk removed 95% or more of the aboveground biomass of the monocarpic biennial scarlet gilia, *Ipomopsis aggregata*, the product of lifetime seed production, seed germination, and seedling survival averaged 3.0 times that of uneaten controls (see also Paige 1992, 1994, 1999). Since the initial study of Paige and Whitham (1987) evidence for increased flower, fruit, and seed production following herbivory has also been found for numerous plant species including *Ipomopsis arizonica* (Maschinski and Whitham 1989), *Gentianella campestris*, *G. amarella* (Nilsson *et al.* 1996; Lennartsson *et al.* 1997), *Arabidopsis thaliana* (Mauricio *et al.* 1997; Weinig *et al.* 2003), and *Erysimum strictum* (Rautio *et al.* 2005) to name but a few.

There is also evidence that genetic variation for tolerance/overcompensation exists. For example, studies comparing

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historically grazed and ungrazed populations of the plant *G. campestris* indicate that repeatedly grazed populations overcompensate, while ungrazed populations remain completely intolerant (Lennartsson *et al.* 1997). Furthermore, numerous genetic lineages within a plant species exhibit repeatable patterns of overcompensation, whereas others express only patterns of equal or undercompensation (Mauricio *et al.* 1997; Tiffin and Rausher 1999; Juenger and Bergelson 2000; Weinig *et al.* 2003). Although these observations provide evidence that genetic variation for compensation exists, little is known about the genetic mechanisms leading to enhanced growth and reproduction in plant species exhibiting growth compensation.

A recent study by Scholes and Paige (2011) showed that *Arabidopsis* sometimes responds to the removal of apical dominance at the whole-genome level through endoreduplication, the replication of the genome without mitosis, leading to endopolyploidy, an increase in cellular chromosome number. Different ecotypes of *A. thaliana* show different degrees of endoreduplication in response to loss of apical dominance, and the degree of endopolyploidy achieved is positively correlated with measures of fitness (*i.e.*, the higher the DNA content the higher the fitness in the context of removal of apical dominance). Endoreduplication may have genetic effects that could lead to rapid regrowth and enhanced fitness by increasing gene expression through additional gene copies (Barow 2006). Although we know a great deal about the genetic basis of endoreduplication *per se* (Vlieghe *et al.* 2005; Imai *et al.* 2006; Yoshizumi *et al.* 2006) and have evidence that it plays a role in fitness compensation (Scholes and Paige 2011) we still do not know the underpinning genes or gene pathways affecting fitness compensation following endoreduplication in *Arabidopsis* (or any other plant species exhibiting growth compensation).

As a first step, we have taken advantage of the known compensatory variation in the annual plant *A. thaliana*, combined with commercially available microarrays and QTL analyses to begin to assess the molecular basis of overcompensation (increased fitness) following apical damage. In addition, we use a gene knockout and complementation approach to assess the phenotypic effects of one promising candidate gene uncovered from the microarray/QTL screen. Specifically, we (1) characterize fitness variation, following the removal of apical dominance, of recombinant inbred lines (RILs) generated from a cross between Landsberg *erecta* × Columbia; (2) determine seasonal variation in the compensatory response; (3) identify QTL responsible for the variation in compensation; (4) quantify differential gene expression underlying clipped and unclipped individuals of the Columbia ecotype using a commercially available microarray platform; (5) combine QTL and microarray data to narrow the genes responsible for the compensatory response; (6) evaluate the compensatory response of Transfer DNA (T-DNA) knockout lines of a promising candidate gene, glucose-6-phosphate-1-dehydrogenase (*G6PDH1*, At5g35790.1); (7) perform quantitative RT-PCR (qRT-PCR) on *G6PDH1* to verify differences in expression between overcompensating (Columbia) and undercompensating (Landsberg *erecta*) plants; and (8) construct and assess the fitness response of a transgenic line for the complementation of *G6PDH1*. Twenty-five years ago we published the first empirical data supporting the idea that herbivore damage can lead to enhanced fitness (Paige and Whitham 1987). Here we present the first evidence for the molecular basis of this response.

Materials and Methods

Fitness variation

A total of 96 RILs (Lister and Dean 1993) of *A. thaliana* developed from a cross between Columbia (an overcompensating genotype) and Landsberg *erecta* (an undercompensating genotype) were used to assess fitness variation following the removal of apical dominance (to simulate mammalian herbivory) (Scholes and Paige 2011). The 96 F_2 lines were advanced through inbreeding and single-seed descent for more than eight generations (Lister and Dean 1993) and are available through The Arabidopsis Information Resource. The RILs and their parental lines (Columbia and Landsberg *erecta*) were grown for two seasons (Spring 2007 and Fall 2008) in a greenhouse on the campus of the University of Illinois, Champaign, under 12 hr of light ($\sim$100 μE/m^2/sec) and dark. Plants were grown individually in 3.5-inch pots using LI Sunshine mix. Temperatures within the greenhouse ranged from 22° to 26°. Seeds/seedlings were kept moist during germination, and plants were watered daily to maintain soil moisture without saturating the soil. Plants were not fertilized. Ten plants per line (960 plants) were grown from seed, and half (five per line) were randomly chosen and clipped at a 6-cm inflorescence height down to $\sim$1 cm to simulate mammalian herbivory; the remaining five served as undamaged controls. At the end of the flowering season the numbers of siliques per plant were recorded. Our previous studies have shown that siliques are a good measure of plant fitness in that there are no significant differences in seed weights or germination success between clipped and unclipped plants of either Columbia or Landsberg *erecta*. In addition, clipped plants of Columbia produced significantly greater numbers of seed, whereas clipped plants of Landsberg *erecta* produced significantly fewer seeds (Scholes and Paige 2011) in comparison to unclipped controls. The seeds from unclipped plants collected during the first season were used to generate the second-season plants.

Potential differences in silique production were assessed using an Analysis of Variance (Systat 13) comparing plants with apical meristem damage to undamaged controls for each recombinant inbred line. Comparisons were made both within and between years to assess fitness variation among RILs and within-line repeatability across the 2 years. Silique counts were square-root-transformed to approximate normality.

RILs were classified as under- (silique production significantly lower than the undamaged control), equal (silique production not statistically different from the undamaged control), or overcompensators (silique production significantly higher than the undamaged control) based on an Analysis of Variance for each RIL and year.

QTL analysis

QTL were identified by importing phenotypic (differential fitness data) and genotypic data sets (Nottingham Arabidopsis Stock Centre, AtEnsembl, http://atensembl.arabidopsis.info) into QTL Cartographer version 2.5 (Wang *et al.* 2010). Fitness data were pooled from 2 years using the average response across years and subtracting clipped from unclipped plants for each RIL. There were 14 of 96 lines for which we had only 1 year's data; these were used in our QTL mapping study as well using Least Square (LS) means of fitness to adjust for unbalanced measures. A total of 141 markers equally distributed on all chromosomes with an average interval of ~4.5 cM were selected (Zeng 1994). The data were initially analyzed using composite interval mapping (CIM) (Jansen and Stam 1994; Zeng 1994) to find QTL. Cofactors for CIM were selected from the forward and backward regression option. Significant QTL (LOD score of 2.5 and above) (Zeng 1994) from CIM were used to find other significant QTL and interactions among QTL elsewhere in the genome using multiple interval mapping. The model that minimized Akaike's information criterion with penalty = 1 (Jansen 1993) was selected and applied to estimate the additive effect and the proportion of the fitness variation explained by each QTL. Effect sizes were calculated in QTL Cartographer version 2.5 (Wang *et al.* 2010) as the average percentage residual variance attributed to a QTL after removing the effects of covariates and all other QTL.

Although QTL can help in identifying regions of the genome responsible for compensation, it is difficult to identify specific candidate genes, as a single QTL likely contains hundreds of genes [a single QTL ranges from 10 to 20 cM in size with ~1 cM of *Arabidopsis* covering 210 kb of the genome (Peters *et al.* 2001)] of which some may and some may not be responsible for observed patterns of fitness compensation. Considering the number of QTL obtained, we combined QTL mapping with microarray expression data to help in identifying potential candidate genes. Wayne and McIntyre (2002), for example, successfully combined data from QTL and microarrays to identify genes responsible for ovariole number in *Drosophila melanogaster.*

Microarray analysis

To identify potential candidate genes located within a QTL region, we carried out a microarray analysis on the Columbia ecotype (one that exhibits patterns of overcompensation) comparing clipped and unclipped individuals (data online at http://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc+GSE44781). Plants were grown in a greenhouse on the campus of the University of Illinois, Champaign, under 12 hr of light (~100 μE/m^2/sec) and dark. Forty plants were grown individually in 3.5-inch pots using LI Sunshine mix. Temperatures within the greenhouse ranged from 22° to 26°. Seeds/seedlings were kept moist during germination, and plants were watered daily to maintain soil moisture without saturating the soil. Plants were not fertilized. Axillary tissue was collected 6 days after clipping from both clipped (meristematic regrowth tissue) and unclipped plants (axillary meristematic tissue that naturally arises prior to clipping—similar in position, size, and location at the base of the unclipped plants' primary inflorescence); three Affymetrix oligonucleotide arrays with eight pooled clipped plants/chip and two Affymetrix oligonucleotide arrays with eight pooled unclipped plants/chip were compared in this experiment. We used the *Arabidopsis* Affymetrix GeneChip containing >22,500 probe sets representing ~24,000 gene sequences. This array is based on information from the International Arabidopsis Sequencing Project completed in December 2000 and is constructed by light-directed synthesis of oligonucleotides directly onto a glass "chip" approximately the size of glass coverslip. Each gene is represented on the array by a set of 20 oligonucleotide probes representing 25-mer sequences from some portion of the gene. Gene expression in a target sample is assessed by hybridization.

Total RNA was extracted with standard TRIzol (Life Technologies, Carlsbad, California) protocols from clipped (n = 3 chips) and unclipped (n = 2 chips) plants. The quality of the RNA was checked at 260 and 280 nm for determination of sample purity and concentration using a nano-drop. Messenger RNA was reverse-transcribed and labeled with the MessageAmp kit (Ambion, Austin, TX) and biotin-labeled dCTP and dGTP (ENZO Diagnostics, Farmingdale, NY). Affymetrix *Arabidopsis* GeneChip Arrays (Version 2.0) were hybridized at the University of Illinois Keck Center. Feature intensities on each chip were quantified with MAS 5.0 software. Following hybridization, the perfect match (PM) probes for all arrays were initially quantile-normalized with the Affy package in Bioconductor (Irizarry *et al.* 2003) to remove nonbiological variation among arrays. Only the PM data were used for the remainder of the analysis, and mismatch (MM) probes were ignored because they tend to increase random noise in the data. Data were analyzed using a t-test for each gene comparing clipped and unclipped plants. We controlled for multiple testing with a false discovery rate of $P < 0.01$.

Genes with significant expression upon clipping based on the microarray analysis were then analyzed for gene ontology. Biological process and molecular function information for each gene was obtained via AmiGo Slimmer Tool (v.1.8) analysis of the Gene Ontology (http://www.geneontology.org) database using the Plant GO Slim term set.

qRT-PCR was also performed on Columbia and Landsberg *erecta* plants to verify differences in expression in *G6PDH1* between overcompensating and undercompensating ecotypes, respectively. Total RNA was isolated with

TRIzol (Invitrogen, Carlsbad, CA) from rosette/cauline leaf material from clipped and unclipped Columbia and Landsberg *erecta* plants. Rosette/axillary meristematic tissues were collected at five time points [1 day before the inflorescence reached 6 cm (the height threshold for clipping), 1 day after, 5 days after, 15 days after, and at 50% flowering) in both clipped and unclipped plants to capture the time course of variation in gene expression patterns. Rosette leaves were collected for 1 day before and 1 day after treatments, and axillary meristems (regrowth tissue arising from the base of the plant off of the remaining portion of the primary inflorescence) were collected for the remaining time points. Of course, axillary meristems became more mature as time passed in terms of size and stage of development. The rationale for collecting axillary meristems at later points in time deals with the fact that plants translocate their nutrients to the developing tissues (axillary meristems, cauline leaves, siliques). The rationale for choosing samples before clipping was to check the actual change in gene expression following clipping and to assess any inherent differences between the genotypes in gene expression. The first-strand cDNA was synthesized using reverse transcriptase (SuperScript III, Invitrogen). The reverse transcription was carried out as recommended by the manufacturer. Three biological replicates and three technical replicates (*i.e.*, three reads from each sample) were used for each ecotype and time interval. qRT-PCR was performed on each ecotype (Columbia and Landsberg *erecta*) and a reference gene from microarray data (ubiquitin) using SYBR green (a fluorescent dye). The *G6PDH1* expression data were analyzed using the approach of Pfaffl (2001), where the ratio of a target gene (*G6PDH1* in Columbia or Landsberg *erecta*) is expressed in a sample *vs.* a reference gene (ubiquitin), followed by an analysis of variance and linear contrasts comparing Columbia to Landsberg *erecta*. Expression data were square-root-transformed to approximate normality.

T-DNA knockout evaluation

A gene knockout experiment gives firsthand information on the role of a candidate gene in the response of interest (in this case, the degree of compensation) and a direct way of measuring the function of the gene product *in situ*. In *Arabidopsis*, T-DNA knockout plants are available for nearly all genes identified to date. A T-DNA inserted within the gene (in the 5′ UTR, ORF, or 3′ UTR) silences the gene, and plants harboring a T-DNA on both chromosomes are devoid of any gene product (or most of the gene product depending upon the position of the insert) for the gene of interest. Therefore, we assessed the role of the candidate gene (see results below) uncovered in our combined QTL mapping and microarray experiment above, using a T-DNA knockout approach followed by a clipping experiment and a fitness analysis. Mutant knockouts included G6PDH_1 (Sail_1252), G6PDH_2 (Salk_019323), and G6PDH_3 (Gabi_86405A). T-DNA inserts were confirmed by designing primers for the genomic region and T-DNA insertion using the T-DNA Primer Design Tool (Salk Institute Genomic Analysis Laboratory, http://signal.salk.edu/tdnaprimers.2.html). The primers LP–TGCCATTCATTTTTAAGCTGG, RP- AGATGCAA GGTAATGTGCACC and LB–ATATTGACCATCATACTCATTGC were used to genotype plants. The PCR reactions produced diagnostic banding patterns for homozygous, heterozygous, and wild-type individuals. Three homozygous knockout lines with differing T-DNA insertions were compared for fitness differences among clipped and unclipped plants. Columbia (an overcompensating plant that shares identical genetic background to the knockout plants except for the knocked-out gene) served as a control on the effects of the gene knockout. Plants were grown individually under 12 hr of light and dark (~70 μE/m^2/sec) in 3.5-inch pots with LI Sunshine mix in an environmental chamber on the campus of the University of Illinois. The temperature within the growth chamber was set at 22° C. Seeds/seedlings were kept moist during germination and plants were watered daily to maintain soil moisture without saturating the soil. Plants were not fertilized. A total of 40 plants per line were grown from seed, and half (20 per line) were randomly chosen and clipped to ~1 cm above ground level (removing apical dominance) at 6 cm of inflorescence growth to simulate mammalian herbivory; the remaining 20 served as undamaged controls. Fitness comparisons were made in terms of the numbers of siliques produced. The data were square-root-transformed and analyzed using an analysis of variance (SAS v. 9.2; SAS, Cary, NC) followed by linear contrasts comparing clipped to unclipped plants within each treatment group so that we could assess whether knockout treatments altered the compensatory outcome from that of overcompensation observed in the Columbia wild type.

Complementation of G6PDH1

To further assess the effects of *G6PDH1* on fitness compensation, we used a gene complementation approach wherein we replaced *G6PDH1* in a T-DNA knockout line (G6PDH_3; Gabi_86405A). To amplify 6032 bp of *G6PDH1* using *Kod* polymerase, we used the following forward and reverse primers: For1—CACCCGTGTCGACCTCCACTATTGCCTCAA GTTGATGTTGAGTTCCG and Rev1 —CCAATCTTCATCTTCG TCTTCATGGTACCTAACG. The region included ~2.0 kb of the upstream promoter, exons, and introns and ~1.1 kb of the downstream region. The PCR product was subcloned into a pENTR/d-TOPO vector as per the manufacturer's recommendation and later cloned to pMDC 123 (Curtis and Grossniklaus 2003) using the gateway LR reaction (Left and Right recombination sites). As both entry clone and binary vector had the same selection marker (kanamycin), the entry clone was linearized using the restriction enzyme *Mlu*I. This enzyme linearizes without affecting the gene or the gateway-site-specific recombination sites. The gateway-site-specific recombination yielded the binary vector (pMHS 207), which was transformed to *Agrobacterium tumefaciens* strain GV3101:pMP90 by the freeze-thaw method (Holsters *et al.* 1978). Plant

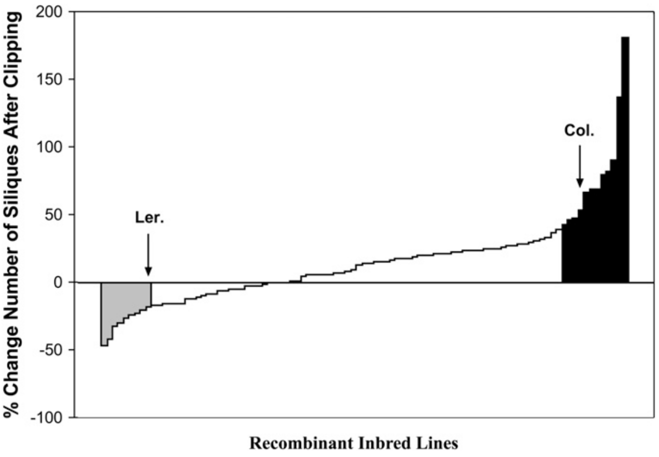

Figure 1 Percentage change in number of siliques per line between clipped and unclipped plants for Columbia (right arrow) and Landsberg erecta (left arrow) parental lines and 93 recombinant inbred lines from a cross between Columbia and Landsberg erecta over 2 years; 14 lines had only 1 year of data. Solid area indicates overcompensating lines; shaded area indicates undercompensating lines.

transformation was done using Clough and Bent's (1998) floral dip protocol. Primary transformants were selected by spraying glufosinate at 250 mM concentration. Transgenic seed was carried through to the T_2 generation for subsequent fitness analyses. Given that the transgenic line was grown in a separate experiment, under conditions identical to those used in comparing Columbia, Landsberg *erecta*, and three T-DNA knockout mutants to one another, a *t*-test was used to compare clipped to unclipped transgenic plants to see if restoring gene function led to a pattern of overcompensation as one would predict if *G6PDH1* played a significant role in overcompensation.

Results

Fitness variation among RILs

The RILs used from a cross between Columbia and Landsberg *erecta* showed variation in compensatory responses ranging from undercompensation to overcompensation within both seasons/years (Spring 2007: treatment × line interaction, $F = 1.65$, d.f. = 92, 654, $P < 0.0001$; Fall 2008: treatment × line interaction, $F = 3.26$, d.f. = 83, 640, $P < 0.0001$) (Figure 1). Although there was a significant treatment × line × year effect ($F = 1.28$, d.f. = 86, 1294, $P = 0.045$), the majority (68%) of lines had similar compensatory responses across years (48 lines equally compensated in both years, 4 overcompensated, and 2 undercompensated). Of the remaining lines for which we had 2 years of data, 19 shifted from overcompensation to equal compensation, 5 shifted from equal compensation to undercompensation, and only 1 shifted from overcompensation to undercompensation ($P < 0.05$ for those that changed category). There were 14 lines for which we had only one year's data, of which 13 equally compensated and 1 overcompensated.

Table 1 Estimates of QTL positions, effects, and interactions

Chromosome	Marker	Position (cM)	LOD	Additive effect[a]	R^2_{par} [b]
1	10	49	2.76	21.7	11.4
4	22	101	3.05	21.7	10.1
5	23	69	3.41	63.6	26.7

Significant QTL determined at LOD > 2.5.

[a] All alleles increasing compensatory response originate from the Columbia ecotype.

[b] R^2_{par}: partial R^2 provides an estimate of the amount of phenotypic variance explained by each QTL.

QTL/microarray analyses

A total of three main QTL for compensation was found on chromosomes 1, 4, and 5 explaining 11.4, 10.1, and 26.7% of the variation in compensation, respectively (Table 1). The three QTL showed additive effects varying between 21.7 and 63.6 siliques and no evidence for epistatic interactions. All alleles increasing fitness were contributed by the Columbia ecotype (Table 1), although the compensatory response distribution suggests contributions from Landsberg *erecta* (*i.e.*, evidence for transgressive segregation; see Figure 1).

From the microarray analysis a total of 109 genes were found to be differentially expressed between clipped and unclipped plants of Columbia (see Supporting Information, File S1 and File S2 for gene list). A total of 30, 19, 17, 16, and 27 differentially expressed genes were located on chromosomes 1–5, respectively, between clipped and unclipped plants. Based on the gene ontology analysis, these genes can be generally classified into stress response genes, metabolic genes, and growth/reproductive genes (Table 2). When mapped with the QTL data, only a single gene colocalizes within one of the QTL markers (QTL 3 located on chromosome 5 at 69 cM; Table 1), a *G6PDH1* (EC 1.1.1.49).

T-DNA knockout fitness analyses and gene expression patterns

T-DNA knockout experiments verified the role of *G6PDH1* in the compensatory response (Figure 2). Overall, results show a marginally significant clipping treatment × line interaction for silique production ($F = 2.21$, d.f. = 4, 114, $P = 0.073$). Results indicate that Landsberg *erecta* equally compensated with a nonsignificant trend toward undercompensation ($P = 0.094$; see Figure 2) while all three knockouts of *G6PDH1* showed patterns of equal compensation [$P = 0.471$, $P = 0.419$, and $P = 0.265$ for knockouts 1 (Sail 1252), 2 (Salk 019323), and 3 (Gabi_86405A); see Figure 2], respectively, with a trend toward undercompensation, whereas Columbia overcompensated following clipping ($P = 0.019$). *G6PDH1* expression data through time comparing Landsberg *erecta*, an undercompensating ecotype, and Columbia, an overcompensating ecotype, showed higher levels of expression (1.4- to 2.2-fold) in Columbia following the removal of apical dominance at all time points following clipping (overall expression differences between ecotypes: Columbia 0.907 ± 0.064 and Landsberg *erecta* 0.684 ± 0.064, $F = 5.99$, d.f. = 1, 20, $P = 0.024$; ecotype × time, $F = 3.83$, d.f. = 4, 20, $P = 0.018$) (Figure 3).

Table 2 Gene ontology analysis of 109 overexpressed genes in Columbia wild type after clipping

Biological process	No. of genes	Selected genes						
Response to stress	19	ATP1^{a,b,c}	CGL1^{d}	FNR1^{a}	GOLS2^{e}	PDE345^{e}	TCH4^{b,d}	WR3^{c}
Reproduction	9	AGL8^{a,f}	GRH1^{g}	GSH1^{e}	MPK6^{h,i}	RP1^{j}		
Carbohydrate metabolic process	9	CGL1^{d}	CINV1^{b,g}	G6PD1^{a,g}	GALAK^{a,d,h}	GOLS2^{e}	IAR4^{e}	
Transport	9	ATP1^{a,b,c}	GDI2^{k}	WR3^{c}				
Response to biotic stimulus	6	CYP38^{e}	FNR1^{a}	GSH1^{e}	MPK6^{h,i}	WIN1^{d}		
Generation of precursor metabolites and energy	5	FNR1^{a}	IAR4^{e}	ORF291^{c}	PDE345^{e}			
Flower development	4	AGL8^{a,f}	GRH1^{g}	GSH1^{e}	MPK6^{h,i}			
Secondary metabolic process	2	GSH1^{e}	MPK6^{h,i}					
Photosynthesis	1	FNR1^{a}						
Cell differentiation	1	AGL8^{a,f}						
Growth	1	GRH1^{g}						

Shown are a subset of biological processes and a selection of important genes. Superscripts indicate molecular function. See File S1 and File S2 for full gene ontology analysis.

[a] Nucleotide/DNA/RNA binding.

[b] Hydrolase activity.

[c] Transporter activity.

[d] Transferase activity.

[e] Catalytic activity.

[f] Sequence-specific DNA-binding transcription factor activity.

[g] Protein binding.

[h] Kinase activity.

[i] Signal transducer activity.

[j] Structural molecule activity.

[k] Enzyme regulator activity.

Complementation of G6PDH1

The results of our complementation studies support the role of *G6PDH1* in the compensatory response. This transgenic line showed patterns more similar to the overcompensating Columbia line than either Landsberg *erecta* or the three knockout lines (see Figure 2). Clipped plants of the transgenic line complemented with *G6PDH1* tended ($P = 0.064$) to produce more siliques/plant than unclipped plants (127.7 ± 5.0 fruits per plant) whereas unclipped plants produced 113.3 ± 5.3 fruits per plant ($t = 1.975$, d.f. = 1, 18, $P = 0.064$).

Discussion

Although there is evidence that genetic variation for fitness compensation exists, little is known about the genetic underpinnings leading to enhanced growth and reproduction in species exhibiting growth compensation following herbivory. Using a QTL analysis, we uncovered three QTL on chromosomes 1, 4, and 5, explaining 11.4, 10.1, and 26.7% of the variation in compensation, respectively. These three QTL showed additive effects increasing silique production by 21.7–63.6 siliques upon clipping. The increase in fitness is attributable to alleles contributed by the Columbia ecotype (Table 1) as opposed to alleles from Landsberg *erecta*, although, as noted above, the compensatory response distribution suggests contributions from Landsberg *erecta* (*i.e.*, evidence for transgressive segregation) (Figure 1).

Furthermore, combining QTL and microarray analyses we have uncovered one gene that appears to play a significant role in the phenomenon of overcompensation in *Arabidopsis*, *G6PDH1* (At5g35790.1). For a relatively important gene, residing in the middle of the QTL with the greatest effect size, the LOD score was relatively low (3.41, Table 1). This might be explained by not having markers very close to the estimated position of the QTL, having some missing data from the QTL analysis, or that the QTL might be involved in an important epistatic interaction within the area that may suppress the expected QTL effect (Darrah *et al.* 2006). Nonetheless, T-DNA knockouts, expression assays, and complementation studies confirm the importance of *G6PDH1* in fitness compensation (see below).

G6PDH1 is the key regulatory enzyme in the oxidative pentose phosphate pathway (OPPP) that plays a central role in plant metabolism by converting glucose to ribose-5-phosphate. The OPPP is a primary source of the reductant NADPH for biosynthetic processes such as the assimilation of nitrogen into amino acids, fatty-acid synthesis, and resistance to oxidative damage. Intermediates, such as ribose-5-phosphate, are also withdrawn from the OPP pathway for phenylpropanoid production via the shikimate pathway (Figure 4) (Kruger and Von Schaewen 2003; Scharte *et al.* 2009).

Knockout studies of three T-DNA insertion lines of *G6PDH1* (sharing the same genetic background as Columbia) showed patterns of equal compensation, with a trend toward undercompensation, rather than overcompensation, as observed in the Columbia wild type (Figure 2). Two of the three T-DNA knockout mutants (*G6PDH1*-1, Sail 1252, and *G6PDH1*-2, Salk 019323) (Figure 2) showed overall lower levels of fitness (*i.e.*, both clipped and unclipped plants), while the third, *G6PDH1*-3, Gabi_86405A, showed higher overall levels of fitness that were within the range of the wild types, suggesting potential positional effects of T-DNA insertion resulting in partial knockdown of *G6PDH1*-3. Specifically, the insertion of *G6PDH1*-3 is positioned within

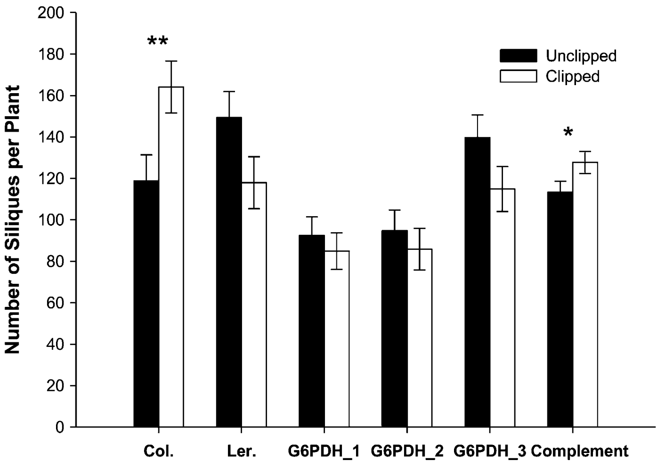

Figure 2 Silique production for clipped and unclipped T-DNA knockout lines of G6PDH1_1–3 of Columbia, the two ecotypes, Landsberg *erecta* (Ler.), and Columbia (Col.) and a transgenic line complemented with G6PDH1 (G6PDH1_3; Gabi_86405A). Note that the gene complementation was conducted in a separate experiment and thus analyzed separately. Shown are means ± 1 SE. Asterisks indicate significance at $^{**}P < 0.05$ and $^{*}P = 0.064$.

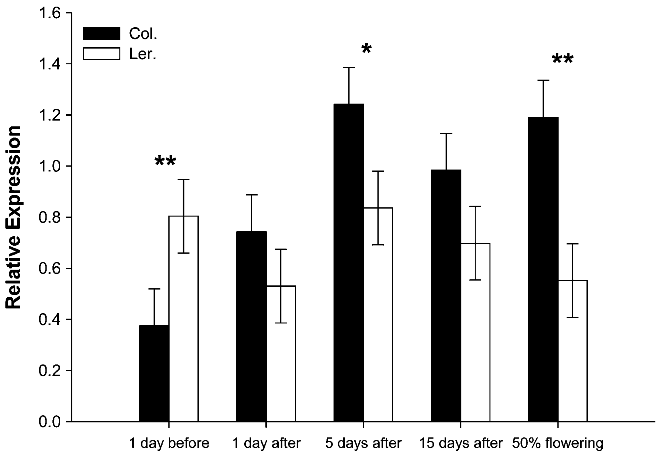

Figure 3 G6PDH1 gene expression through time before and after the removal (clipping) of the plants' apical meristem, simulating mammalian herbivory, for Columbia wild type (Col.) and Landsberg *erecta* (Ler.). The *G6PDH1* expression data were analyzed using the approach of Pfaffl (2001), where the ratio of a target gene (*G6PDH1* in Columbia or Landsberg *erecta*) is expressed in a sample *vs.* a reference gene (ubiquitin). Shown are means ± 1 SE. Asterisks indicate significance at $^{**}P < 0.05$ and $^{*}P < 0.06$.

the ORF, rather than the UTRs of *G6PDH1*-1 and -2 (see Figure 5 for sites of insertion). Nonetheless, *G6PDH1*-3 plants also equally compensated with a trend toward undercompensation as in the other two knockout mutants.

In addition, *G6PDH1* expression data through time comparing Landsberg *erecta*, an undercompensating ecotype, and Columbia, an overcompensating ecotype, showed higher levels of expression (1.4- to 2.2-fold) in Columbia following the removal of apical dominance; these data are consistent with our knockout experiments wherein lowering or knocking out *G6PDH1* resulted in equal-to-undercompensation instead of overcompensation (Figure 3). There is considerable sequence variation in *G6PDH1*, with three nonsynonymous substitutions, each causing a change in an amino acid, between Columbia and Landsberg *erecta* that may explain the differential patterns of expression in *G6PDH1* following apical damage and regrowth and perhaps the differences in compensation (Max Planck Institute for Developmental Biology, POLYMORPH Project, http://polymorph-clark20.weigelworld.org/cgi-bin/retrieve_cds_snp.cgi). In addition, our transgenic line complemented with *G6PDH1* restored the compensatory response from equal compensation, with a trend toward undercompensation, in the knockout line (G6PDH1_3; Gabi_86405A) to overcompensation (at $P = 0.064$). We suspect that positional effects of the transgene or unmeasured environmental influences may have constrained the magnitude of the compensatory response typically observed in Columbia. Collectively, these results indicate the importance of *G6PDH1* in regulating the compensatory response following the removal of apical dominance.

We propose that plants with the capability of overcompensating (increasing both biomass and fitness when compared to undamaged controls) reprogram their transcriptional activity in at least three important ways: through a suite of defensive mechanisms, through an increase in expression of genes involved in energy metabolism, and through an increase in DNA content (via endoreduplication; see Scholes and Paige 2011), with the increase in DNA content feeding back on pathways involved in defense and metabolism through increased gene expression. Initially, following apical damage, the *G6PDH1* gene elicits a suite of defensive reactions that are likely associated with cellular damage from herbivory. These may include reactive oxygen species to ward off infection and induced chemical defenses, such as glucosinolates, via the shikimate pathway (Scharte *et al.* 2009). When analyzing genes that were significantly differentially expressed (from our microarray data), several of the genes affected were found to be enzymes (*e.g.*, a suite of invertase genes, *G6PDH1*, and galactinol synthase) involved in carbohydrate metabolism, and these genes were significantly up-regulated and likely play a significant role in overcoming tissue loss. Of particular note, cytosolic invertase 1 is adjacent to a QTL located on chromosome 1. In addition, up-regulation of *G6PDH1* ultimately leads to the biosynthesis of nucleic acids (see Figure 4), consistent with the significant increase in DNA content (through endoreduplication) observed in overcompensating ecotypes of *A. thaliana* when compared to undercompensating ecotypes (Scholes and Paige 2011). Interestingly, removal of apical dominance reduces the level of auxin leading to axillary bud break and stem regeneration, and low levels of auxin trigger an exit from mitotic cycles into the endocycle (Ishida *et al.* 2010). Thus, there is a direct link between endoreduplication and the removal of apical dominance.

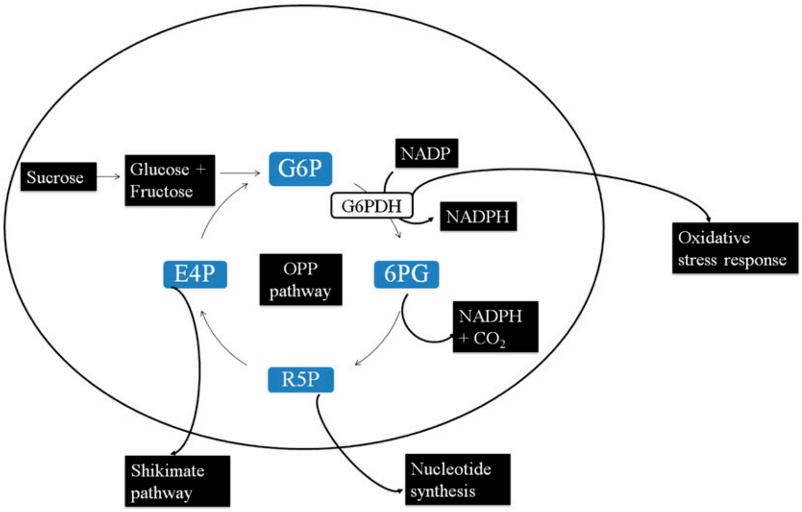

Figure 4 Schematic representation of the cytosolic oxidative pentose-phosphate pathway, adapted from Hauschild and Von Schaewen (2003). G6P (glucose-6-phosphate) is oxidized by G6PDH to yield 6-phospho-gluconate (6PG) and in the process reduces NADP to NADPH and functions in reducing oxidative damage, eventually leading to the production of ribulose-5-phosphate (R5P) and erythrose-4-phosphate (E4P), which are used for nucleotide synthesis (essential in the synthesis of aromatic amino acids) and defensive chemistry (such as glucosinolates) via the shikimate pathway, respectively.

Weinig *et al.* (2003) previously mapped QTL for resistance and tolerance (compensation) to apical meristem damage by rabbits under natural conditions of the field over two seasons in RILs from a Columbia × Landsberg *erecta* cross (Lister and Dean 1993) of *Arabidopsis*. Although QTL for resistance were found within each seasonal cohort, no QTL for tolerance were detected. This is in contrast to our study here, wherein we uncovered three QTL. We surmise that the differences in our findings can be attributed to the differences in natural herbivory under field conditions *vs.* artificial herbivory in a greenhouse. Natural herbivory resulted in wide variance in regrowth and fitness within any given line whereas our clipping experiments in the greenhouse resulted in far less variance, resulting in higher repeatability in fitness compensation, making it easier to uncover QTL. Whereas Weinig *et al.* (2003) interpreted this to mean that there were many genes of small effect involved in tolerance (compensation), our results indicate fewer genes of larger effect; *i.e.*, in our study we uncovered a single gene of major effect, *G6PDH1* (when knocked-out plants equally compensated with a trend toward undercompensation following apical damage, contributing significantly to the phenomenon of overcompensation). In both studies, there were also significant environmental effects (genotype × environment interactions) detected, with 25 of 79 lines for which we had two seasons of data responding differently in fitness compensation from one season to the next (all shifting to lower fitness levels). The remaining 54 lines all maintained the same level of fitness compensation.

Results here support the utility of using a combinatorial approach of QTL mapping and microarray data in uncovering potential candidate genes. As Wayne and McIntyre (2002, pp. 14,903) pointed out, "The use of microarray technology . . . allows an efficient, objective, quantitative evaluation of genes in the QTL and has the potential to reduce the overall effort needed in identifying genes causally associated with quantitative traits of interest." Using these combined approaches, we uncovered a single differentially expressed gene colocated within one of three QTL regions in the recombinant inbred Lister–Dean lines created from a cross between Landsberg *erecta* and Columbia. Knockout and complementation studies of this candidate strongly suggest an important role of this gene and the pathway in which it resides in the compensatory response of *Arabidopsis*. Of course we want to be clear that this is likely not the only important gene involved in the compensatory response, given the additional QTL and the pathway in which *G6PDH1* resides.

Gaining an understanding of the genetic basis of overcompensation (increased seed yield after damage), in particular,

Figure 5 Schematic representation of G6PDH1 showing the position of each of the three T-DNA insertions. Exons (solid), introns (shaded), and start and stop codons are shown. The T-DNA inserts are represented by inverted triangles. See text for a discussion of potential positional effects.

following apical damage should be of great interest to agriculturists who, through recent advances in genetic technology and selective breeding, might incorporate these traits into crop plants such as oilseed rape (*Brassica napus*), a close relative of *Arabidopsis*. The isoform of *G6PDH1* could also be engineered in crops such as sugarcane or rice where ratoon cropping is conducted (ratoon cropping resembles simulated herbivory where the apical meristem is removed leading to increased plant yields through regrowth). Thus, our findings should be of great value in that the results of this study set the stage for genetically engineering or selecting plants that not only tolerate apical damage, but also actually increase seed yield from such damage. Furthermore, from an evolutionary perspective, the genetic basis of overcompensation uncovered here in the model system *A. thaliana* may be readily applied to natural systems, improving our understanding of plant regrowth following herbivory and the complexities of plant–animal interactions. With the results of this study, we are beginning to gain significant insights as to the underpinning genetic basis that contributes to the phenomenon of overcompensation.

Acknowledgments

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GENETICS

Supporting Information
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Overcompensation in Response to Herbivory in *Arabidopsis thaliana*: The Role of Glucose-6-Phosphate Dehydrogenase and the Oxidative Pentose-Phosphate Pathway

Madhura H. Siddappaji, Daniel R. Scholes, Martin Bohn, and Ken N. Paige

DOI: 10.1534/genetics.113.154351

File S1: Supporting Data

I. *QTL Analysis*

Result of MIM analysis for Model 1 of Trait 1

```
    71450316   -filetype MImapqtl.out

            QTL Cartographer v. 1.15c, May 2001
            This output file (mimrltM.txt) was created by MIMapQTL...

            It is 22:58:16 on Tuesday, 05 March 2013
#########################################################################
            The Initial Model is

-trait         1      Analyzed trait [trait]
-maxqtl      18    Maximum number of allowed QTL in the model
-maxepis    36    Maximum number of epistatic terms allowed
-xic           1    Code for the IC criterion
-walk         1.0    Walking speed for position refinement and QTL search, in cM
-LRthresh  0.0    Likelihood ratio threshold for adding/deleting a QTL
-workcode    sMPrtseC       Code indicating what to do
-modelfile   qtlcarti.mqt

-Aqtl       5    Number of QTL with additive effects
-Dqtl       0    Number of QTL with dominance effects
-AAqtl    0    Number of QTL with additive by additive effects
-ADqtl    0    Number of QTL with additive by dominance effects
-DAqtl    0    Number of QTL with dominance by additive effects
-DDqtl    0    Number of QTL with dominance by dominance effects
________________
-Total       5    Number of parameters in this model
-Maximum   19    Number of parameters allowed in this model (2sqrt(n))

   Here is a summary of the QTL
Note: c1 <c2> - Recombinant frequency between QTL and adjacence marker of left
<right>
---------------------------------------------------------------------------------
               Position (Main effect)                              Epistatic effect Position
               ----------------------------                        ----------------------------------
 QTL       Effect Value    C   M      c1          c2                (QTL) (C)   (M)     (c1)       (c2)
-s
   1   A       49.1234          1   10   0.05662800 0.00329000
   2   A      -46.0581          3    8   0.00100000 0.04531300
   3   A        56.5110         4   22   0.04767200 0.00754200
   4   A      -77.2541          5   18   0.01960600 0.01224700
   5   A        88.2851         5   19   0.00100000 0.02561900
-e
```

```
###########################################################################
        After PARAMETER refinement,
-trait          1      Analyzed trait [trait]
-maxqtl        18    Maximum number of allowed QTL in the model
-maxepis        36    Maximum number of epistatic terms allowed
-xic            1    Code for the IC criterion
-walk          1.0    Walking speed for position refinement and QTL search, in cM
-LRthresh      0.0    Likelihood ratio threshold for adding/deleting a QTL
-workcode    sMPrtseC      Code indicating what to do
-modelfile   qtlcarti.mqt

-Aqtl       5    Number of QTL with additive effects
-Dqtl       0    Number of QTL with dominance effects
-AAqtl    0    Number of QTL with additive by additive effects
-ADqtl    0    Number of QTL with additive by dominance effects
-DAqtl    0    Number of QTL with dominance by additive effects
-DDqtl    0    Number of QTL with dominance by dominance effects
________________
-Total      5    Number of parameters in this model
-Maximum   19    Number of parameters allowed in this model (2sqrt(n))

  Here is a summary of the QTL
Note: c1 <c2> - Recombinant frequency between QTL and adjacence marker of left
<right>
-----------------------------------------------------------------------------------
              Position (Main effect)                              Epistatic effect Position
              ----------------------------                      ----------------------------------
 QTL Effect Value       C     M      c1         c2                   (QTL) (C)   (M)     (c1)       (c2)
-s
  1       A     21.6663     1   10  0.05662800 0.00329000
  2       A   -18.1787     3     8    0.00100000 0.04531300
  3       A     21.6842     4   22   0.04767200 0.00754200
  4       A   -58.2673      5  18  0.01960600 0.01224700
  5       A    63.6223      5  19   0.00100000 0.02561900
-e
###########################################################################
        We use this model for the Variance-Covariance matrix.

-trait          1      Analyzed trait [trait]
-maxqtl      18    Maximum number of allowed QTL in the model
-maxepis    36    Maximum number of epistatic terms allowed
-xic            1    Code for the IC criterion
-walk          1.0    Walking speed for position refinement and QTL search, in cM
-LRthresh   0.0    Likelihood ratio threshold for adding/deleting a QTL
-workcode    sMPrtseC      Code indicating what to do
-modelfile   qtlcarti.mqt
```

```
-Aqtl      5   Number of QTL with additive effects
-Dqtl      0   Number of QTL with dominance effects
-AAqtl   0   Number of QTL with additive by additive effects
-ADqtl   0   Number of QTL with additive by dominance effects
-DAqtl   0   Number of QTL with dominance by additive effects
-DDqtl   0   Number of QTL with dominance by dominance effects
_________________
-Total      5    Number of parameters in this model
-Maximum   19    Number of parameters allowed in this model (2sqrt(n))

   Here is a summary of the QTL
Note: c1 <c2> - Recombinant frequency between QTL and adjacence marker of left
<right>
-----------------------------------------------------------------------------------
               Position (Main effect)                          Epistatic effect Position
               -----------------------------                          ----------------------------------
 QTL Effect    Value        C   M      c1         c2               (QTL) (C)   (M)     (c1)    (c2)
-s
   1       A        21.6663    1   10   0.05662800 0.00329000
   2       A         -18.1787   3    8   0.00100000 0.04531300
   3       A        21.6842    4   22   0.04767200 0.00754200
   4       A        -58.2673    5  18   0.01960600 0.01224700
   5       A        63.6223     5  19    0.00100000 0.02561900
-e
##############################################################################
          This is the Variance-Covariance Matrix.

Phenotypic Variance:      4901
Genetic Variance:          3664
Residual Variance:          1236

---------------------------------------------------------------------------
---------------------------------------------------------------------------
QTL(s) Type    1         2         3         4         5
---------------------------------------------------------------------------
1      A      469.3      -98.48       28.36        8.37       237.1
2      A                  330.1       -7.186       228.1       -388.3
3      A                               469.1       147.6       -114.6
4      A                                            3378       -4930
5      A                                                        3906
---------------------------------------------------------------------------
  Sum             557       197.2       496.2          1105         1309
Total           3664
▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪▪
          Here are the R2 values

Genetic:       0.7477
```

```
Residual:      0.2523
-----------------------------------------------------------------------
-----------------------------------------------------------------------
QTL(s) Type    1         2         3         4         5
-----------------------------------------------------------------------
1      A     0.0958     -0.0201      0.0058      0.0017      0.0484
2      A               0.0674     -0.0015      0.0466     -0.0792
3      A                         0.0957      0.0301     -0.0234
4      A                                   0.6893     -1.0059
5      A                                             0.7971
-----------------------------------------------------------------------
 Sum          0.1137      0.0402      0.1013      0.2255      0.2670
Total         0.7477

**********************************************************************
               Estimates of QTL positions, effects and interactions
------------------------------------------------------------------------------------------
------------------------------------------------------------------------------------------
QTL(pair)    Type    Chrom.  Marker   Position     LOD        Effect          Effect (%)
------------------------------------------------------------------------------------------
1               A       1        10      48.9199      2.76      21.6663          11.4
2               A       3         8      28.5101      2.25     -18.1787           4.0
3               A       4        22     100.9100      3.05       21.6842         10.1
4               A       5        18      67.1601      1.96     -58.2673          22.6
5               A       5        19      68.5001      3.41      63.6223          26.7
------------------------------------------------------------------------------------------

These are the breeding values of the individuals.
------------------------------------
Individual    Equation 14    Equation 15
------------------------------------
       1     -108.1162      -45.9587
       2       56.0318       15.9832
       3       74.7818       14.8005
       4       65.3369       66.2320
       5       42.5712       12.2108
       6       35.3581       39.6197
       7      117.5375        0.0564
       8       20.8846       67.0736
       9       11.4620       16.1371
      10        30.2853       17.6694
      11        38.5752       40.2654
      12        54.7789       85.9728
      13       183.0493      109.9992
      14        75.1014        0.7822
      15        39.3201       -3.7158
```

16	67.7519	67.7758
17	58.9501	80.2842
18	169.3721	23.1663
19	-31.4108	-69.1495
20	67.6778	107.5116
21	-21.3201	28.4675
22	57.2362	45.9443
23	47.1255	-23.9477
24	62.2847	99.6097
25	3.2780	39.5434
26	48.8415	43.6531
27	-28.9091	-72.0085
28	-14.0556	24.1166
29	6.6778	6.5722
30	36.4544	17.7909
31	55.7960	57.7139
32	-14.9711	-31.6804
33	63.3501	35.1051
34	30.1880	55.3054
35	24.5452	69.4538
36	0.0227	2.5632
37	7.2866	11.1554
38	-74.0114	-16.4867
39	88.5096	52.8547
40	29.6563	41.5370
41	95.8859	83.7961
42	1.8184	14.0665
43	43.5952	30.4732
44	80.0895	81.8627
45	-96.0828	-11.6944
46	93.1192	94.1341
47	46.2224	59.5988
48	6.3933	12.9213
49	90.9432	47.1804
50	16.0498	21.0818
51	16.0642	23.4472
52	17.2377	33.5381
53	30.5482	62.7538
54	13.9164	18.8401
55	-14.3917	-14.0593
56	32.4041	-14.4069
57	30.9462	25.8180
58	-81.4133	-26.4686
59	62.4313	33.6639
60	28.1634	-34.8551
61	54.5752	5.8643

```
      62     -17.0297      -20.7719
      63       1.9633        5.2396
      64      27.5334       33.0489
      65      58.7193       61.0769
      66    -115.0340      -32.4583
      67      79.0594       94.0740
      68      60.2534       23.1922
      69      42.0166       37.6528
      70      41.8056      -10.3027
      71      46.9872        6.7104
      72      63.1472      110.7074
      73       8.6213       11.3527
      74      36.8359       46.0165
      75      51.1000       49.2893
      76      74.4380       66.7694
      77      26.5311       32.9470
      78       9.4383       54.1679
      79      35.6732       94.9896
      80      50.5226        4.9794
      81      22.3130       34.8999
      82      48.4159       34.3798
      83      13.1523      -23.6851
      84      -0.6919        6.3906
      85     -70.2524       -6.0560
      86     -17.5487        0.1258
      87    -145.7010      -53.0890
      88      88.7238       39.7092
      89      60.3896       56.1905
      90      51.6220       37.9031
      91      96.4155       90.3001
      92      -3.5232       -1.5387
      93     -65.9182       10.3026
      94      34.2078       28.1844
      95     167.0550       83.2006
      96      40.8446       49.5807
      97    -123.1481      -48.1993
      98      65.7914       73.1303
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These are the QTL genotype and probability values of the individuals.
---------------------------------------------------------------------
Individual    GID     QTL Genotype    Probability
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0001        01     11111        0.2414
0001        02     11112        0.0022
0001        03     11121        0.1519
0001        04     11122        0.0014
0001        05     11211        0.0656
0001        06     11221        0.0412
0001        07     12111        0.2346
0001        08     12112        0.0021
0001        09     12121        0.1476
0001        10     12122        0.0013
0001        11     12211        0.0637
0001        12     12221        0.0401
0001        13     21111        0.0021
0001        14     21121        0.0013
0001        15     22111        0.0020
0001        16     22121        0.0013
0002        01     11111        0.0014
0002        02     21111        0.5060
0002        03     21112        0.0202
0002        04     21121        0.3184
0002        05     21122        0.0127
0002        06     21211        0.0833
0002        07     21212        0.0033
0002        08     21221        0.0524
0002        09     21222        0.0021
0003        01     11111        0.1056
0003        02     11112        0.0042
0003        03     11121        0.0665
0003        04     11122        0.0027
0003        05     11211        0.1056
0003        06     11212        0.0042
0003        07     11221        0.0665
0003        08     11222        0.0027
0003        09     12111        0.0024
0003        10     12121        0.0015
0003        11     12211        0.0024
0003        12     12221        0.0015
0003        13     21111        0.1831
0003        14     21112        0.0073
0003        15     21121        0.1152
0003        16     21122        0.0046
0003        17     21211        0.1831
0003        18     21212        0.0073
0003        19     21221        0.1152
0003        20     21222        0.0046
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0003	21	22111	0.0042
0003	22	22121	0.0027
0003	23	22211	0.0042
0003	24	22221	0.0027
0004	01	11122	0.0023
0004	02	21112	0.0031
0004	03	21122	0.8347
0004	04	21222	0.1374
0004	05	22122	0.0192
0004	06	22222	0.0032
0005	01	11111	0.0016
0005	02	21111	0.5567
0005	03	21112	0.0223
0005	04	21121	0.3503
0005	05	21122	0.0140
0005	06	21211	0.0330
0005	07	21212	0.0013
0005	08	21221	0.0208
0006	01	12211	0.0024
0006	02	22111	0.0046
0006	03	22211	0.8465
0006	04	22221	0.1465
0007	01	12111	0.1134
0007	02	12112	0.1180
0007	03	12121	0.1175
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0007	07	12221	0.1175
0007	08	12222	0.1223
0007	09	22111	0.0069
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0007	13	22211	0.0069
0007	14	22212	0.0072
0007	15	22221	0.0072
0007	16	22222	0.0075
0008	01	12112	0.0222
0008	02	12122	0.0352
0008	03	22112	0.3621
0008	04	22122	0.5754
0008	05	22212	0.0020
0008	06	22222	0.0031
0009	01	11112	0.0042
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0009	03	11212	0.0024
0009	04	11222	0.1756
0009	05	12112	0.0043
0009	06	12122	0.3195
0009	07	12212	0.0024
0009	08	12222	0.1802
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0010	02	11122	0.2319
0010	03	11221	0.0093
0010	04	11222	0.2319
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0010	06	12122	0.2319
0010	07	12221	0.0093
0010	08	12222	0.2319
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0010	10	21222	0.0088
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0010	12	22222	0.0088
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0011	02	11212	0.0017
0011	03	11221	0.0179
0011	04	11222	0.4472
0011	05	12122	0.0025
0011	06	12212	0.0017
0011	07	12221	0.0181
0011	08	12222	0.4514
0011	09	21221	0.0011
0011	10	21222	0.0274
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0011	12	22222	0.0276
0012	01	21111	0.0032
0012	02	21112	0.0809
0012	03	21121	0.0051
0012	04	21122	0.1285
0012	05	21211	0.0011
0012	06	21212	0.0273
0012	07	21221	0.0017
0012	08	21222	0.0434
0012	09	22111	0.0079
0012	10	22112	0.1968
0012	11	22121	0.0125
0012	12	22122	0.3128
0012	13	22211	0.0027
0012	14	22212	0.0664
0012	15	22221	0.0042
0012	16	22222	0.1055

0013	01	12212	0.0222
0013	02	12222	0.0352
0013	03	22112	0.0020
0013	04	22122	0.0031
0013	05	22212	0.3621
0013	06	22222	0.5754
0014	01	12111	0.0999
0014	02	12112	0.1181
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0015	01	11211	0.0086
0015	02	11221	0.0054
0015	03	12111	0.0015
0015	04	12211	0.2833
0015	05	12212	0.0113
0015	06	12221	0.1782
0015	07	12222	0.0071
0015	08	21211	0.0087
0015	09	21221	0.0055
0015	10	22111	0.0016
0015	11	22211	0.2884
0015	12	22212	0.0115
0015	13	22221	0.1815
0015	14	22222	0.0073
0016	01	12222	0.0028
0016	02	22122	0.0054
0016	03	22212	0.0037
0016	04	22222	0.9882
0017	01	21211	0.0947
0017	02	21212	0.1210
0017	03	21221	0.1248
0017	04	21222	0.1595
0017	05	22211	0.0947
0017	06	22212	0.1210

0017	07	22221	0.1248
0017	08	22222	0.1595
0018	01	11112	0.0032
0018	02	11122	0.2352
0018	03	11222	0.0226
0018	04	12112	0.0035
0018	05	12122	0.2576
0018	06	12222	0.0247
0018	07	21112	0.0026
0018	08	21122	0.1950
0018	09	21222	0.0187
0018	10	22112	0.0029
0018	11	22122	0.2135
0018	12	22222	0.0205
0019	01	12111	0.5798
0019	02	12112	0.0232
0019	03	12121	0.3649
0019	04	12122	0.0146
0019	05	12211	0.0032
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0019	07	22111	0.0076
0019	08	22121	0.0048
0020	01	12212	0.0010
0020	02	12222	0.0016
0020	03	22112	0.0020
0020	04	22122	0.0032
0020	05	22211	0.0147
0020	06	22212	0.3684
0020	07	22221	0.0234
0020	08	22222	0.5855
0021	01	11222	0.0012
0021	02	12111	0.0019
0021	03	12112	0.0028
0021	04	12121	0.0061
0021	05	12122	0.0090
0021	06	12211	0.0033
0021	07	12212	0.0048
0021	08	12221	0.0103
0021	09	12222	0.0152
0021	10	21111	0.0026
0021	11	21112	0.0038
0021	12	21121	0.0081
0021	13	21122	0.0119
0021	14	21211	0.0043
0021	15	21212	0.0064
0021	16	21221	0.0137

0021	17	21222	0.0202
0021	18	22111	0.0316
0021	19	22112	0.0465
0021	20	22121	0.0997
0021	21	22122	0.1469
0021	22	22211	0.0534
0021	23	22212	0.0787
0021	24	22221	0.1688
0021	25	22222	0.2487
0022	01	11111	0.0052
0022	02	11112	0.0522
0022	03	11121	0.0339
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0022	05	11211	0.0062
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0022	07	11221	0.0406
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0022	10	12122	0.0078
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0022	12	12222	0.0094
0022	13	21112	0.0019
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0022	15	21122	0.0122
0022	16	21212	0.0022
0022	17	21221	0.0015
0022	18	21222	0.0146
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0023	02	11121	0.2586
0023	03	11211	0.0022
0023	04	11221	0.0014
0023	05	21111	0.1999
0023	06	21121	0.1258
0023	07	21211	0.0011
0024	01	11112	0.0545
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0024	03	11212	0.3311
0024	04	11222	0.5262
0024	05	21222	0.0015
0025	01	11111	0.0074
0025	02	11112	0.1847
0025	03	11121	0.0117
0025	04	11122	0.2935
0025	05	11212	0.0010
0025	06	11222	0.0016
0025	07	12111	0.0074

0025	08	12112	0.1847
0025	09	12121	0.0117
0025	10	12122	0.2935
0025	11	12212	0.0010
0025	12	12222	0.0016
0026	01	11111	0.1406
0026	02	11211	0.8539
0026	03	11221	0.0032
0026	04	21211	0.0024
0027	01	12111	0.5754
0027	02	12121	0.3621
0027	03	12211	0.0031
0027	04	12221	0.0020
0027	05	22111	0.0352
0027	06	22121	0.0222
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0028	02	11112	0.0193
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0028	12	21122	0.0024
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0028	15	21221	0.0186
0028	16	21222	0.0144
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0029	03	11211	0.0054
0029	04	21111	0.0028
0030	01	11111	0.0397
0030	02	11121	0.0250
0030	03	11211	0.2411
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0030	05	12111	0.0034
0030	06	12121	0.0022
0030	07	12211	0.0208
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0031	06	22211	0.1443
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0032	01	11111	0.0224
0032	02	11121	0.0141
0032	03	11211	0.0041
0032	04	11221	0.0026
0032	05	12111	0.1610
0032	06	12112	0.0064
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0032	13	21112	0.0016
0032	14	21121	0.0244
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0032	16	21221	0.0044
0032	17	22111	0.2791
0032	18	22112	0.0112
0032	19	22121	0.1756
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0032	21	22211	0.0508
0032	22	22212	0.0020
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0032	24	22222	0.0013
0033	01	12221	0.0010
0033	02	21211	0.0042
0033	03	21212	0.0033
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0033	05	21222	0.0065
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0033	07	22122	0.0015
0033	08	22211	0.1830

0033	09	22212	0.1412
0033	10	22221	0.3661
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0034	02	22111	0.1352
0034	03	22112	0.0054
0034	04	22211	0.8212
0034	05	22212	0.0328
0034	06	22221	0.0031
0035	01	12112	0.0011
0035	02	12122	0.0017
0035	03	22112	0.3831
0035	04	22122	0.6088
0035	05	22212	0.0021
0035	06	22222	0.0033
0036	01	12112	0.0058
0036	02	12121	0.0063
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0036	04	12212	0.0058
0036	05	12221	0.0063
0036	06	12222	0.4870
0036	07	22122	0.0014
0036	08	22222	0.0014
0037	01	11111	0.6103
0037	02	11112	0.0244
0037	03	11121	0.0798
0037	04	11122	0.0032
0037	05	11211	0.1005
0037	06	11212	0.0040
0037	07	11221	0.0131
0037	08	21111	0.1214
0037	09	21112	0.0049
0037	10	21121	0.0159
0037	11	21211	0.0200
0037	12	21221	0.0026
0038	01	11111	0.3597
0038	02	11112	0.0144
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0038	04	11122	0.0091
0038	05	11211	0.2299
0038	06	11212	0.0092
0038	07	11221	0.1447
0038	08	11222	0.0058
0038	09	21111	0.0010
0039	01	11211	0.0016
0039	02	11221	0.0010

0039	03	21111	0.0032
0039	04	21121	0.0020
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0039	06	21212	0.0234
0039	07	21221	0.3684
0039	08	21222	0.0147
0040	01	11111	0.0059
0040	02	11112	0.0028
0040	03	11121	0.0023
0040	04	11122	0.0011
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0040	10	12112	0.0028
0040	11	12121	0.0023
0040	12	12122	0.0011
0040	13	12211	0.2244
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0040	19	21221	0.0054
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0040	21	22211	0.0137
0040	22	22212	0.0065
0040	23	22221	0.0054
0040	24	22222	0.0025
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0041	05	21122	0.0029
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0041	08	22222	0.0122
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0042	27	22212	0.0021
0042	28	22221	0.0021
0043	01	11122	0.0019
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0044	03	21112	0.0018
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0045	03	11121	0.1776
0045	04	11122	0.0037

0045	05	11211	0.2838
0045	06	11212	0.0059
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0046	07	21212	0.0351
0046	08	21221	0.0033
0047	01	11111	0.0016
0047	02	11211	0.2886
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0047	14	22221	0.0042
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0048	06	21111	0.0539
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0048	08	22111	0.0012
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0049	08	22221	0.0086
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0050	02	12111	0.0048
0050	03	12211	0.8792
0050	04	12212	0.0352
0050	05	12221	0.0033
0050	06	21211	0.0012
0050	07	22211	0.0539
0050	08	22212	0.0022
0051	01	12121	0.0019
0051	02	12122	0.0475
0051	03	12222	0.0078
0051	04	22112	0.0029
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0051	07	22221	0.0051
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0052	01	11111	0.1488
0052	02	11211	0.0301
0052	03	12111	0.0733
0052	04	12211	0.0148
0052	05	21111	0.4076
0052	06	21121	0.0015
0052	07	21211	0.0825
0052	08	22111	0.2008
0052	09	22211	0.0406
0053	01	11111	0.1565
0053	02	11112	0.0063
0053	03	11211	0.2784
0053	04	11212	0.0111
0053	05	11221	0.0010
0053	06	21111	0.1887
0053	07	21112	0.0075
0053	08	21211	0.3358
0053	09	21212	0.0134
0053	10	21221	0.0012
0054	01	12111	0.0026
0054	02	21111	0.0215
0054	03	22111	0.9302
0054	04	22112	0.0372
0054	05	22121	0.0035
0054	06	22211	0.0051
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0055	02	11222	0.0029
0055	03	12112	0.0028

0055	04	12121	0.0304
0055	05	12122	0.7593
0055	06	12221	0.0050
0055	07	12222	0.1250
0055	08	21122	0.0011
0055	09	22121	0.0019
0055	10	22122	0.0465
0055	11	22222	0.0077
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0056	05	11211	0.2534
0056	06	11212	0.0101
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0056	12	12122	0.0010
0056	13	12211	0.2534
0056	14	12212	0.0101
0056	15	12221	0.1594
0056	16	12222	0.0064
0057	01	12122	0.0023
0057	02	22112	0.0031
0057	03	22121	0.0328
0057	04	22122	0.8212
0057	05	22221	0.0054
0057	06	22222	0.1352
0058	01	11111	0.0216
0058	02	11121	0.0136
0058	03	11211	0.1503
0058	04	11221	0.0945
0058	05	12111	0.0552
0058	06	12121	0.0348
0058	07	12211	0.3849
0058	08	12221	0.2422
0058	09	22211	0.0018
0058	10	22221	0.0012
0059	01	12111	0.0277
0059	02	12211	0.0282
0059	03	21111	0.0137
0059	04	21211	0.0139
0059	05	22111	0.4529
0059	06	22121	0.0017

0059	07	22211	0.4601
0059	08	22221	0.0017
0060	01	11111	0.1534
0060	02	11121	0.0966
0060	03	11211	0.1534
0060	04	11221	0.0966
0060	05	12111	0.1534
0060	06	12121	0.0966
0060	07	12211	0.1534
0060	08	12221	0.0966
0061	01	12211	0.0015
0061	02	22111	0.0866
0061	03	22121	0.0545
0061	04	22211	0.5262
0061	05	22221	0.3311
0062	01	12112	0.0033
0062	02	12121	0.0359
0062	03	12122	0.8986
0062	04	12222	0.0049
0062	05	22121	0.0022
0062	06	22122	0.0550
0063	01	11112	0.0020
0063	02	11121	0.0016
0063	03	11122	0.0082
0063	04	11212	0.0015
0063	05	11221	0.0012
0063	06	11222	0.0062
0063	07	12111	0.0165
0063	08	12112	0.0864
0063	09	12121	0.0678
0063	10	12122	0.3554
0063	11	12211	0.0125
0063	12	12212	0.0653
0063	13	12221	0.0512
0063	14	12222	0.2686
0063	15	22111	0.0010
0063	16	22112	0.0053
0063	17	22121	0.0042
0063	18	22122	0.0218
0063	19	22212	0.0040
0063	20	22221	0.0031
0063	21	22222	0.0165
0064	01	11112	0.0023
0064	02	11122	0.6143
0064	03	11222	0.0033
0064	04	12122	0.0142

0064	05	21112	0.0013
0064	06	21122	0.3545
0064	07	21222	0.0019
0064	08	22122	0.0082
0065	01	12211	0.0027
0065	02	22111	0.0052
0065	03	22211	0.9506
0065	04	22212	0.0380
0065	05	22221	0.0035
0066	01	12111	0.0833
0066	02	12112	0.0033
0066	03	12121	0.0524
0066	04	12122	0.0021
0066	05	12211	0.5060
0066	06	12212	0.0202
0066	07	12221	0.3184
0066	08	12222	0.0127
0066	09	22211	0.0014
0067	01	11211	0.0534
0067	02	11212	0.0021
0067	03	12211	0.0016
0067	04	21111	0.0048
0067	05	21211	0.8724
0067	06	21212	0.0349
0067	07	21221	0.0032
0067	08	22211	0.0264
0067	09	22212	0.0011
0068	01	11111	0.0361
0068	02	11121	0.0227
0068	03	11211	0.2194
0068	04	11221	0.1381
0068	05	12211	0.0051
0068	06	12221	0.0032
0068	07	21111	0.0489
0068	08	21121	0.0307
0068	09	21211	0.2968
0068	10	21221	0.1867
0068	11	22111	0.0011
0068	12	22211	0.0068
0068	13	22221	0.0043
0069	01	12112	0.0043
0069	02	12121	0.0048
0069	03	12122	0.0214
0069	04	12212	0.0036
0069	05	12221	0.0040
0069	06	12222	0.0179

0069	07	22111	0.0159
0069	08	22112	0.0702
0069	09	22121	0.0791
0069	10	22122	0.3493
0069	11	22211	0.0133
0069	12	22212	0.0586
0069	13	22221	0.0660
0069	14	22222	0.2917
0070	01	11111	0.0114
0070	02	12111	0.4964
0070	03	12112	0.0206
0070	04	12121	0.0283
0070	05	12122	0.0012
0070	06	12211	0.0257
0070	07	12212	0.0011
0070	08	12221	0.0015
0070	09	21111	0.0081
0070	10	22111	0.3519
0070	11	22112	0.0146
0070	12	22121	0.0200
0070	13	22211	0.0182
0070	14	22221	0.0010
0071	01	11111	0.1070
0071	02	11112	0.0043
0071	03	11121	0.0674
0071	04	11122	0.0027
0071	05	11211	0.0176
0071	06	11221	0.0111
0071	07	21111	0.4003
0071	08	21112	0.0160
0071	09	21121	0.2519
0071	10	21122	0.0101
0071	11	21211	0.0659
0071	12	21212	0.0026
0071	13	21221	0.0415
0071	14	21222	0.0017
0072	01	11112	0.0195
0072	02	11122	0.0310
0072	03	11212	0.1183
0072	04	11222	0.1881
0072	05	12112	0.0079
0072	06	12122	0.0126
0072	07	12212	0.0480
0072	08	12222	0.0763
0072	09	21112	0.0194
0072	10	21122	0.0308

0072	11	21212	0.1176
0072	12	21222	0.1869
0072	13	22112	0.0079
0072	14	22122	0.0125
0072	15	22212	0.0477
0072	16	22222	0.0758
0073	01	11111	0.9492
0073	02	11112	0.0380
0073	03	11121	0.0035
0073	04	11211	0.0052
0073	05	12111	0.0015
0073	06	21111	0.0027
0074	01	11111	0.0094
0074	02	11112	0.0111
0074	03	11121	0.0114
0074	04	11122	0.0135
0074	05	11211	0.0279
0074	06	11212	0.0330
0074	07	11221	0.0338
0074	08	11222	0.0400
0074	09	12111	0.0143
0074	10	12112	0.0169
0074	11	12121	0.0173
0074	12	12122	0.0205
0074	13	12211	0.0423
0074	14	12212	0.0501
0074	15	12221	0.0512
0074	16	12222	0.0607
0074	17	21111	0.0113
0074	18	21112	0.0134
0074	19	21121	0.0137
0074	20	21122	0.0163
0074	21	21211	0.0336
0074	22	21212	0.0398
0074	23	21221	0.0407
0074	24	21222	0.0482
0074	25	22111	0.0172
0074	26	22112	0.0204
0074	27	22121	0.0208
0074	28	22122	0.0247
0074	29	22211	0.0510
0074	30	22212	0.0604
0074	31	22221	0.0618
0074	32	22222	0.0732
0075	01	11111	0.0052
0075	02	11211	0.9529

0075	03	11221	0.0035
0075	04	12211	0.0220
0075	05	21211	0.0164
0076	01	11122	0.0023
0076	02	21112	0.0031
0076	03	21122	0.8226
0076	04	21222	0.1496
0076	05	22122	0.0190
0076	06	22222	0.0035
0077	01	12122	0.0024
0077	02	22111	0.0044
0077	03	22112	0.1104
0077	04	22121	0.0338
0077	05	22122	0.8445
0077	06	22222	0.0046
0078	01	11111	0.0294
0078	02	11112	0.0966
0078	03	11121	0.0535
0078	04	11122	0.1755
0078	05	11211	0.0490
0078	06	11212	0.1610
0078	07	11221	0.0891
0078	08	11222	0.2926
0078	09	12111	0.0017
0078	10	12112	0.0054
0078	11	12121	0.0030
0078	12	12122	0.0099
0078	13	12211	0.0028
0078	14	12212	0.0091
0078	15	12221	0.0050
0078	16	12222	0.0165
0079	01	11112	0.0116
0079	02	11122	0.0184
0079	03	11212	0.0019
0079	04	11222	0.0030
0079	05	12112	0.0075
0079	06	12122	0.0120
0079	07	12212	0.0012
0079	08	12222	0.0020
0079	09	21112	0.1893
0079	10	21122	0.3008
0079	11	21212	0.0312
0079	12	21222	0.0495
0079	13	22112	0.1232
0079	14	22122	0.1958
0079	15	22212	0.0203

0079	16	22222	0.0322
0080	01	11111	0.0033
0080	02	11121	0.0021
0080	03	11211	0.6076
0080	04	11221	0.3823
0080	05	21211	0.0029
0080	06	21221	0.0018
0081	01	11111	0.0030
0081	02	12111	0.0035
0081	03	21111	0.4409
0081	04	21112	0.0176
0081	05	21121	0.0016
0081	06	21211	0.0024
0081	07	22111	0.5061
0081	08	22112	0.0202
0081	09	22121	0.0019
0081	10	22211	0.0028
0082	01	11111	0.0015
0082	02	11211	0.0093
0082	03	12111	0.0664
0082	04	12112	0.0027
0082	05	12211	0.4035
0082	06	12212	0.0161
0082	07	12221	0.0015
0082	08	21111	0.0015
0082	09	21211	0.0093
0082	10	22111	0.0662
0082	11	22112	0.0026
0082	12	22211	0.4018
0082	13	22212	0.0161
0082	14	22221	0.0015
0083	01	11211	0.0125
0083	02	11221	0.0079
0083	03	12111	0.0030
0083	04	12121	0.0019
0083	05	12211	0.5426
0083	06	12212	0.0217
0083	07	12221	0.3414
0083	08	12222	0.0137
0083	09	22211	0.0332
0083	10	22212	0.0013
0083	11	22221	0.0209
0084	01	11111	0.5389
0084	02	11112	0.0018
0084	03	11121	0.0097
0084	04	11211	0.1836

0084	05	11221	0.0033
0084	06	12111	0.1913
0084	07	12121	0.0034
0084	08	12211	0.0652
0084	09	12221	0.0012
0084	10	21111	0.0015
0085	01	11111	0.2579
0085	02	11112	0.0103
0085	03	11121	0.1623
0085	04	11122	0.0065
0085	05	11211	0.0425
0085	06	11212	0.0017
0085	07	11221	0.0267
0085	08	11222	0.0011
0085	09	21111	0.2489
0085	10	21112	0.0100
0085	11	21121	0.1566
0085	12	21122	0.0063
0085	13	21211	0.0410
0085	14	21212	0.0016
0085	15	21221	0.0258
0085	16	21222	0.0010
0086	01	11111	0.4281
0086	02	11112	0.0171
0086	03	11121	0.0016
0086	04	11211	0.0705
0086	05	11212	0.0028
0086	06	12111	0.3903
0086	07	12112	0.0156
0086	08	12121	0.0015
0086	09	12211	0.0643
0086	10	12212	0.0026
0086	11	21111	0.0029
0086	12	22111	0.0027
0087	01	11111	0.0084
0087	02	11121	0.0053
0087	03	12111	0.3645
0087	04	12112	0.0146
0087	05	12121	0.2294
0087	06	12122	0.0092
0087	07	12211	0.0020
0087	08	12221	0.0012
0087	09	21111	0.0049
0087	10	21121	0.0031
0087	11	22111	0.2103
0087	12	22112	0.0084

0087	13	22121	0.1323
0087	14	22122	0.0053
0087	15	22211	0.0011
0088	01	11111	0.0050
0088	02	11121	0.0032
0088	03	11211	0.0304
0088	04	11221	0.0191
0088	05	21111	0.0818
0088	06	21121	0.0514
0088	07	21211	0.4966
0088	08	21221	0.3125
0089	01	11122	0.0052
0089	02	11212	0.0035
0089	03	11221	0.0380
0089	04	11222	0.9506
0089	05	21222	0.0027
0090	01	11111	0.0561
0090	02	11112	0.0022
0090	03	11211	0.3411
0090	04	11212	0.0136
0090	05	11221	0.0013
0090	06	12111	0.0556
0090	07	12112	0.0022
0090	08	12211	0.3379
0090	09	12212	0.0135
0090	10	12221	0.0013
0090	11	21111	0.0120
0090	12	21211	0.0730
0090	13	21212	0.0029
0090	14	22111	0.0119
0090	15	22211	0.0724
0090	16	22212	0.0029
0091	01	11122	0.0077
0091	02	11221	0.0019
0091	03	11222	0.0465
0091	04	12222	0.0011
0091	05	21121	0.0050
0091	06	21122	0.1250
0091	07	21212	0.0028
0091	08	21221	0.0304
0091	09	21222	0.7593
0091	10	22122	0.0029
0091	11	22222	0.0175
0092	01	11111	0.0150
0092	02	11121	0.0095
0092	03	11211	0.0298

0092	04	11221	0.0187
0092	05	12111	0.0336
0092	06	12121	0.0211
0092	07	12211	0.0665
0092	08	12221	0.0418
0092	09	21111	0.0486
0092	10	21121	0.0306
0092	11	21211	0.0964
0092	12	21221	0.0607
0092	13	22111	0.1086
0092	14	22121	0.0683
0092	15	22211	0.2152
0092	16	22221	0.1354
0093	01	11122	0.0024
0093	02	12111	0.0177
0093	03	12112	0.0662
0093	04	12121	0.0628
0093	05	12122	0.2349
0093	06	12211	0.0032
0093	07	12212	0.0120
0093	08	12221	0.0114
0093	09	12222	0.0427
0093	10	21122	0.0029
0093	11	22111	0.0213
0093	12	22112	0.0798
0093	13	22121	0.0757
0093	14	22122	0.2833
0093	15	22211	0.0039
0093	16	22212	0.0145
0093	17	22221	0.0138
0093	18	22222	0.0515
0094	01	11111	0.4808
0094	02	11121	0.0018
0094	03	11211	0.0026
0094	04	12111	0.0049
0094	05	21111	0.5002
0094	06	21121	0.0019
0094	07	21211	0.0027
0094	08	22111	0.0051
0095	01	11122	0.0011
0095	02	11212	0.0043
0095	03	11222	0.0068
0095	04	12112	0.0232
0095	05	12121	0.0015
0095	06	12122	0.0368
0095	07	12211	0.0056

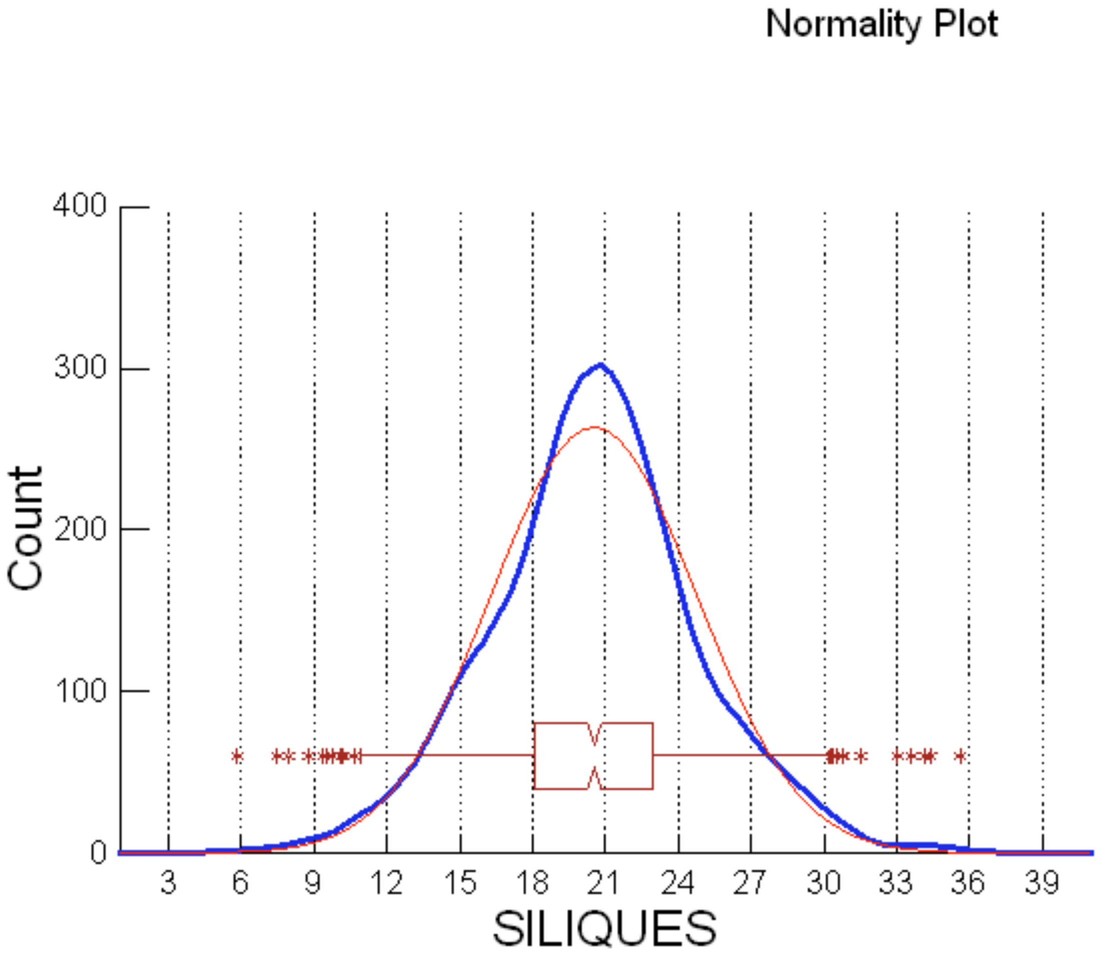
0095	08	12212	0.1408
0095	09	12221	0.0090
0095	10	12222	0.2237
0095	11	21122	0.0013
0095	12	21212	0.0051
0095	13	21222	0.0082
0095	14	22111	0.0011
0095	15	22112	0.0280
0095	16	22121	0.0018
0095	17	22122	0.0444
0095	18	22211	0.0068
0095	19	22212	0.1698
0095	20	22221	0.0108
0095	21	22222	0.2699
0096	01	11111	0.0281
0096	02	11112	0.0345
0096	03	11121	0.0341
0096	04	11122	0.0419
0096	05	11211	0.1705
0096	06	11212	0.2097
0096	07	11221	0.2070
0096	08	11222	0.2547
0096	09	12211	0.0039
0096	10	12212	0.0048
0096	11	12221	0.0048
0096	12	12222	0.0059
0097	01	12111	0.2664
0097	02	12121	0.1676
0097	03	12211	0.0256
0097	04	12221	0.0161
0097	05	22111	0.2937
0097	06	22121	0.1848
0097	07	22211	0.0282
0097	08	22221	0.0177
0098	01	12212	0.0066
0098	02	12222	0.0776
0098	03	21222	0.0068
0098	04	22122	0.0045
0098	05	22212	0.0709
0098	06	22222	0.8336

II. *Phenotypic Fitness Data for QTL Mapping and for assessing compensatory responses*

Year 1 Data

ANOVA

SOURCE	SS	DF	MS	F	P
TRT$	1368	1	1368	0.166	0.684
LINE	8150.17	92	88589	10.755	0.000
TRT$*LINE	1250.508	92	13.592	1.650	0.000
ERROR	5387.187	654	8.237		



* Data approximate normality with sqrt transformation with homogeneity of variances (Levene's Test 0.701, p=0.403)

Clipping Treatment	Line	Siliques
uc	1	558
uc	1	498
uc	1	233
uc	1	.
uc	1	.
uc	2	295
uc	2	34
uc	2	398
uc	2	321
uc	2	442
uc	3	358
uc	3	321
uc	3	479
uc	3	354
uc	3	355
uc	4	386
uc	4	196
uc	4	241
uc	4	157
uc	4	283
uc	5	224
uc	5	402
uc	5	267
uc	5	432
uc	5	223
uc	6	382
uc	6	415
uc	6	308
uc	6	.
uc	6	.
uc	7	496
uc	7	540
uc	7	546
uc	7	824
uc	7	309
uc	8	567
uc	8	515
uc	8	501
uc	8	334
uc	8	305
uc	9	443
uc	9	845
uc	9	681
uc	9	573
uc	9	.
uc	10	223
uc	10	333
uc	10	439

uc	10	176
uc	10	.
uc	11	423
uc	11	509
uc	11	380
uc	11	370
uc	11	471
uc	12	632
uc	12	718
uc	12	518
uc	12	502
uc	12	594
uc	13	450
uc	13	77
uc	13	545
uc	13	477
uc	13	400
uc	14	361
uc	14	228
uc	14	428
uc	14	479
uc	14	.
uc	15	354
uc	15	413
uc	15	377
uc	15	291
uc	15	375
uc	16	167
uc	16	344
uc	16	360
uc	16	.
uc	16	.
uc	17	372
uc	17	188
uc	17	430
uc	17	329
uc	17	.
uc	18	503
uc	18	499
uc	18	.
uc	18	.
uc	19	660
uc	19	641
uc	19	904
uc	19	266
uc	19	540
uc	20	443
uc	20	489
uc	20	367
uc	20	273

uc	20	319
uc	21	380
uc	21	362
uc	21	.
uc	21	.
uc	21	.
uc	22	56
uc	22	370
uc	22	333
uc	22	767
uc	22	.
uc	23	257
uc	23	370
uc	23	331
uc	23	242
uc	23	239
uc	24	613
uc	24	501
uc	24	571
uc	24	600
uc	24	794
uc	25	196
uc	25	187
uc	25	95
uc	25	213
uc	25	198
uc	27	392
uc	27	273
uc	27	376
uc	27	463
uc	27	413
uc	28	695
uc	28	408
uc	28	640
uc	28	438
uc	28	456
uc	30	.
uc	30	.
uc	30	.
uc	30	.
uc	30	.
uc	31	255
uc	31	483
uc	31	420
uc	31	.
uc	31	.
uc	31	.
uc	31	.
uc	32	401
uc	32	741

uc	32	527
uc	32	472
uc	32	679
uc	33	412
uc	33	304
uc	33	333
uc	33	341
uc	33	315
uc	34	321
uc	34	385
uc	34	654
uc	35	252
uc	35	259
uc	35	226
uc	35	.
uc	35	.
uc	36	624
uc	36	489
uc	36	519
uc	36	.
uc	36	.
uc	36	.
uc	37	402
uc	37	560
uc	37	258
uc	37	280
uc	37	500
uc	39	.
uc	39	.
uc	39	.
uc	39	.
uc	40	496
uc	40	435
uc	40	543
uc	40	424
uc	40	.
uc	41	546
uc	41	498
uc	41	233
uc	41	.
uc	41	.
uc	42	190
uc	42	465
uc	42	390
uc	42	.
uc	42	.
uc	43	267
uc	43	295
uc	43	383
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c	97	558
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c	98	.
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c	99	347

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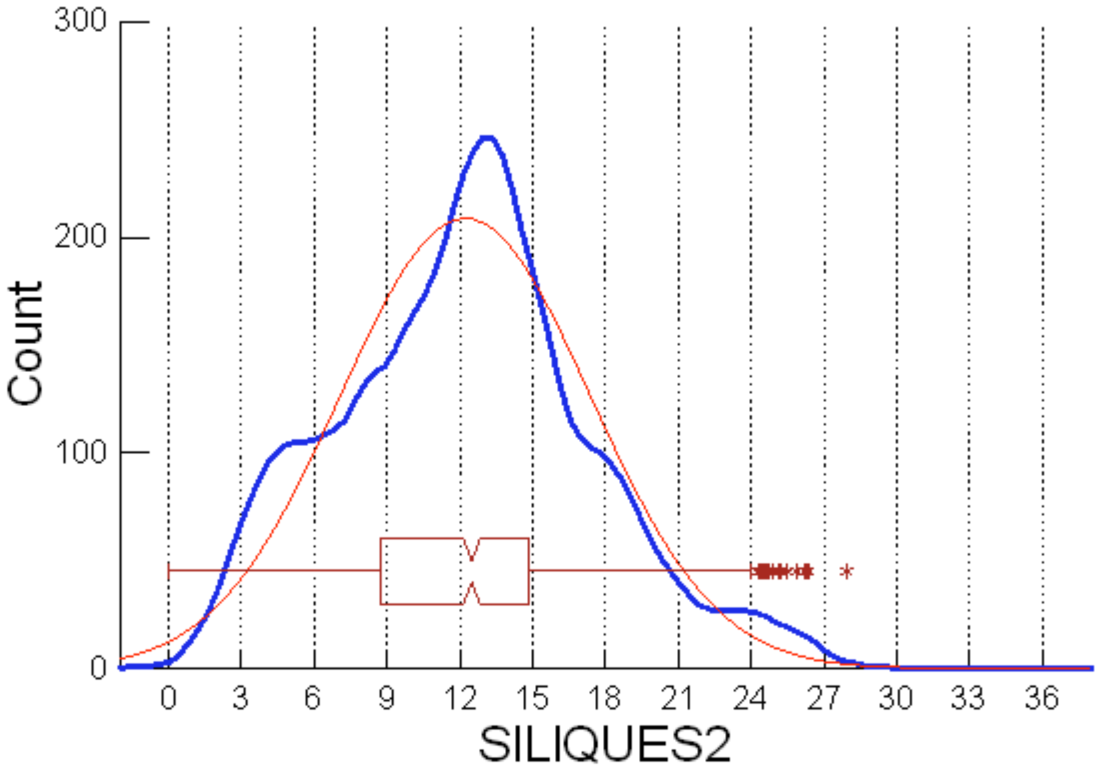
c	686	377
c	686	430
c	686	433
c	686	439
c	686	381

<u>**Year 2 Data**</u>

ANOVA

SOURCE	SS	DF	MS	F	P
TRT$	0.189	1	0.189	0.056	0.813
LINE	18,243.861	83	219.806	65.354	0.000
TRT$*LINE	911.029	83	10.976	3.264	0.000
ERROR	2,152.515	640	3.363		



Normality Plot

* Data approximate normality with a sqrt transformation with homogeneity of variances (Levene’s Test 0.147, p=0.702)

Clipping Treatment	Line	Siliques
uc	1	265
uc	1	221
uc	1	273
uc	1	197
uc	1	219
uc	2	295
uc	2	34
uc	2	398
uc	2	321
uc	2	442
uc	3	358
uc	3	321
uc	3	479
uc	3	354
uc	3	355
uc	4	386
uc	4	196
uc	4	241
uc	4	157
uc	4	283
uc	5	224
uc	5	402
uc	5	267
uc	5	432
uc	5	223
uc	6	172
uc	6	295
uc	6	275
uc	6	273
uc	6	.
uc	7	142
uc	7	138
uc	7	147
uc	7	148
uc	7	162
uc	8	27
uc	8	35
uc	8	32
uc	8	21
uc	8	27
uc	9	21
uc	9	25
uc	9	19
uc	9	27
uc	9	26
uc	10	19

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uc	10	23
uc	10	16
uc	10	17
uc	11	15
uc	11	17
uc	11	9
uc	11	8
uc	11	21
uc	12	52
uc	12	49
uc	12	61
uc	12	49
uc	12	68
uc	13	162
uc	13	178
uc	13	252
uc	13	282
uc	13	297
uc	14	193
uc	14	127
uc	14	157
uc	14	178
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uc	15	57
uc	15	38
uc	15	39
uc	15	72
uc	15	.
uc	16	175
uc	16	39
uc	16	37
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uc	16	79
uc	17	93
uc	17	143
uc	17	151
uc	17	171
uc	17	93
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uc	18	.
uc	18	.
uc	18	.
uc	19	31
uc	19	9
uc	19	27
uc	19	21
uc	19	9
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uc	20	73

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uc	53	164
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uc	79	273
uc	79	315
uc	79	371
uc	79	324
uc	80	92
uc	80	185
uc	80	295
uc	80	254
uc	80	261
uc	81	78
uc	81	87
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uc	81	85
uc	81	79
uc	82	224
uc	82	294
uc	82	187
uc	82	195
uc	82	270
uc	83	632
uc	83	694
uc	83	687
uc	83	609
uc	83	603
uc	84	390
uc	84	398
uc	84	331
uc	84	410
uc	84	321
uc	85	670

uc	85	598
uc	85	611
uc	85	610
uc	85	611
uc	86	110
uc	86	65
uc	86	79
uc	86	84
uc	86	95
uc	87	45
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uc	87	40
uc	87	55
uc	88	85
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uc	89	529
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uc	93	451
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uc	93	383
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uc	94	212
uc	94	195
uc	94	183
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uc	95	198

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uc	95	.
uc	95	.
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uc	96	195
uc	96	38
uc	96	55
uc	96	55
uc	96	193
uc	97	199
uc	97	238
uc	97	183
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uc	97	241
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uc	98	.
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uc	99	495
uc	99	512
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uc	686	233
uc	686	259
uc	686	291
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c	1	129
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c	1	159
c	2	417
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c	2	337
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c	2	365
c	3	500
c	3	530
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c	3	527
c	3	441
c	4	262
c	4	385
c	4	317
c	4	365

c	4	312
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c	5	326
c	5	459
c	5	199
c	5	476
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c	6	298
c	6	275
c	6	296
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c	7	205
c	7	195
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c	7	210
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c	13	312
c	13	275
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c	14	187
c	14	190
c	14	209

c	14	207
c	15	75
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c	15	39
c	15	74
c	15	83
c	16	93
c	16	87
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c	16	83
c	16	.
c	17	87
c	17	193
c	17	129
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c	18	.
c	18	.
c	18	.
c	19	15
c	19	8
c	19	12
c	19	9
c	19	23
c	20	92
c	20	78
c	20	73
c	20	72
c	20	65
c	21	21
c	21	9
c	21	23
c	21	21
c	21	17
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c	22	157
c	22	193
c	22	183
c	23	195
c	23	139
c	23	294
c	23	233
c	23	242
c	24	172
c	24	178
c	24	175
c	24	162
c	24	173

c	25	49
c	25	114
c	25	66
c	25	225
c	25	55
c	27	183
c	27	147
c	27	185
c	27	176
c	27	221
c	28	135
c	28	143
c	28	257
c	28	133
c	28	143
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c	30	69
c	30	66
c	30	51
c	30	50
c	31	30
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c	31	21
c	31	45
c	31	109
c	31	.
c	31	.
c	32	198
c	32	207
c	32	172
c	32	185
c	32	205
c	33	49
c	33	114
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c	35	.
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c	37	151
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c	39	39
c	39	83
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c	40	4
c	40	11
c	40	9
c	41	31
c	41	27
c	41	21
c	41	11
c	41	43
c	42	11
c	42	15
c	42	16
c	42	9
c	42	15
c	43	11
c	43	11
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c	44	132
c	44	141
c	44	152
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c	45	.
c	45	.
c	45	.
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c	46	217
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c	46	175
c	47	.
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c	47	.
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c	48	97

c	48	98
c	48	73
c	48	62
c	49	.
c	49	.
c	49	.
c	50	103
c	50	97
c	50	98
c	50	73
c	50	62
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c	52	197
c	52	183
c	52	284
c	53	158
c	53	142
c	53	162
c	53	239
c	53	284
c	55	65
c	55	64
c	55	54
c	55	56
c	55	71
c	56	.
c	56	.
c	56	.
c	56	.
c	56	.
c	57	98
c	57	112
c	57	138
c	57	150
c	57	120
c	58	129
c	58	135
c	58	214
c	58	182
c	58	179
c	59	130
c	59	145
c	59	98
c	59	110

c	59	130
c	60	60
c	60	78
c	60	97
c	60	65
c	60	75
c	61	.
c	61	.
c	61	.
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c	63	392
c	63	294
c	63	407
c	64	198
c	64	265
c	64	232
c	64	211
c	64	187
c	65	241
c	65	292
c	65	141
c	65	183
c	65	271
c	66	138
c	66	141
c	66	197
c	66	138
c	66	142
c	67	.
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c	67	.
c	67	.
c	68	168
c	68	175
c	68	207
c	68	168
c	68	182
c	69	147
c	69	153
c	69	162
c	69	184

c	69	115
c	70	102
c	70	215
c	70	314
c	70	275
c	70	185
c	71	198
c	71	152
c	71	172
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c	73	182
c	73	215
c	74	185
c	74	292
c	74	178
c	74	.
c	74	.
c	75	240
c	75	175
c	75	182
c	75	212
c	75	215
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c	76	.
c	76	.
c	76	.
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c	77	158
c	77	142
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c	78	262
c	78	292
c	78	263
c	78	198
c	78	212
c	79	351
c	79	323
c	79	347
c	79	410

c	79	225
c	80	208
c	80	275
c	80	308
c	80	185
c	80	165
c	81	104
c	81	97
c	81	102
c	81	105
c	81	97
c	82	304
c	82	297
c	82	360
c	82	307
c	82	337
c	83	621
c	83	610
c	83	590
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c	83	638
c	84	450
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c	84	495
c	84	391
c	84	398
c	85	598
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c	85	591
c	85	575
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c	86	83
c	86	76
c	86	79
c	86	65
c	87	45
c	87	65
c	87	23
c	87	71
c	87	76
c	88	98
c	88	97
c	88	65
c	88	90
c	88	125
c	89	209
c	89	308
c	89	304
c	89	382

c	89	401
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c	90	.
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c	90	.
c	90	.
c	91	205
c	91	198
c	91	197
c	91	155
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c	92	179
c	92	182
c	92	192
c	92	173
c	92	152
c	93	408
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c	93	507
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c	95	98
c	95	195
c	95	.
c	95	.
c	95	.
c	96	158
c	96	175
c	96	130
c	96	195
c	96	212
c	97	365
c	97	327
c	97	336
c	97	355
c	97	342
c	98	135
c	98	193
c	98	185
c	98	193
c	98	192
c	98	98
c	98	95
c	99	308
c	99	316

c	99	372
c	99	298
c	99	345
c	686	355
c	686	337
c	686	336
c	686	355
c	686	342

III. *Transcriptomic Data*

http://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE44781

List of differentially expressed genes

Number	Microarray Element	Gene
1	262038_at	AT1G35580
2	267516_at	AT2G30520
3	251028_at	AT5G02230
4	258448_at	AT3G22290
5	252308_at	AT3G49310
6	264501_at	AT1G09390
7	264977_at	AT1G27090
8	247353_at	AT5G63620
9	245817_at	AT1G26160
10	265953_at	AT2G37480
11	246320_at	AT1G16560
12	247553_at	AT5G60910
13	247694_at	AT5G59750
14	254270_at	AT4G23100
15	255417_at	AT4G03190
16	248551_at	AT5G50200
17	253964_at	AT4G26480
18	250895_at	AT5G03850
19	249694_at	AT5G35790
20	260395_at	AT1G69780
21	257148_at	AT3G27240
22	265227_s_at	ATMG01280 AT2G07695
23	245790_at	AT1G32200
24	260821_at	AT1G06820
25	262059_at	AT1G80030
26	266465_at	AT2G47750
27	255148_at	AT4G08470
28	265228_at	ATMG01190 AT2G07698
29	264871_at	AT1G24180
30	246745_at	AT5G27770
31	255797_at	AT2G33630

32	252290_at	AT3G49140
33	250382_at	AT5G11580
34	247433_at	AT5G62540
35	252960_at	AT4G38750
36	253243_at	AT4G34560
37	251666_at	AT3G57050
38	248309_at	AT5G52540
39	251082_at	AT5G11580
40	254306_at	AT4G22330
41	247131_at	AT5G66190
42	263014_at	AT1G23400
43	264095_at	AT1G79230
44	256502_at	AT1G36730
45	260536_at	AT2G43400
46	266904_at	AT2G34590
47	267609_at	AT2G26780
48	248094_at	AT5G55220
49	248103_at	AT5G55160
50	260286_at	AT1G80600
51	253035_at	AT2G38400
52	263973_at	AT2G42740
53	265817_at	AT2G18050
54	267035_at	AT4G38240
55	253886_at	AT4G27710
56	260896_at	AT1G29310
57	249900_at	AT5G22640
58	256193_at	AT1G30200
59	249538_at	AT5G38840
60	259258_at	AT3G07670
61	261408_s_at	AT1G07660 AT1G07820
62	244939_at	ATCG00065
63	251449_at	AT3G59920
64	253779_at	AT4G28490
65	261944_at	AT1G64650
66	257903_at	AT3G28460
67	264353_at	AT1G03260
68	251409_at	AT3G60245
69	263755_at	AT2G21340
70	245269_at	AT4G14500
71	245627_at	AT1G56600
72	253164_at	AT4G35725
73	250318_at	AT5G12200
74	250434_at	AT5G10390
75	252562_s_at	AT3G46320 AT3G45930[AT3G46320
76	262963_at	AT1G54220
77	256729_at	AT3G25680
78	260571_at	AT2G43790
79	261557_at	AT1G63640

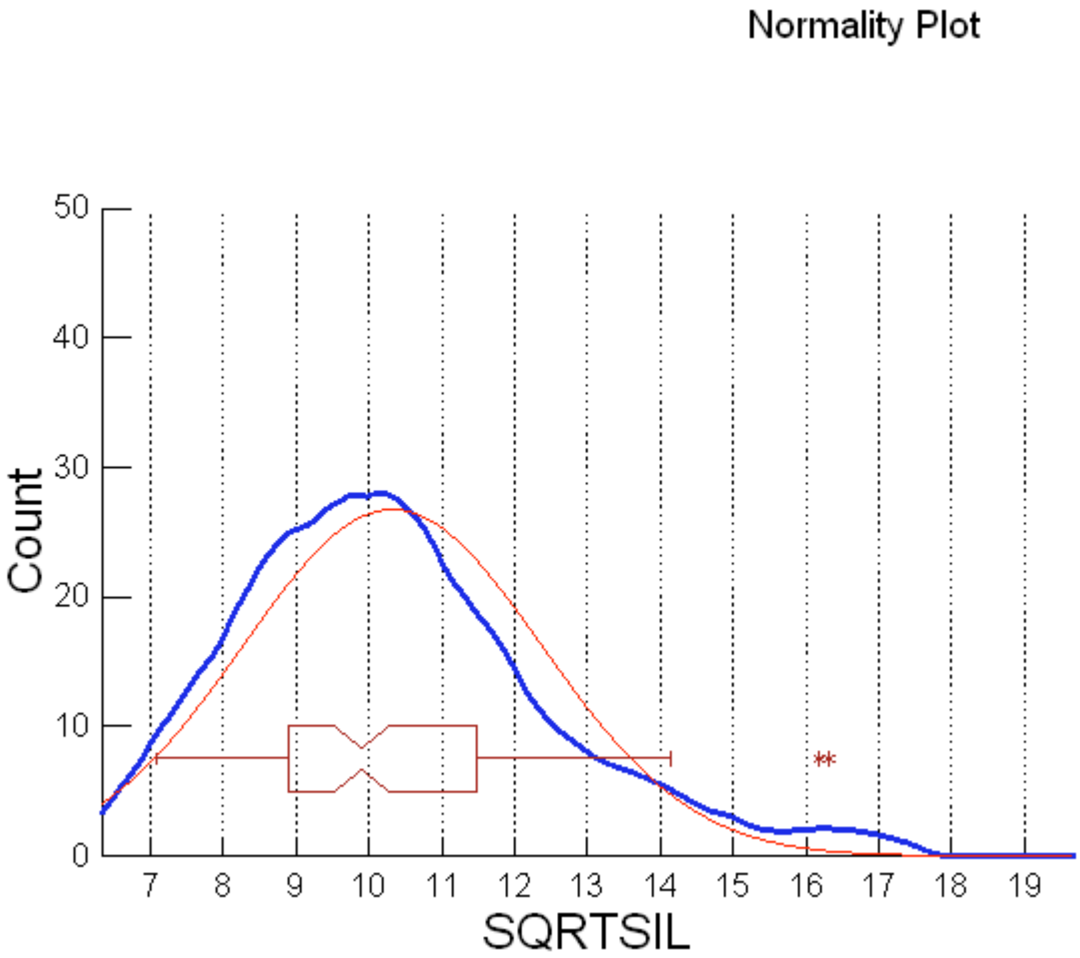
80	266638_at	AT2G35490
81	258922_at	AT3G10610
82	245263_at	AT4G17740
83	264262_at	AT1G09200
84	253704_at	AT4G29490
85	247260_at	AT5G64500
86	257431_at	AT2G36360
87	262985_s_at	AT1G70600 AT1G23290[AT1G70600
88	247140_at	AT5G66250
89	258766_at	AT3G10700
90	245176_at	AT2G47440
91	247925_at	AT5G57560
92	258755_at	AT3G11945
93	261424_at	AT1G18700
94	262174_at	AT1G74910
95	264454_at	AT1G10320
96	266438_at	AT2G43180
97	260510_at	AT1G51580
98	248676_at	AT5G48850
99	255537_at	AT4G01690
100	267517_at	AT2G30520
101	257215_at	AT3G15070
102	248669_at	AT5G48730
103	245284_at	AT4G14210
104	247306_at	AT5G63870
105	252235_at	AT3G49910
106	259193_at	AT3G01480
107	250941_at	AT5G03320
108	265735_at	AT2G01140
109	264421_at	AT1G43170

IV. *Knockout mutant data*

ANOVA

Source	SS	DF	MS	F	P
Trt	1.494	1	1.494	0.471	0.494
Line	126.048	4	31.512	9.928	0.000
Trt * Line	28.013	4	7.003	2.206	0.073
Error	361.824	114	3.174		

Effect	trt	line	trt	line	P
trt*line	c	sail1252	uc	sail1252	0.471
trt*line	c	salk0193	uc	salk0193	0.419
trt*line	c	Gabi864	uc	Gabi864	0.265
trt *line	c	col	uc	col	0.019
trt*line	c	ler	uc	ler	0.094



* Data approximate normality with sqrt transformation with homogeneity of variances (Levene's Test .203, p=0.653).

Treatment	Line	Siliques
c	sail1252	89
c	sail1252	92
c	sail1252	91
c	sail1252	70
c	sail1252	89
c	sail1252	78
c	sail1252	63
c	sail1252	133
c	sail1252	59
c	sail1252	89
c	sail1252	92
c	sail1252	91
c	sail1252	70
c	sail1252	89
c	sail1252	78
c	sail1252	63
c	sail1252	133
c	sail1252	59
uc	sail1252	70
uc	sail1252	79
uc	sail1252	95
uc	sail1252	98
uc	sail1252	112
uc	sail1252	98
uc	sail1252	132
uc	sail1252	89
uc	sail1252	59
uc	sail1252	70
uc	sail1252	79
uc	sail1252	95
uc	sail1252	98
uc	sail1252	112
uc	sail1252	98
uc	sail1252	132
uc	sail1252	89
uc	sail1252	59
c	salk019323	83
c	salk019323	102
c	salk019323	123
c	salk019323	98
c	salk019323	71
c	salk019323	59
c	salk019323	65
c	salk019323	83
c	salk019323	102
c	salk019323	123

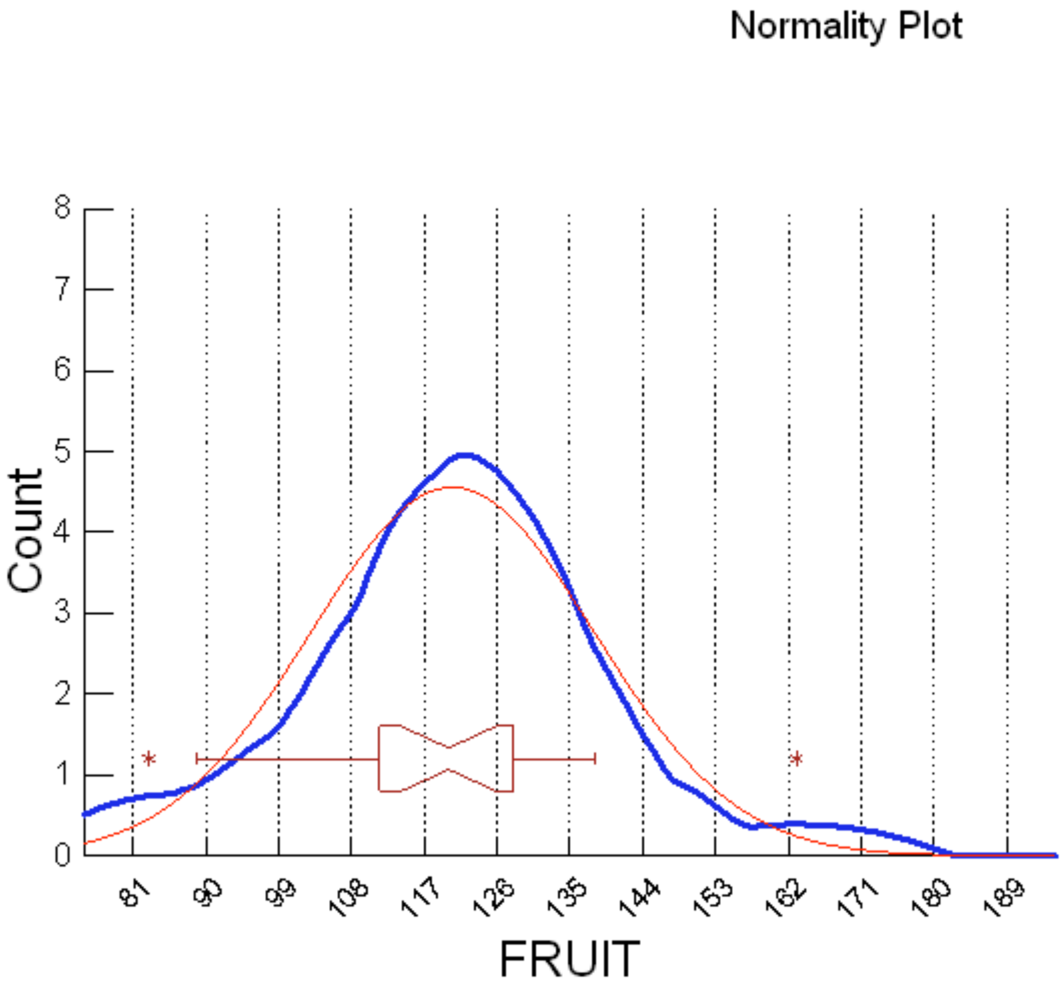
c	salk019323	98
c	salk019323	71
c	salk019323	59
c	salk019323	65
uc	salk019323	125
uc	salk019323	79
uc	salk019323	92
uc	salk019323	88
uc	salk019323	92
uc	salk019323	98
uc	salk019323	89
uc	salk019323	125
uc	salk019323	79
uc	salk019323	92
uc	salk019323	88
uc	salk019323	92
uc	salk019323	98
uc	salk019323	89
c	N173950	200
c	N173950	81
c	N173950	57
c	N173950	57
c	N173950	188
c	N173950	106
c	N173950	200
c	N173950	81
c	N173950	57
c	N173950	57
c	N173950	188
c	N173950	106
uc	N173950	139
uc	N173950	262
uc	N173950	266
uc	N173950	71
uc	N173950	50
uc	N173950	50
uc	N173950	139
uc	N173950	262
uc	N173950	266
uc	N173950	71
uc	N173950	50
uc	N173950	50
c	col	193
c	col	159
c	col	152
c	col	187
c	col	149
c	col	165
c	col	186
c	col	115

c	col	171
uc	col	106
uc	col	119
uc	col	116
uc	col	119
uc	col	118
uc	col	128
uc	col	132
uc	col	112
uc	col	119
c	ler	133
c	ler	125
c	ler	115
c	ler	119
c	ler	115
c	ler	142
c	ler	112
c	ler	111
c	ler	89
uc	ler	125
uc	ler	190
uc	ler	147
uc	ler	132
uc	ler	162
uc	ler	197
uc	ler	114
uc	ler	137
uc	ler	140

V. ***Complementation Data***

Analysis of Variance

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
TREATM$	1,036.80	1	1,036.80	3.901	0.064
Error	4,784.20	18	265.789		



* Data normally distributed with homogeneity of variances (Levene's Test .119, p=0.734).

Treatment	**Siliques**
C	138
C	128
C	137
C	118
C	105
C	117

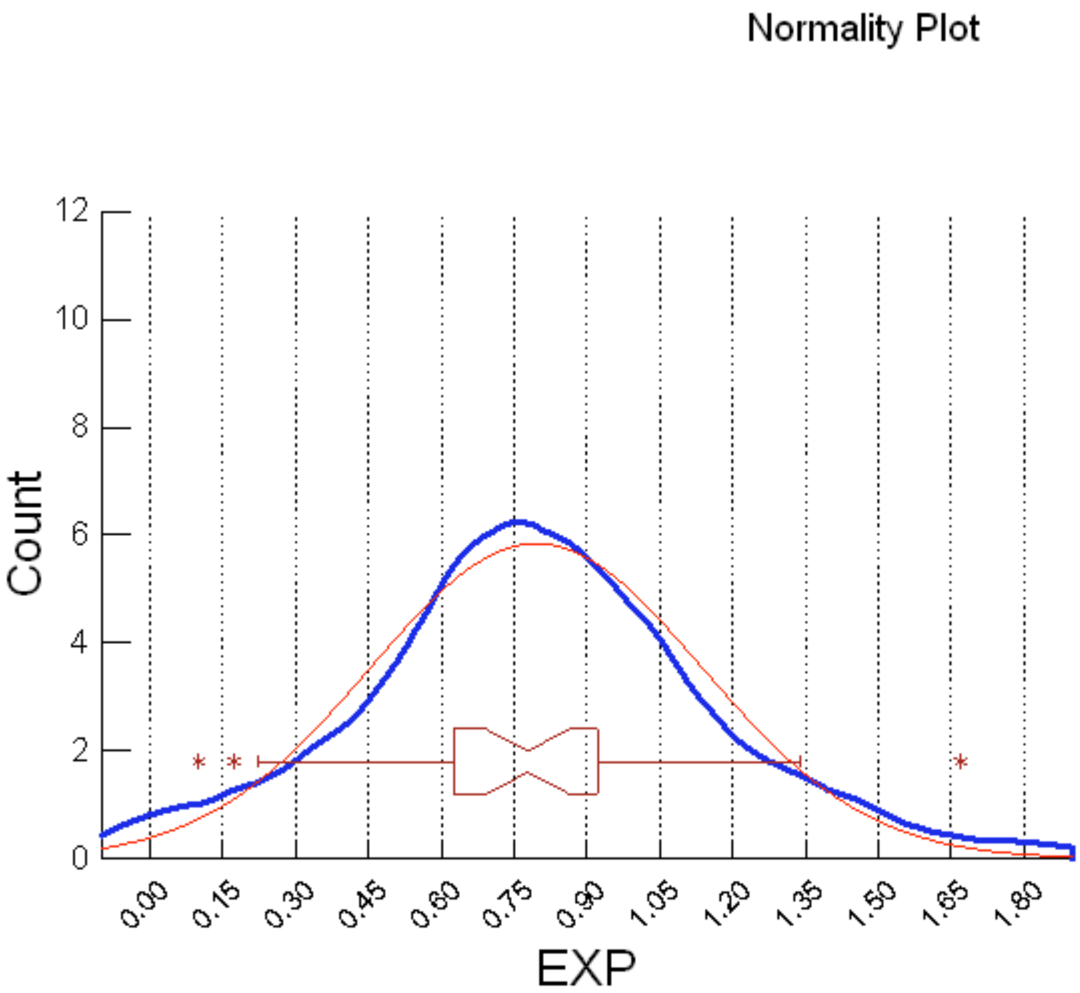
C	119
C	163
C	124
C	128
Uc	128
Uc	108
Uc	118
Uc	128
Uc	110
Uc	121
Uc	113
Uc	89
Uc	135
Uc	83

VI. *Expression Data*

Analysis of Variance

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
TT$	0.373	1	0.373	6.001	0.024
GRP	0.809	4	0.202	3.253	0.033
TT$*GRP	0.954	4	0.239	3.837	0.018
Error	1.244	20	0.062		

Standard Effect	Trt	group	_trt	_group	Estimate	Error	DF	t	Pr
trt*group	Col	1	ler	1	-0.4293	0.2036	20	-2.11	0.0478
trt*group	Col	2	ler	2	0.2133	0.2036	20	1.05	0.3073
trt*group	Col	3	ler	3	0.4053	0.2036	20	1.99	0.0604
trt*group	Col	4	ler	4	0.2867	0.2036	20	1.41	0.1745
trt*group	Col	5	ler	5	0.6393	0.2036	20	3.14	0.0052



* Data normally distributed with a sqrt transformation with homogeneity of variances (Levene’s Test .686, p=0.608).

Treatment	**Expression**	**Group**
col	0.1	1
col	0.566	1
col	0.458	1
col	0.656	2
col	0.755	2
col	0.819	2
col	1.208	3
col	1.175	3
col	1.342	3
col	1.261	4
col	0.775	4
col	0.917	4
col	1.054	5
col	0.849	5
col	1.67	5
ler	0.922	1

ler	0.624	1
ler	0.866	1
ler	0.742	2
ler	0.624	2
ler	0.224	2
ler	0.877	3
ler	1.049	3
ler	0.583	3
ler	0.781	4
ler	0.843	4
ler	0.469	4
ler	0.768	5
ler	0.714	5
ler	0.173	5

File S2
Combined Phenotypic Genotypic data

Available for download as a CSV file at
http://www.genetics.org/lookup/suppl/doi: 10.1534/genetics.113.154351 /-/DC1