

Empirical Analysis of Transcriptional Activity in the *Arabidopsis* Genome

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Functional analysis of a genome requires accurate gene structure information and a complete gene inventory. A dual experimental strategy was used to verify and correct the initial genome sequence annotation of the reference plant *Arabidopsis*. Sequencing full-length cDNAs and hybridizations using RNA populations from various tissues to a set of high-density oligonucleotide arrays spanning the entire genome allowed the accurate annotation of thousands of gene structures. We identified 5817 novel transcription units, including a substantial amount of antisense gene transcription, and 40 genes within the genetically defined centromeres. This approach resulted in completion of ~30% of the *Arabidopsis* ORFeome as a resource for global functional experimentation of the plant proteome.

The genome sequence of *Arabidopsis thaliana* serves as a reference for plants (1). The initial identification of transcriptional units in the *Arabidopsis* genome sequence was carried out largely by ab initio gene predictions, sequence homology, sequence motif analysis, and other nonexperimental methods (2–7). This led to an estimate of 25,500 protein-coding genes (2). Though gene prediction software has steadily improved, the ability of these programs to precisely determine gene structures in sequenced genomes remains unsatisfactory (8–10). A recent attempt to verify experimentally the accuracy of the *Arabidopsis* genome annotation with conventional molecular approaches proved quite inefficient in identifying full-length (fl) open-reading frames (ORFs) (11).

Global experimental approaches are expected to greatly improve genome annotation (12, 13).

A genome sequence that is empirically annotated can provide the foundation for the determination of its ORFeome, the complete set of ORF clones for all protein-coding genes. Access to a “gold standard” cDNA/ORF clone collection (14–16), representing the entire *Arabidopsis* proteome, is urgently needed as a common resource for research (17). Here we report the experimental definition of the transcriptional units for all *Arabidopsis* genes by fl-cDNA discovery and by hybridization of RNA populations to whole-genome arrays (WGs) (fig. S1).

Annotation and fl cDNAs. Dramatic improvements in genome annotation have been achieved for several organisms by means of

sequences of fl-cDNAs (8, 15, 18, 19). For *Arabidopsis*, three collections of fl-cDNAs have been used for this purpose (8, 20–23). Of the 26,828 predicted genes in the *Arabidopsis* genome, 25,540 were annotated as protein-coding, with the rest being annotated as pseudo- and partial genes (fig. S3). A unique location in the genome can be identified for the majority (99%) of cDNAs (fig. S4). From this analysis, three classes of genes were detected in the annotated genome (fig. S5): (i) annotated expressed (AE) genes; (ii) annotated non-expressed (ANE) genes, and (iii) newly discovered genes located in the intergenic regions (non-annotated expressed; NAE). Seventy percent (18,093) of the 25,540 annotated genes were found to be transcriptionally active on the basis of identification of an expressed sequence tag (EST) or cDNA, and these represent the class of the AE genes. The remaining 7447 genes (30%) are the hypothetical, ANE (24) genes. Only 10,507 (58%) of the AE genes have at least one fl-cDNA clone (Fig. 1). The remaining 7586 genes (42%) have evidence of their expression from At-ESTs and/or non-fl-cDNAs (Fig. 1). Among the 10,507 genes with a fl-cDNA sequence, the annotated structures of 32% of them (3336) were inaccurately annotated. Incorporation of fl-cDNA sequences resulted in the dramatic improvement of the genome annotation (fig. S6). The vast majority of predicted gene structures in the initial release of the *Arabidopsis* genome annotation (August 2001 V1.0) were not derived from experimental evidence of transcription.

Genome annotation, intergenic regions, and comparative genomics. Alignment of the various At-ESTs and fl-cDNAs on the V1.0 genome annotation reveals that a considerable number of cDNAs mapped within in-

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tergenic regions (IGRs) (fig. S5). Clustering analysis (22) reveals that as many as 1347 NAE genes may reside in the IGRs. The density and distribution of the new unpredicted genes are shown in fig. S7 (22). The availability of a substantial number of *Brassica*, rice, and wheat ESTs allowed us to examine whether any of the aANE genes (Fig. 1) show similarity to these non-*Arabidopsis* ESTs. This analysis suggests that 45% of the ANE *Arabidopsis* genes are transcriptionally active [BLAST e-value < 10^{-25} , (22)] (Fig. 1A). Furthermore, alignment of the *Brassica*, rice, or wheat ESTs within the IGRs identified an additional 1042 transcriptionally active regions (BLAST e-value < 10^{-25} , Fig. 1B). Overall, our analysis revealed that the *Arabidopsis* genome contains ~28,000 genes of which 15,033 (59%) annotated genes lack a fl-cDNA clone and, therefore, have not been experimentally verified.

Mapping transcriptional units using high-density oligonucleotide tiling arrays.

In the absence of a corresponding fl-cDNA for 15,033 annotated genes (7586 AE and 7447 ANE genes) and for the ~1350 newly discovered genes located in the IGRs (Fig. 1B), new methods are needed to obtain evidence for the existence of this remaining large number of “untouched” genes. Recently, microarray technology has been used for mapping transcription units in genomes (12, 13, 25). Despite the fact that the *E. coli* genome is well characterized, nearly 25% of the transcripts were previously unidentified (26). Except for *Saccharomyces cerevisiae* (27, 28), however, tiling arrays have not been applied on a genome-wide scale for unbiased examination of transcriptional activity in the eukaryote.

To identify transcription units in the *Arabidopsis* genome, we used custom high-density oligonucleotide arrays that tile the entire genome and RNA samples prepared from a diverse set of tissues and treatments to ensure broad representation of transcriptional activity. Four pilot arrays, identical in design except for the regions of the genome sequence covered, were used to test the feasibility of the approach (fig. S8) (22). In brief, labeled cRNAs were prepared from different plant tissues and hybridized to the four arrays. Figure 2A shows a deconvoluted and merged image of these arrays after hybridization with cRNA from three different plant tissues (flower, etiolated seedlings, and inflorescence). Differential gene expression was revealed across the 5 Mb region. For example, gene At1g12110 (Fig. 2B) is expressed only in seedlings; gene At1g10770 (Fig. 2C), only in flowers; and gene At1g10630, in all three tissues (Fig. 2D). In addition, the hybridization profiles revealed the structures of the individual genes as confirmed by the sequences of fl-cDNAs corresponding to each of these genes (Fig. 2, B to D). Further analysis with mRNAs isolated from light grown (L+), dark grown (L-) and cold-stressed light grown (L+ cold) seedlings (22) representing different growth conditions revealed that 950

(88%) of the AE transcription units present on the four chips could be detected (Fig. 3A, AE). One-half of the ANE transcription units present on these four chips were also detected (Fig. 3A, ANE). Expression was detected for 61% percent of the newly discovered genes present on the four pilot chips (Fig. 3A, NAE).

Validation of tiling chip–detected transcription units was carried out through reverse transcriptase–polymerase chain reaction (RT-PCR) amplification, cloning, and sequencing (fig. S9) (22). RT-PCR products were detected for 78% of the tested transcriptional units (table S1). Fifty-seven percent of the RT-PCR products yielded “perfect” ORF clones from both AE and ANE genes (table S1). The remaining 42% of the clones were without ORFs due to stop codons introduced during RT-PCR amplification (table S1).

Whole-genome arrays. We next designed a set of 12 oligonucleotide arrays representing ~94% of the *Arabidopsis* ge-

nome sequence [110 Mb (22) (fig. S10)]. Each array contains ~834,000 25-mer oligos (22). Four RNA populations (22) were hybridized to these arrays, and a transcription map for the entire *Arabidopsis* genome was determined (figs. S11 to S15) (22). Expression of 84% of the AE genes and 37% of the ANE genes was detected when these four RNA samples were used (Fig. 3B, AE and ANE). In addition, we were also able to detect a large number (~54%) of transcriptionally active sites corresponding to the chromosomal locations where the newly discovered genes were found (Fig. 3B, NAE). Transcriptional activity was also detected in 2000 intergenic regions (23%) that were thought to be devoid of transcriptional activity (Fig. 3B, IGR).

The five chromosomes were equally transcriptionally active under various growth conditions or developmental stages (fig. S16).

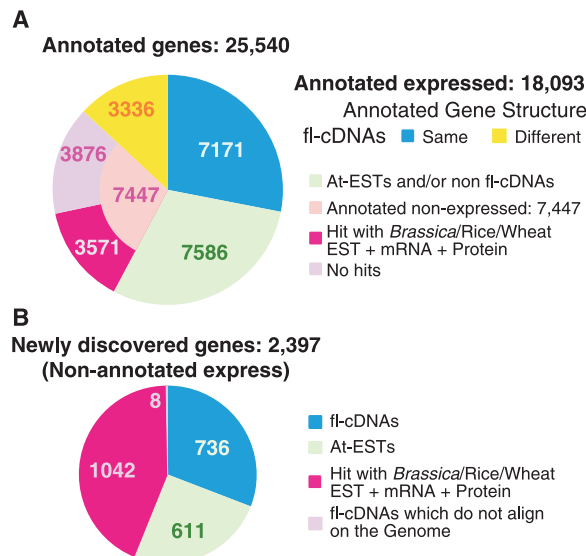


Fig. 1. Quality of the *Arabidopsis* genome annotation V1.0. (A) AE and ANE genes (hypothetical). (B) Newly discovered genes. The fl-cDNAs include: community full length (CFL); Ceres (8); Riken *Arabidopsis* full length [RAFL, (20)] and Chip (C) clones isolated during this study. See (46) for percentage distribution in the two types of annotated genes.

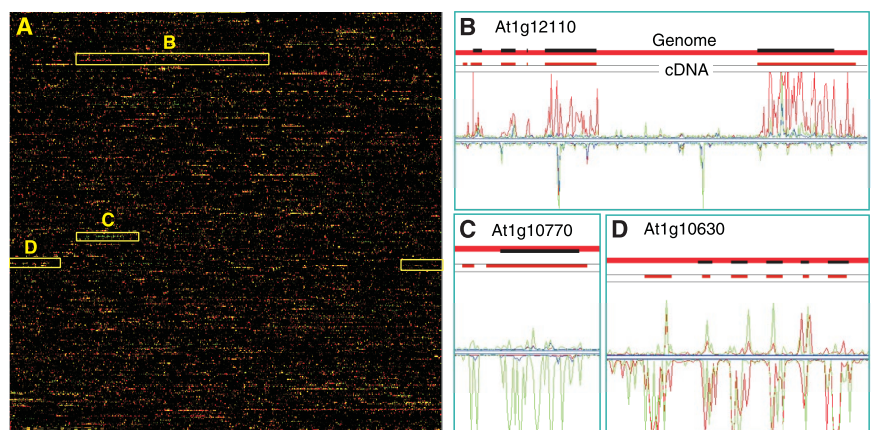


Fig. 2. Pilot Affymetrix tiling genome arrays for mapping transcription units. (A) Deconvoluted hybridization image of array 1A hybridized with three different mRNAs from seedlings, flowers, and young inflorescence. The chip images from three independent hybridizations were overlaid electronically and shown on (A). (B) Detection of a transcription unit specifically expressed in a 3-day-old etiolated seedlings treated with ethylene. (C) Detection of a transcription unit specifically expressed in flowers. (D) Detection of a transcription unit expressed in all three tissues.

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Transcriptional activity across the chromosomes using four different messenger RNAs (mRNAs) is quantitatively distinct (Fig. 4). The transcriptional activity across each chromosome was different in various tissues tested (Fig. 4). For example, the right arm of chromosome 2 showed more transcriptionally active sites in suspension cell cultures [Fig. 4, compare (E) with (C) in chr. 2] than in flowers. In addition, in certain cases the transcriptional activity was strand-specific. For example, in roots there was more transcription from the forward-strand than from the reverse complement strand (Fig. 4D, chr. 1). The gene density is approximately the same in both strands. The distribution of tissue-specific transcripts across the five chromosomes is shown in

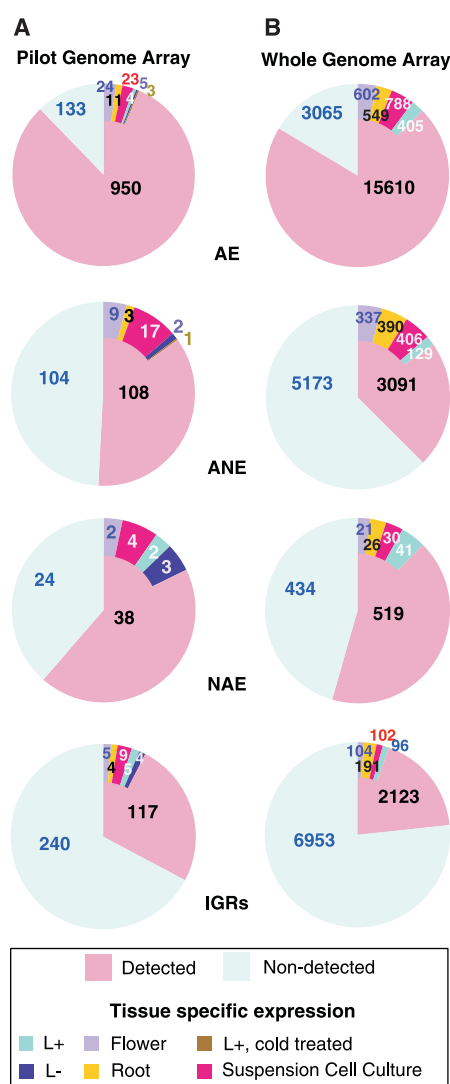


Fig. 3. Quantification of total and tissue-specific transcriptional units detected by the pilot (A) and whole genome (B) arrays of AE genes, ANE genes, NAE genes, and IGRs. See (22) for additional details. The number of genes detected for each category present in the arrays are as follows: (A) AE, 950/1083 (88%); ANE, 108/212 (51%); NAE, 38/62 (61%); IGRs, 117/357 (33%). (B) AE, 15,610/18,675 (84%); ANE, 3091/8264 (37%); NAE, 519/953 (54%); IGRs, 2123/9076 (23%).

Fig. 5. Functional classification of the tissue-specific transcripts revealed variation in the types of genes expressed in a tissue-specific manner (fig. S17). For example, 16% of the flower-specific AE transcription units encode proteins involved in metabolism, whereas only 6.5% of the same class of genes were detected in suspension cell cultures (fig. S17C, compare flower with suspension cell culture).

More detailed analyses of the whole-genome transcription map focused on examination of regions of the genome, such as pseudogenes and centromeres, thought to be relatively transcriptionally silent and also on genomic locations showing antisense RNA expression. (Fig. 6A). We detected transcription for ~20% of the 1332 ANE “pseudogenes” (Fig. 6A), suggesting that these ORFs may be misannotated. Alternatively, as recently described for mouse (29), such actively transcribed “pseudogenes” may function to regulate gene activity. In total, ~7600 annotated genes (~30% of all annotated genes) were identified that showed significant antisense RNA expression (Fig. 6B), suggesting that double-strand RNA formation may be a general phenomenon in plant cells (30). We found complementary patterns of tissue-specific expression of sense and antisense RNAs for many genes, indicating a possible biological role for these transcripts (31). Lastly, we surveyed regions located within the genetically defined centromeres for transcriptional activity [(2, 32); Fig. 6C]. Transcriptional activity was confirmed for ~90% of the AE genes. Transcriptional activity was also observed for ~45% of the “unexpressed” genes, and we identified 29 new transcribed genes within the five centromere regions. Surprisingly, two

unusually highly expressed sites, “hot spots,” were identified within the genetically defined centromeres of two chromosomes (2, 22, 32) (Fig. 6D). The centromere region of chromosome 2 (CEN2) contains a large (~600 kb) insertion of a rearranged copy of the mitochondrial genome (2). This entire genomic location showed high level of transcriptional activity. In addition, several unannotated regions within the centromere region of chromosome 3 (CEN3) were identified that displayed a significantly higher level of transcriptional activity from both forward and reverse complement DNA strands (Fig. 6D). These highly transcribed sequences within CEN3 were largely composed of transposon or retrotransposon-like sequences but also contained some unique sequences.

Overall, evidence from both cDNA sequencing and WGA expression studies allowed detection of transcriptional activity for 5817 previously ANE (hypothetical) genes (Fig. 3B, ANE; figs. S6, A and C).

Determination of the *Arabidopsis* ORFeome. Large-scale ORFeome projects not only aid in the improvement of whole genome annotation, but also provide valuable resources to the community for functional genomic studies and proteomics (33, 34). We constructed 8750 error-free ORF clones [Table 1 (22, 35)] representing approximately 32% of the annotated genes. Functional classification of the constructed ORFeome revealed a similar distribution of the various functional classes compared with the complete set of annotated genes (fig. S19). Figure S20 shows the distribution of the ORF clones constructed among the various available fl-cDNAs.

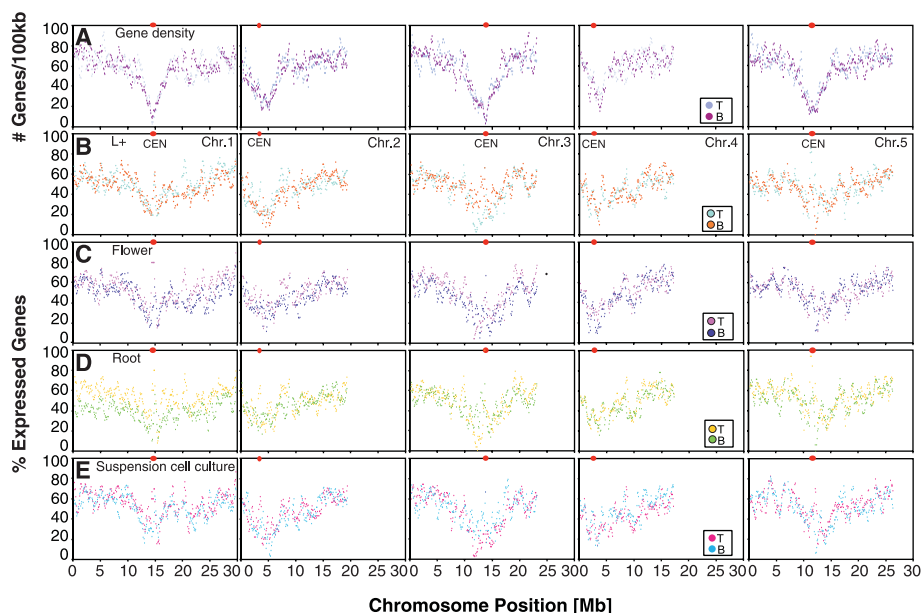


Fig. 4. Global gene expression detected by whole genome arrays in the *Arabidopsis* chromosomes. (A) Predicted gene density on each strand of the five chromosomes. (B) Percentage of expressed genes on each strand of the five chromosomes in light-grown seedlings. (C) Flowers. (D) Roots. (E) Suspension cell culture. Forward strand is indicated as top (T), whereas reverse strand as bottom (B). The genetically defined centromeres were indicated as red dots.

Utility of WGA for genomic analysis.

We used a strategy for mapping transcription units that included both a traditional cDNA cloning and DNA sequencing approach and a novel high-throughput approach that utilizes tiling array technology (12, 13, 25). Sequencing ESTs and fl-cDNAs verified 40% of the annotated genes, dramatically improved genome annotation, and allowed the construction of 30% of the ORFeome. As with other large-scale cDNA-based gene col-

lection projects (8, 15, 18), the traditional approach of sequencing fl-cDNAs reaches a point of diminishing returns: two-thirds of the total annotated *Arabidopsis* genes still have no corresponding fl-cDNA. The WGA technology allowed us to identify transcripts for the ANE genes and enabled construction of the remaining 30% of the *Arabidopsis* ORFeome. We were able to detect ~60% of the total annotated genes (AE and ANE) using only a limited number of RNA samples (four). A more comprehensive survey of tissues and cell types should enable a more complete description of the transcriptome.

WGAs serve as a “molecular roadmap” for detecting transcription units and their structures across the chromosomes. This capability arrives at a convenient time, because several major efforts to generate fl-cDNAs for identification of a full set of ORF clones of expressed genes are under way [the Mammalian Gene Collection (15, 16) and FANTOM (36)]. As these collections become more complete, the marginal utility of each added EST decreases, and the prospect

for discovering new genes diminishes. Use of full-genome tiling arrays is a natural way to complete the identification of transcription units. In addition, the data presented here raise the prospect that novel, tissue-specific transcription units can be identified in *Arabidopsis* by means of WGAs, cloned, and functionally studied with biochemical and reverse genetic approaches (37). The WGAs allowed us to detect transcription from many of the “pseudogenes,” providing additional evidence that this class of genes may function in the regulation of their paralogous counterparts (29). Our studies also revealed that a large fraction of *Arabidopsis* genes showed expression of an antisense RNA transcript that, in many cases, was tissue-specific. These results suggest that the production of double-stranded RNAs may play a greater role in the regulation of normal plant development than is currently understood.

The use of genome tiling array technology is not restricted to transcription unit mapping of RNA polymerase II transcripts. WGAs can also be used for detecting mitochondrial- or plastid-derived RNAs and potentially could be used for the identification of a variety of small noncoding RNAs (nc-RNAs) (38). By design, WGAs contain DNA sequences absent from traditional gene expression arrays, such as the promoters, introns, and intergenic “dark matter.” Thus, they are well suited for global mapping of DNA binding sites by location analysis (39, 40) and provide an “unbiased view” of DNA binding sites that recent studies suggest may lie within coding regions at a greater frequency than previously suspected (41). Genome tiling arrays can

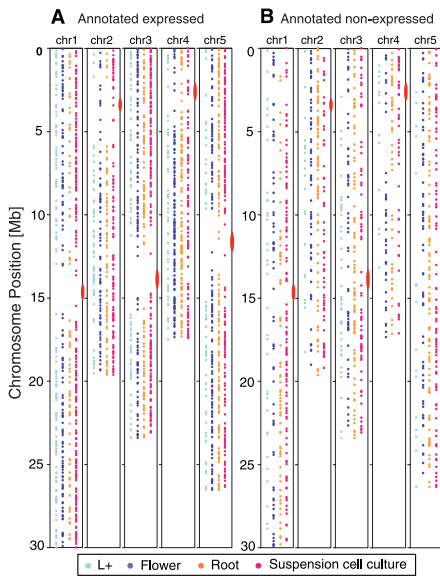


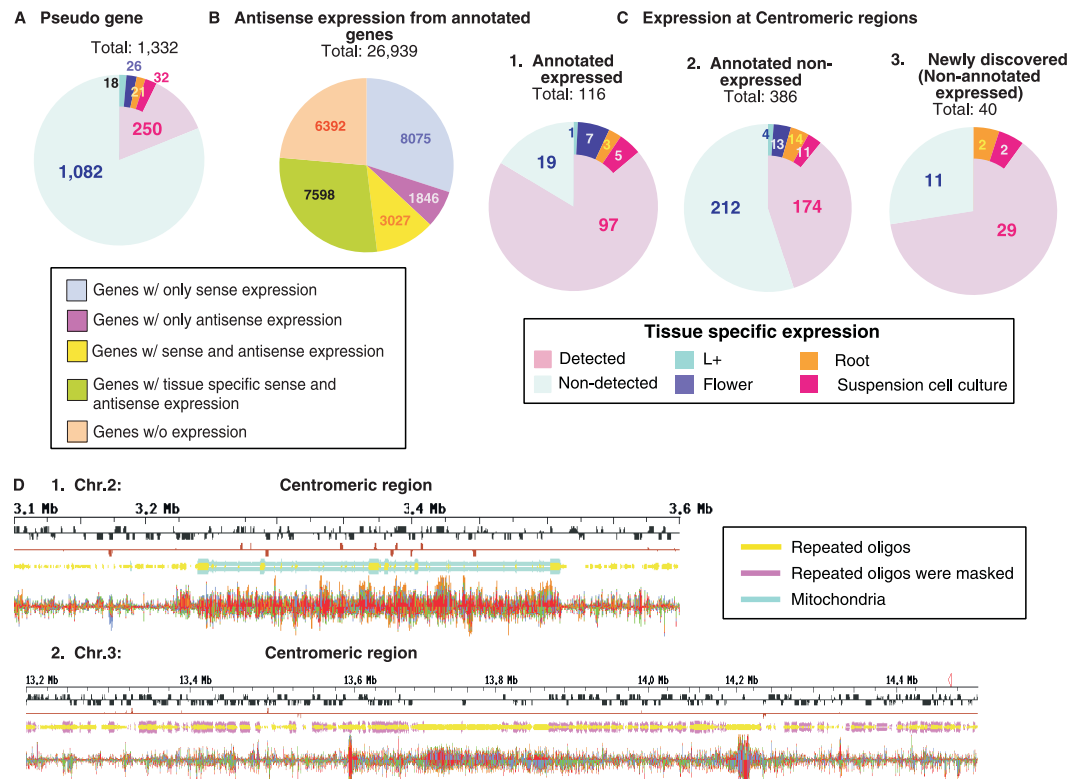
Fig. 5. Chromosomal locations of tissue-specific expressed transcription units. (A) AE genes. (B) ANE genes.

Table 1. ORF clones constructed.

Class of genes	Type of ORF clone*	
	U	C
Annotated expressed	7685	486
Annotated non-expressed	N/A	275
Newly discovered	171	27
Annotated as pseudogenes	19	87
Total	7875	875

*See (22) for clone terminology.

Fig. 6. WGA analysis of transcription of pseudogenes, antisense RNAs, and centromere-located genes. Proportion of AE and ANE genes for (A) predicted pseudo-genes, (B) antisense genes, or (C) centromere regions. (D) Transcriptionally active “hot spots” with the genetically defined centeromeres for chromosomes 2 and 3. See SOM text for further description.



also be used to detect DNA sequence polymorphisms and potentially to detect differences in cytosine methylation patterns among *Arabidopsis* ecotypes, which would be useful for rapid genome-wide mapping of quantitative trait loci (QTL) (42). Finally, WGAs might also be used for direct mapping of point mutations without the use of segregated populations.

The impact of these findings and of the experimental resources developed is not restricted to *Arabidopsis*. For example, 85% of *Arabidopsis* genes have close homologs in the rice genome (43). Therefore, this resource will aid in the elucidation of the function(s) of the vast majority of genes in plant genomes (43, 44), providing fundamental knowledge that we hope will eventually lead to the engineering of new plant species.

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- A large collection of ~20,150 RIKEN *Arabidopsis* full-length (RAFL)-cDNAs were produced by the RIKEN Genome Sciences Center (21) and the complete sequence of the majority of RAFLs was determined in this study [fig. S2; (22)].
- Materials and Methods are available as supporting material on Science Online.
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- The distribution of the various types of fl-cDNAs that correspond to genes with the same or different annotated gene structure is as follows: same annotated structure, CFL, 20%; Ceres, 33%; RAFL, 43%; C-clones, 3%; different annotated structure, CFL, 10%; Ceres, 27%; RAFL, 61%.
- We thank M. Johnston for critical reading of the manuscript, K. Mayer for gene functional category information, and T. Gingeras for support of this project. We also thank S. Elledge for providing us with the pUNI50 vector and P. Surko, J. Borevitz, and T. Mockler for useful discussions. Supported by the NSF Plant Genome Research Program under awards DBI-9975718, DBI-0196098 (to J.R.E.), DBI-9872752 (to R.W.D.), and USDA CRIS no. 5335-21430-005-00D (to A.T.). This study has also been supported by Research Grant for Genome Research from RIKEN (to K.S.) and by Research Grant for the RIKEN Genome Exploration Research Project from the Ministry of Education, Culture, Sports, Science and Technology of the Japanese Government (to Y.H.). Affymetrix genome tiling array expression data have been deposited in the Gene Expression Omnibus (GEO) database (www.ncbi.nlm.nih.gov/geo/). Accession numbers are as follows: pilot tiling arrays, GSM8999 through GSM9010 and GSM9196 through GSM9207; whole genome arrays, GSM8942 through GSM8977 and GSM9208 through GSM9219. GEO accessions for pilot and whole genome array analysis files: GSE601, GSE636-639. GenBank accession numbers can be found on table S6.

Supporting Online Material

www.sciencemag.org/cgi/content/full/302/5646/842/DC1

Materials and Methods

SOM Text

Figs. S1 to S27

Tables S1 to S6

References

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REPORTS

Direct Atom-Resolved Imaging of Oxides and Their Grain Boundaries

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Using high-resolution transmission electron microscopy, we obtained structure images of strontium titanate (SrTiO₃) with a clearly resolved oxygen sublattice along different crystallographic directions in the bulk lattice and for a Σ3 tilt grain boundary. Comparison with image simulations showed that the grain boundary contains oxygen vacancies. Measurements of atom displacements near the grain boundary revealed close correspondence with theoretical calculations.

Direct imaging of atoms in oxides, especially in defect regions, is of considerable importance for understanding the properties of materials. Because oxygen has a high electronegativity, its presence can have a marked effect on these properties. This can occur

through the binding of free electrons, which leads to a loss of electrical conductivity (e.g., in metal oxides) through the presence of vacancies in the oxygen sublattice, which in turn can give rise to considerable ionic conductivity (as in electroceramic materials).

Oxygen has a strong effect on mechanical properties, which are directly linked with the strong interatomic forces. But oxygen can also have an indirect influence: Most properties of materials are sensitively influenced by the presence of crystal defects, and the oxygen concentration at such defects can drastically deviate from the average bulk value, even in thermal equilibrium. This is one of the reasons why grain boundaries (GBs) in electroceramics can be electrically charged and form a double Schottky barrier against the movement of ions (1, 2), which is of ultimate importance in polycrystalline electroceramic materials. Recently, it was shown that dislocations in SrTiO₃ can be oxygen deficient (3) and that this can lead to a change

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Supplemental Online Materials

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Materials and Methods

Supporting Text

Supporting Figures (S1-S27)

Supporting Tables (TS1-TS5)

Supporting References

Materials and Methods

a. Plant material

Arabidopsis thaliana (ecotype Columbia) seeds were surface sterilized in 5% sodium hypochlorite and 0.15% Tween 20 for 8 min, rinsed in distilled water, and placed onto sterilized filter paper disks on top of 0.8% agar-containing Petri dishes. The plates contained 0.5X Murashige-Skoog salts (Life Technologies, Inc.), 0.5 mM MES, pH5.7, 1% sucrose, and 1X vitamin B5. The seeds were cold-treated at 4 °C for 2 days and then incubated in the dark (etiolated; L-) or in the light (light grown; L+) for 7 days at 25 °C. Cold-treated seedlings were obtained by incubating 7-day old light grown seedlings (L+) for 24 hours at 4 °C. Flower buds were collected from mature *Arabidopsis* plants (4-6 weeks old) which were grown as described in the *Arabidopsis* Biological Resources Center manual (ABRC; <http://www.biosci.ohio-state.edu/~plantbio/Facilities/abrc/abrchome.htm>). *Arabidopsis* suspension-culture cells were derived from hypocotyls of etiolated seedlings (1). They were a generous gift from Dr. Jonathan Jones (Sainsbury Laboratory, Norwich, UK). The culture was maintained at 24 °C in the dark with constant shaking and was subcultured every week. The growth medium contained Murashige-Skoog basal salts, Gamborg's B5 vitamins (Life Technologies, Inc.), 3% sucrose, and 1 mg/L 2,4-dichlorophenoxyacetic acid (2,4-D). The cells were harvested two-days after subculture. Root

tissue was obtained by incubating surface-sterilized seeds in flasks (5-10 seeds per flask) containing 100 ml Gamborg's B-5 medium (Life Technologies, Inc.). The seedlings were incubated for 3-4 weeks with constant agitation (125-150 rpm) under constant light, and root tissue was collected and immediately ground in liquid N₂ for total RNA isolation.

b. Molecular biological techniques

(i) RNA isolation

Total RNA was isolated from various plant tissues using the Qiagen RNeasy kit (Valencia, CA) or with the TRIzol reagent procedure (Invitrogen, Carlsbad, CA). When TRIzol reagent was used for RNA isolation, the Qiagen RNeasy kit was used for further clean up according to the manufacturer's instructions. When necessary, poly(A)⁺ RNA was purified by oligo(dT) cellulose (Qiagen, Valencia, CA) according to the manufacturer's instructions. The quality and quantity of RNA isolated was checked by both gel electrophoresis and spectrophotometry.

(ii) Clone terminology

During this work, the following terminology was used for the various open-reading frame (ORF) cDNA clones constructed and sequenced.

U Clone: A pUNI clone that contains the ORF of a RIKEN *Arabidopsis* Full-Length (RAFL) cDNA clone. It was generated by PCR and is error-free.

C Clone: A pUNI clone that contains an ORF of a transcription unit detected by the hybridization of RNA to the genome tiling_chips (C). It was obtained by RT-PCR and is error-free.

(iii) Sequencing and Annotation of RAFL, U and C Clones

A primer-walking approach was chosen for sequencing the RAFL clones using BigDye Terminator chemistry V2.0 and V3.0 (Applied Biosystems, Foster city, CA). Since the entire genome sequence of *Arabidopsis* is available, we chose to use the predicted genome annotation as a guide to call primers to cover an entire clone. The algorithm developed for this process picks primers to give equally spaced high-quality sequences from reads along both strands of each clone. This approach allows an entire sequence of a clone to be determined at once. The U clones were sequenced using the same oligos used for the RAFL clones. In order to find an error-free ORF, we determined the sequences of four cDNA clones for each unique U clone. The C clones were also sequenced with the same strategy as the RAFL clones. Four cDNA clones for each C clone were also sequenced in order to identify an error-free ORF.

The Phred/Phrap/Consed (2-4) suite of programs was used to assemble sequence reads and perform “finishing” of the assembled sequences. cDNA clones were mapped on the genome using the methodology described below (section *c*). The experimentally-determined sequence of each clone was compared to the genomic sequence to check for insertions, deletions, frameshifts, splicing errors, upstream start codons, and downstream stop codons. The ORF of each full-length cDNA clone was selected by choosing the longest ORF among all of the three possible reading frames in the derived DNA sequence. Using the predicted protein as a query sequence, cDNA clone annotation was verified by searching each sequence against a database of the annotated *Arabidopsis* proteins, Ceres, and community-sequenced full-length cDNAs (CFL) using BLAST (5).

Analysis of 13,481 fully-sequenced non-unique RAFL clones (99% of the total clones sequenced) representing 11,600 unique genes (Fig. S2) revealed that 70% of the clones were indeed fl-cDNAs (Fig. S21B). The remaining 30% of cDNAs were associated with various problems, such as point mutations and 5' or 3' partial deletions, compared with the genome

sequence (Fig. S21C). The RAFLs designated as “problem-associated” may be due to alternative splicing (partial/unprocessed), RNA editing, sequence errors and mutations introduced during the experimental process (uncategorized and mismatched classes of clones in Fig. S21C). The finding that numerous problems were identified in the RAFLs necessitates the use of alternative experimental approaches to obtain fl-cDNAs for genes with defective ORFs and for identification cDNAs corresponding to the “untouched” genes.

Annotation of RAFL clones was carried out using the *Arabidopsis* genome annotation version 3.0 (September 2002) of Genbank (ftp://ftp.ncbi.nih.gov/genomes/A_thaliana). The RAFL cDNA clones are available from the RIKEN Bioresource Center (<http://www.brc.riken.go.jp/lab/epd/Eng/index.html>). The DNA sequences of the U and C clones have been deposited in GenBank and their accession numbers are available at: <http://signal.salk.edu>. The clones are also publicly available through the *Arabidopsis* Biological Resource Center (<http://www.biosci.ohio-state.edu/~plantbio/Facilities/abrc/abrchome.htm>).

(iv) Construction of ORF Clones

Full-length ORF clones were constructed using two different approaches:

(1) PCR amplification of ORF of sequenced RAFL clones that were annotated as full-length cDNAs. These clones are named U (pUNI). The RAFL ORFs were amplified by PCR using gene specific primers, and 2.5 U of Pfu Turbo DNA polymerase (Stratagene, La Jolla, CA). The PCR reaction conditions were: denaturation at 95 °C for 2 min, 10 cycles of 30 sec at 95 °C, 1 min at 56 °C and 6 min at 68 °C followed by final elongation at 68°C for 7 min. The amplified ORF DNAs were purified using the Qiagen PCR product purification kit (Valencia, CA).

(2) RT-PCR. These cDNA clones are named C (chip). First-strand cDNA was synthesized using 5 µg poly(A)⁺ RNA with oligo dT₁₈ as a primer and 1000 units of SuperScriptII RT

enzyme (Invitrogen, Carlsbad, CA) as described in (6). First-strand cDNA was re-suspended into 50 μ l of dH₂O after phenol/chloroform extraction followed by EtOH precipitation. Using gene specific primers, the ORFs were amplified using 0.5 μ l of first-strand cDNA and 3.75 units of Expand High-Fidelity DNA polymerase (Roche Applied Science, Mannheim, Germany). The amplification conditions were: denaturation for 2 min at 94 °C, touch-down PCR (7) was performed, consisting of 12 cycles of 15 sec denaturation at 94 °C, 30 sec annealing at 63 °C with negative ramp 6 °C at 0.5 °C per cycles and 3 min at 68 °C, followed by 18 cycles of 15 sec at 94 °C, 30 sec at 57 °C and 3 min at 68 °C. A final elongation cycle was undertaken at 68 °C for 7 min. Amplified cDNA PCR products were isolated with the Qiagen PCR purification kit (Valencia, CA).

The U and C ORF PCR products were digested with *SfiA* and *SfiB* and were cloned into the pUNI51 vector (Fig.S18) and their DNA sequences were determined. This recombination-based universal cloning vector was derived from pUNI50 (8) by introducing a new polylinker containing two *SfiI* sites(A and B). This feature allowed cloning of a full-length ORF unidirectionally using *SfiI* A and B sites at the 5' and 3' of the ORF, respectively. The ORFs are error-free and can be transferred into any desirable expression vector by *in vitro cre/lox* recombination (8).

The design of gene specific primers used for U and C ORF clone construction is as follows:

Forward primer; 59 mer:

5'-GAATTCGGCCGTCAAGGCCA-GAAGGAGA-TATA-ACC-ATG-(X)₁₈-3'

Reverse primer; 41 mer:

5'-AGTCGACGGCCCATGAGGCC-(X)₂₁-3'

The forward primer contains 21 bp specific to each cDNA downstream of the ATG. Upstream of the ATG, the sequence contains the prokaryotic (9) and eukaryotic (10) ribosome-binding sites (boxed). The reverse primer contains 21 bp cDNA specific sequence (3' UTR) that is located 10 bp downstream of the STOP signal. The 5' end sequences of both primers contain restriction sites for *SfiA* and *SfiB*, respectively.

(v) *Expression of pUNI clones*

We have tested the efficiency of the pUNI system for protein production in several ways including enzyme assays (ACC synthase) and the large-scale expression of protein in *E. coli*. A pHOST *E. coli* expression vector and a randomly chosen set of 96 pUNI U clones were recombined *in vitro* by the addition of CRE recombinase protein (8). Figure S22 shows all tested clones expressed high levels of protein (11). Introduction of a *lox* site into currently available prokaryotic and eukaryotic expression vectors will allow the transfer and expression of the ORFs for functional studies.

(vi) *Functional classification*

Functional classification of the RAFL and ORF clones (U and C) was performed using the Munich Information Center for Protein Sequences (MIPS) functional categories (http://pedant.gsf.de/cgi-bin/wwwfly.pl?Set=Arabidopsis_thaliana_MAtDB&Page=index).

c. *Mapping cDNAs on the Arabidopsis genome*

1. In order to determine the number of annotated genes for which there is evidence of transcriptional activity, we aligned all available *Arabidopsis* ESTs and full-length cDNAs generated by us and others (NCBI-GenBank Flat File Release 135.0) to the *Arabidopsis* genome as described in sections *cii* and *ciii*.

(i) *Sources of EST and cDNA sequences*

Cluster analysis was performed using Version 2.0 and 3.0 of the *Arabidopsis* genome annotation obtained from GenBank (ftp://ftp.ncbi.nih.gov/genomes/A_thaliana/). The sequences analyzed are: ESTs (ftp://ftp.Arabidopsis.org/home/tair/Sequences/blast_datasets); single-read 5' and 3' end sequences of RAFL clones (<http://rarge.gsc.riken.go.jp/>); full-length cDNAs sequenced by the SSPC (<http://signal.salk.edu>); Ceres (ftp://ftp.tigr.org/pub/data/a_thaliana/ceres/CeresTigr), and a collection of full-length cDNAs sequences determined by the *Arabidopsis* community (community full length; CFL) (ftp://cycle.stanford.edu/pub/projects/arab/AtGenBank_fullcDNA.fasta). The *Brassica*, rice and wheat ESTs were obtained from Genbank (<http://www.ncbi.nlm.nih.gov/>). Table S2 shows the number of each class of cDNA that was mapped onto the *Arabidopsis* genome.

(ii) *Mapping of cDNAs to Annotated Genes*

ESTs and full-length cDNA sequences were aligned to the *Arabidopsis* genome using sim4 (12). Each aligned sequence was assigned to an annotated gene if it overlapped the gene or fell within 600 bp of the gene. cDNAs that showed high sequence similarity to unannotated genomic locations were labeled as “newly-discovered genes”. In cases where a cDNA or EST could be aligned to multiple chromosomal sites, we chose the alignment having the highest percentage match across the entire cDNA sequence. A small fraction of cDNA sequences failed to align to the genome, indicating possible library contamination, errors in the cDNA or genomic sequence (Fig. S4).

(iii) *Identification of Intergenic Transcription Units*

A hierarchical agglomerative clustering algorithm (13) was used to identify groups of cDNAs

that aligned to intergenic sequences which formed potential transcription units. ESTs and cDNAs that did not map to an annotated gene were ordered according to their position on the genome. Adjacent ESTs/cDNAs sequences which overlapped or fell within 3 kb of each other were merged into a single contiguous feature (contig); a safeguard was implemented to prevent features from merging across annotated gene locations. This merging process was repeated until no additional sequences or contigs could be merged, resulting in a set of features that consisted of putative new transcription units. The 3 kb window size was chosen because it represents an average size of an *Arabidopsis* transcription unit (14) and provides a conservative estimate of the number of intergenic transcription units found. Based on the distribution of intergenic region lengths in the *Arabidopsis* genome, two transcription units which are more than 3 kb apart may represent two independent genes.

(iv) *Identification of Potential Transcriptional Activity by Homology*

In order to determine potential transcriptional activity in regions of the genome not represented in the *Arabidopsis* EST or full-length cDNA collections, we performed searches against mRNA, EST, and protein databases (GenBank) of sequences from rice, wheat, and *Brassica*. Two sets of *Arabidopsis* query sequences were used to search for homology among these rice, wheat, and *Brassica* sequences. The first query set consisted of annotated genes to which no EST or cDNA sequences had been mapped. This class of genes is termed annotated non-expressed (ANE; same as hypothetical). We compare the protein sequences of these genes to proteins from other species using BLASTP while TBLASTN was used for analysis of mRNA and EST sequences. The second query set consisted of all regions of the genome after eliminating annotated genes and transcription units identified in the intergenic regions (newly discovered genes) using the clustering algorithm. Annotated genes were augmented by 600 bp and intergenic transcription units widened to 3 kb to minimize false positive alignments near these annotated

and putative transcription units. To compare the nucleotide sequences of this second query set to protein databases, BLASTX was used; BLASTN was used for nucleotide databases. In all cases, only hits with an E-value $<10^{-25}$ were considered to be indicative of homology. The average alignment length for both queries are shown below

EST	Annotated Non-expressed	Intergenic Region
	Length (bp)	Length (bp)
<i>Brassica</i>		
EST	152	188
mRNA	357	173
Protein	398	400
Rice		
EST	172	205
mRNA	400	290
Protein	461	467
Wheat		
EST	186	168
mRNA	350	195
Protein	325	213

(v) *Data Storage and Software Development*

A relational database schema was developed to store data used in this analysis. This schema was realized using the MySQL database server (<http://www.mysql.com/>). Automation of mapping and annotation was carried out using software implemented in the Java programming language (<http://java.sun.com/>); human oversight of the annotation process was carried out within a web-

based workflow system implemented using the PHP programming language (<http://www.php.net/>).

d. Identification of transcription units with high-density oligonucleotide tiling arrays

(i) Design of the pilot tiling array

Affymetrix produced 4 pilot *Arabidopsis* genome tiling chips with 18 micron features. The design was based on the *Arabidopsis* genome annotation V1.0 of GenBank (ftp://ftp.ncbi.nih.gov/genbank/genomes/A_thaliana/). All four chips are identical in design except for the regions of genome sequence that they cover (Figure S8). Each array contains 1.25 Mb of genomic sequences that is represented by 25-mer oligonucleotides. Two chips span a 2.5 Mb region (1.79-3.04 Mb) of chromosome 1 and another two chips span a 2.5 Mb region (17.0-19.5 Mb) of chromosome 2. The 25-mer oligonucleotides were synthesized with 12 bp sequence overlap. For each perfect match (PM) oligonucleotide, a corresponding 1 base mismatch (MM) oligonucleotide (base position 13) was also synthesized on the array. These four arrays contain a total of 1.6×10^6 25-mer that represent both Watson (W) (top strand) and Crick (C) (bottom strand) strands of a 5.0 Mb segment of the *Arabidopsis* genome sequence. According to the V3.0 genome annotation, there are a total of 1,295 predicted genes (chip 1a 326; chip 1b 313; chip 1c 331; and chip 1d 325) represented on the four tiling chips.

(ii) Design of the Whole Arabidopsis Genome Tiling Arrays

The schema for the whole genome tiling arrays is shown in Fig. S10. A single photolithographic mask was designed that covered the entire silicon wafer (49 chips/wafer). The wafer contains four different chip designs: a set of 12 whole genome tiling chips (6 for W/forward, and the other 6 for C/reverse complement), a gene expression (exon scanning) chip, a

splice-site variation detection chip and a 5' mRNA transcription start site mapping chip. Their designs were based on the *Arabidopsis* genome annotation V2.0 (GenBank). The number of probes representing the genome in the three genome designs (12 chips/design) are:

Design No.	Probes	bp
1	8,855,960	110,390,000
2	8,830,090	110,386,250
3	8,830,224	110,377,800

All designs represent 94% of the *Arabidopsis* genome (117,429,178 bp V2.0).

Each array contains an end-to-end “tile” of oligonucleotides (from head to tail) with no overlap in their DNA sequences. The entire genome is tiled in three “frames” with an 8 bp offset between the three different sets (designs 1, 2 and 3 indicated above). Integrated probe hybridization data from experiments carried out using all three tiling sets will provide 8 bp resolution. Complete coverage of one strand of the *Arabidopsis* genome requires six different chips (chip 1-1 to chip 1-6). Since both strands are being tiled in three different offsets, the genome tiling chips use 36 of the 49 available chips on a wafer. We decided to include only perfect match (PM) probes in the whole genome array design, because our studies with the pilot array chip indicated that the mismatch (MM) probes were not necessary for deducing gene structures. Oligos that contain ambiguous bases (including those due to the few remaining gaps in the genomic sequence) are not represented in the tiling oligos, but their locations within the genome are noted. The standard Affymetrix *Arabidopsis* gene expression controls are present on each of these chips and are repeated several times distributed throughout the chip. The design of the remaining chips on the wafer will be reported elsewhere. There are a total of 26,934 predicted transcription units on the 12 chips according to the V3.0 genome annotation. The predicted gene content of each chip in tiling array design #1 is shown below.

Chip	Chromosome	Gene content (Top strand)	Chip	Chromosome	Gene content (Bottom strand)
1-1	1	2189	1-rc-1	1	2167
1-2	1 & 2	2077	1-rc-2	1 & 2	2106
1-3	2 & 3	2542	1-rc-3	2 & 3	2557
1-4	3 & 4	1954	1-rc-4	3 & 4	1947
1-5	4 & 5	2549	1-rc-5	4 & 5	2540
1-6	5	2182	1-rc-6	5	2129

(iii) *Probe Synthesis and Chip hybridization*

Either 10 µg total RNA or 1 µg poly(A)⁺ RNA was converted into double-stranded cDNA using Affymetrix T7-oligo(dT) primers. Six cDNA synthesis reactions containing 10 µg total RNA each were sufficient for a set of 12 whole genome tiling arrays. Biotin-labeled cRNA was generated by *in vitro* transcription reactions, fragmented, and then approximately 20 µg of fragmented cRNA were hybridized to the tiling arrays according to Affymetrix (Santa Clara, CA) instructions. The arrays were washed and stained using an Affymetrix fluidics station as instructed in the manufacturer's user manual. CELTM files from scanned arrays were used for further analysis.

(iv) *Processing tiling chip data*

The creation of new software capable of both visualizing and analyzing the genome tiling arrays was necessary since the concept of genome tiling arrays has not yet been commercialized by Affymetrix. Software capable of chip image deconvolution was developed. The ChipViewer program uses an input file of tiling chip probe information and (x,y) coordinates and multiple CELTM files (containing experimental hybridization data), and produces an output file which contains ordered data for each probe on the chip. Then it sorts the probes of each segment into the

actual sequence order of the segment. As output, it generates a file (and a deconvoluted chip image) which lists the intensity values for each probe. The program displays the chip hybridization signals along with various “tracts” including the gene annotation, alongside the full-length cDNA annotation for each corresponding genome segment being interrogated on a tiling chip.

Furthermore, intensity statistics for arbitrary features located on a chip, such as annotated genes and intergenic clusters were computed. Hybridization data were normalized by dividing each probe intensity value in a given experiment by the median intensity value of all probes in that experiment (including PM, MM, and control probes on the chip). The median intensity value of all probes were determined to be a good estimate of the background noise level in a given experiment. Initially we tested the pilot chips and visualization software by hybridizing the arrays with RNA prepared from a single gene. *In vitro* RNA from an RAFL cDNA clone was synthesized, labeled with biotin and hybridized to one of the four tiling arrays (Fig. S23). Analysis of the hybridization signals using all of the oligos for a particular gene or only the even or odd numbered oligos (Fig. S23), indicate that the gene structures predicted by the visualization software yields the same gene model whether all of the oligos or only the even/odd oligos are used for the prediction. These studies indicated that a genome-wide end-to-end tile of oligos will be equally effective and more space efficient than the overlapping probe design produced for the pilot tiling chips.

(v) *Detection of Transcriptional Activity in Annotated and Newly Discovered Genes in Intergenic Regions*

Tiling array transcription unit analysis was carried out by comparison to the most current version of the *Arabidopsis* genome annotation (TIGR V. 3.0). Each annotated or newly discovered

gene or cluster on a chip was determined to be “expressed” if the median intensity value of the probes in that region is above a certain threshold. Two methods were used to determine the threshold value. The first method involves performing “spike-in” experiments to determine the chip sensitivity. The second method involves the determination of a threshold value which bounded the number of falsely expressed genes using a median intensity value derived from probes of gene promoter regions.

The “Spike-in” Method

In vitro cRNAs were synthesized from three RAFLs; RAFL09-15-L21, RAFL09-92-G13, and RAFL09-94-J11 corresponding to genes At2g43010, At1g11870 and At1g11960, respectively. Plasmid DNA of these RAFLs was linearized with *PvuII* (RAFL09-15-L21 and RAFL09-92-G13) or *SapI* (RAFL09-94-J11). Biotin-labeled cRNAs were synthesized by *in vitro* transcription using T7 RNA polymerase (Enzo Life Science, Farmingdale, NY) with 100 ng of linear plasmid DNA as template, according to the supplier's instructions. Different amounts of each RNA corresponding to 100 ng, 1 ng and 0.01 ng/μl were used for hybridization to arrays 1B and 1C. The lowest concentration of probe that allowed the exon-intron structure of these genes to be detected was 100 pg/μl (see Fig. S21). The number of probes in the coding regions of these genes are: At2g43010, 64; At1g11870, 127; At1g11960, 93. The median intensity value of the probes in the coding region of the spiked clone was computed at the 100 pg/μl concentration and this value was used as a threshold for transcription unit detection. This threshold value corresponds to a detection sensitivity of 1 RNA molecule/10⁵ RNAs.

The “Promoter” Method

The putative promoter regions for all genes on a tiling chip were identified in the following manner: (i) we considered all cDNA sequence evidence which could extend into the 5' UTR of

each gene (including RAFL cDNAs , Ceres full-length cDNAs, Community full-length clones (CFL), and Riken 5' ESTs,). (ii) we defined the putative transcription start site of each gene to include probes located within 50 bp 5' of the start (+1) longest cDNA sequence for that gene (iii) we defined the putative promoter region to include all probes located within 400 bp (~32 oligos) upstream of the putative transcription start site. The transcriptional activity of these promoter regions was set as the background signal. The median intensity values of probes located in each promoter region were computed. Taking each observed promoter median intensity m as a potential threshold value, we counted the number of promoters and the number of genes whose median values were greater than m . These values were plotted as a function of hybridization intensity (Fig. S25). Raising the threshold intensity from the level at which all genes and promoters are considered “expressed,” the number of promoters above the threshold drops sharply down to approximately 5% promoters falsely expressed. The intensity at which 5% of promoters were falsely expressed was computed individually for each chip hybridization experiment. The median intensities of the threshold values determined in this way are comparable with those determined by the “spike-in” method, and provide similar numbers of annotated genes and intergenic clusters expressed on each chip. Figure S26 compares the intensity distribution of the probes in all annotated genes with the intensity distribution of the probes in the promoter regions by superimposing them; both distributions match extremely well except for the high end tail. This demonstrates that the median intensity of the promoter regions is a good estimate of background noise.

(vi) Detection of Transcriptional Activity in “Intergenic” Regions

The “threshold” value determined by the promoter method was also used to examine the transcriptional activity in the intergenic regions. An intergenic region was defined as the DNA

sequence between two adjacent genes or EST/cDNA clusters, except the first and last 1000 bp of the region. (If two adjacent genes or clusters were less than 2000 bp apart, the region between them was not considered.) This was done in order to ensure that expression observed in the intergenic regions is not due to misannotated genes or EST/cDNA clusters which do not represent full-length transcription units. Genes and EST/cDNA clusters were considered as adjacent based only on their position, without regard to the direction of transcription. The ordering of probe intensities on each chip was processed by sliding a 30-probe window along the sequence at steps of one probe. An order of “smoothened” intensity values was generated by assigning the median intensity of the 30 probes (750 bases) in the window to the position of the central probe in the window. The set of smoothened intensities located in each intergenic region was extracted, and a count was made of the number of intensities which were higher than the promoter-based threshold.

(vii) Antisense Expression

We computed the antisense expression level of each annotated gene as described below. The antisense expression level was defined as the median intensity of the oligos opposite the coding region of an annotated gene. As with annotated genes, the region in the opposite strand to an annotated gene was said to be expressed in an experiment if its expression level was greater than or equal to the promoter threshold for that experiment.

Each gene in each experiment falls into one of four categories of sense-antisense transcriptional activity: ++ (both sense and antisense expression), +/- (only sense expression), -/+ (only antisense expression), -/- (no expression). Four tissue types were analyzed, giving rise to an expression profile for each gene specifying its expression category in each tissue.

Since there are four expression categories (+/+, +/-, -/+, -/-) and four tissues (FL, RT, SC, L+), there are a total of $4^4 = 256$ different possible expression profiles. In order to make interpretation of these expression profiles more reasonable, we made two simplifying assumptions. First, we disregard the order of the elements of a gene's expression profile; in other words, we ignore which tissue displayed which type of expression. For example, the profile (+/-, +/-, -/-, -/-) is treated the same as (-/-, +/-, +/-, -/-). Second, we disregard the number of times each expression category appears in each profile. For example, the profile (+/-, +/-, -/-, -/-) is treated the same as (+/-, +/-, +/-, -/-). In both of these cases, the qualitative nature of the transcriptional activity is the same; we are only interested in which categories appear in a given profile. For our purposes, all of the profiles mentioned above can be summarized by the single reduced profile (+/-, -/-).

Given these simplifying assumptions, the number of different expression profiles is reduced to fifteen which can be grouped into five major categories shown below.

Profile	Gene category	Number of genes
(+/+)	Genes with sense and antisense expression	2516
(+/-)	Genes with only sense expression	2944
(-/+)	Genes with only antisense expression	318
(-/-)	Genes without expression	6392
(+/- +/+)	Genes with tissue specific sense and antisense expression	3697
(+/+ -/+)	Genes with tissue specific sense and antisense expression	1113
(-/- +/+)	Genes with sense and antisense expression	511
(-/+ +/-)	Genes with tissue specific sense and antisense expression	146
(+/- -/-)	Genes with only sense expression	5131

(-/- -/+)	Genes with only antisense expression	1528
(-/+ ++ +/-)	Genes with tissue specific sense and antisense expression	402
(+/+ -/- +/-)	Genes with tissue specific sense and antisense expression	1043
(-/+ ++ -/-)	Genes with tissue specific sense and antisense expression	569
(-/- -/+ +/-)	Genes with tissue specific sense and antisense expression	469
(-/+ ++ +/- -/-)	Genes with tissue specific sense and antisense expression	160

(viii) Transcriptional activity across five chromosomes

To examine chromosome-scale variation of transcriptional activity, the following approach was used. Within a window of 500 kb, the portion of expressed genes (probes with a median intensity value greater than the threshold value) was computed. The window was then moved in steps of 100 kb across the entire probe sets on each chip. Finally, the proportion of expressed genes in each window was plotted against the position of the center of the window (Fig. 4).

(ix) Analysis of hot spots on chromosomes 2 and 3.

Probes were scored by a threshold (cutoff intensity value > 200) in either the corresponding whole chromosomes or the regions where exhibited relatively high transcriptional activity (named 'hot spot'). Probes with intensity values > 200 are localized in the CEN 2 and 3 regions.

(x) Validation of expression statistics computed by promoter threshold: P value determination

The problem of determining the statistical significance of gene expression in the tiling chip can be phrased as a test of the hypothesis that the observed expression is due to transcriptional activity; the null hypothesis is that the observed expression is due to chance alone (including factors such as cross-hybridization and noise introduced by the equipment (scanner) used in the experiment). In order to test this hypothesis for a gene with median probe intensity x , we computed the probability that an expression level of x could occur as the result of chance (15). If there is no transcriptional activity within a gene's coding region, we may suppose that the intensities of the probes in this region are a random sample, elements independent and identically distributed (i.i.d.), from the overall distribution of intensities observed in the experiment. Thus, for a gene containing n probe in its coding region, the P-value is defined in terms of the cumulative distribution function of the median of a sample of n i.i.d. elements from the distribution of probe intensities on the chip.

In order to compute these P-values, we used a randomized simulation method (16,17). A principal advantage of such a method is that it does not require the distribution of probe intensities in the experiment to be described parametrically. For each actual experiment, we generated a set of 10,000 simulated experiments. The probe intensities in each simulated experiment were independently chosen, uniformly at random and with replacement, from the intensities observed in the actual hybridization experiment. Thus, each simulated experiment had approximately the same distribution of probe intensities as the actual experiment from which it was generated. The P-value of each gene in the given experiment was defined as the proportion of simulated experiments in which the expression level of the gene in the simulated experiment was at least as high as the expression level of the gene in the actual experiment. Figure S27 shows the

relationship of median intensity values vs. P-value for each gene element in the whole genome array.

P-values were used to estimate the sensitivity and specificity of labeling each gene as expressed or unexpressed by comparing its median intensity to the promoter-based threshold. Consider an experiment with promoter threshold t , and let a P-value less than or equal to 0.01 be significant. The number of true positives (TP) in the experiment is the number of genes with median intensity at least t and P-value at most 0.01, minus 1% of this number. In other words, these are genes having high median intensity values as well as significant P-values. The number of false positives (FP) is the total number of genes with median intensity at least t , minus TP. The number of false negatives (FN) is the number of genes with median intensity less than t and P-value at most 0.01, minus 1% of this number. Sensitivity is then defined as $TP/(TP+FN)$, and specificity is $TP/(TP+FP)$. Tables S3 and S4 provide the specificity and sensitivity values for all the experiments carried out in this study with the pilot and whole genome arrays.

Although this method allows us to assess the statistical significance of gene expression levels with respect to an appropriate model of random hybridization, further studies in two areas are necessary. First, experimental validation should be done to verify that the P-values obtained using this method reflect biological reality; i.e., that genes showing significant expression according to this computational method also show transcriptional activity when interrogated using purely molecular methods. Second, it may be useful to develop a more sophisticated model of random hybridization than the one we have assumed here.

Legends For Supplemental Figures

Figure S1. Dual strategy for experimental verification of the *Arabidopsis* genome annotation and discovery of new transcription units.

Figure S2. Summary of the RAFL clones used in this study.

Figure S3. Gene contents of the *Arabidopsis* genome. Annotation V1.0 used for this analysis.

Figure S4. Alignment of all available *Arabidopsis* fl-cDNAs and At-ESTs on the genome annotation V1.0 (18).

Figure S5. Determination of the annotated-expressed (AE), annotated non-expressed (ANE) and newly discovered genes in intergenic regions (non-annotated expressed; NAE) in the V1.0 genome by alignment of all the available unique fl-cDNAs and At-ESTs. The order of determining uniqueness is CFL, Ceres, RAFLs, C clones, and At-ESTs.

Figure S6. Progressive improvement of the *Arabidopsis* genome annotation V1.0 by incorporation of fl-cDNA sequences.

Figure S7. Presence of expressed non-annotated transcription units in intergenic regions of V1.0 genome. (A) Number of intergenic regions. (B) Potential intergenic clusters with transcriptional activity (see Materials and Methods for clustering). The term cDNA includes fl-cDNAs of CFL, Ceres, RAFL, 5' and 3' RAFL and At-ESTs.

Figure S8. Design and feature density of the tiling arrays. An abbreviated view of array 1A is shown. Chip 1A contains 1.20 MB of chromosome 1 (region 1.79-2.99 MB).

Figure S9. Agarose gel electrophoresis of RT-PCR products corresponding to transcription units detected by cRNA hybridization to the genome tiling arrays. The DNA sequences of the PCR products were determined and the results are presented in Table 1.

Figure S10. Design of the whole *Arabidopsis* genome tiling Affymetrix arrays. See Materials and Methods for more details.

Figures S11-15. Transcriptional activity detected in the five *Arabidopsis* chromosomes using whole genome tiling arrays. Four RNA samples were used to hybridize 4 sets (12 chips/set) of Design 1 arrays. The RNA samples are: L+ (red); flower (blue); root (green) and suspension cell culture (orange). The annotated gene structures are shown above the probe hybridization signals (black). Genes located on the forward strand are drawn above the reference line whereas the ones in the reverse strand are drawn below the line. The genetically defined centromeric regions of each chromosome are highlighted (yellow). The fl-cDNAs that have been isolated for each gene are shown below the annotated gene structures (orange).

Figure S16. Gene numbers detected for each chromosome using whole genome tiling arrays hybridization for 4 different plant tissues.

Figure S17. Functional classification of the tissue-specific expressed transcription units detected by WGAs.

Figure S18. The pUNI cloning system. (A) pUNI51 vector (AY260846) for directional cloning of ORFs at the *SfiA/SfiB* sites. (B) The principle of the pUNI cloning system for transferring ORFs to any expression vector by *cre/lox* mediated *in vitro* recombination (8).

Figure S19. Functional classification of the constructed ORFeome. The tissues used for RNA isolation are shown in the figure.

Figure S20. Status of the *Arabidopsis* ORFeome project as of March 2003. The genome annotation V1.0 was used for the analysis the cDNA data. (A) Distribution of the ORF clones among the various classes of cDNAs that represent the annotated expressed genes are shown in different colors. (B) The same as (A) but for the newly discovered genes in the intergenic regions.

Figure S21. Quality of the RAFL cDNA clones analyzed among the 13,619 clones sequenced in this study. (A) Alignment of the RAFL cDNA sequences on V3.0 genome annotation.(B) Alignment of non-problem associated RAFL cDNA sequences (C) Problems associated with some RAFL clones. See text for more details.

Figure S22. Analysis of the polypeptides expressed from pUNI ORFs in *E.coli* using SDS-PAGE with (A) or without (B) IPTG.

Figure S23. Examination of probe sequence overlap on the determination of gene structures using the pilot genome tiling arrays. cRNA was synthesized *in vitro* using the RAFL09-91-M19 clone (19) corresponding to the At1g06680 gene and was used for hybridization to the 1A pilot tiling array. The gene structure was determined from analysis of the hybridization intensity using ALL

the probe information (Top), or only the EVEN numbered probes (middle) or only the or only ODD number probes (bottom).

Figure S24. Sensitivity of detection by the pilot genome tiling arrays cRNAs were synthesized *in vitro* from three RAFLs, RAFL09-15-L21, RAFL09-92-G13 and RAFL09-94-J11, corresponding to genes At2g43010, At1g11870 and At1g11960, respectively, as described in Materials and Methods. Different amounts of each RNA were used for hybridization to the pilot tiling arrays, 1C and 1B where these genes are located. The median intensity values of the probe hybridization signals for each RNA concentration were determined as described in Materials and Methods and their values are shown in the inserted table at the right bottom corner.

Figure S25. Relationship between median probe hybridization intensity detected in the promoter and annotated gene regions present on: (A) pilot tiling genome arrays, (B) whole genome tiling arrays (top strand), and (C) whole genome tiling arrays (bottom strand). The various RNA samples used are display using different colors. The median intensity value (red arrow on *x*-axis) that corresponds to a 5% false positive was used as the cutoff value for quantification of numbers of genes expressed in each tissue.

Figure S26. Comparison of intensity distributions between the probes associated with annotated genes and those associated with the promoter regions. The two distributions have been superimposed.

Figure S27. Relationship between median intensity value and P-value. (A) All annotated genes (AE and ANE) (B) Newly discovered genes (non-annotated expressed; NAE) in intergenic regions. The P-values were calculated with the whole genome array 1 hybridized with L+ RNA. The genes fall in four domains shown: TP, true positive; FP, false positive; FN, false negative; and TN, true negative.

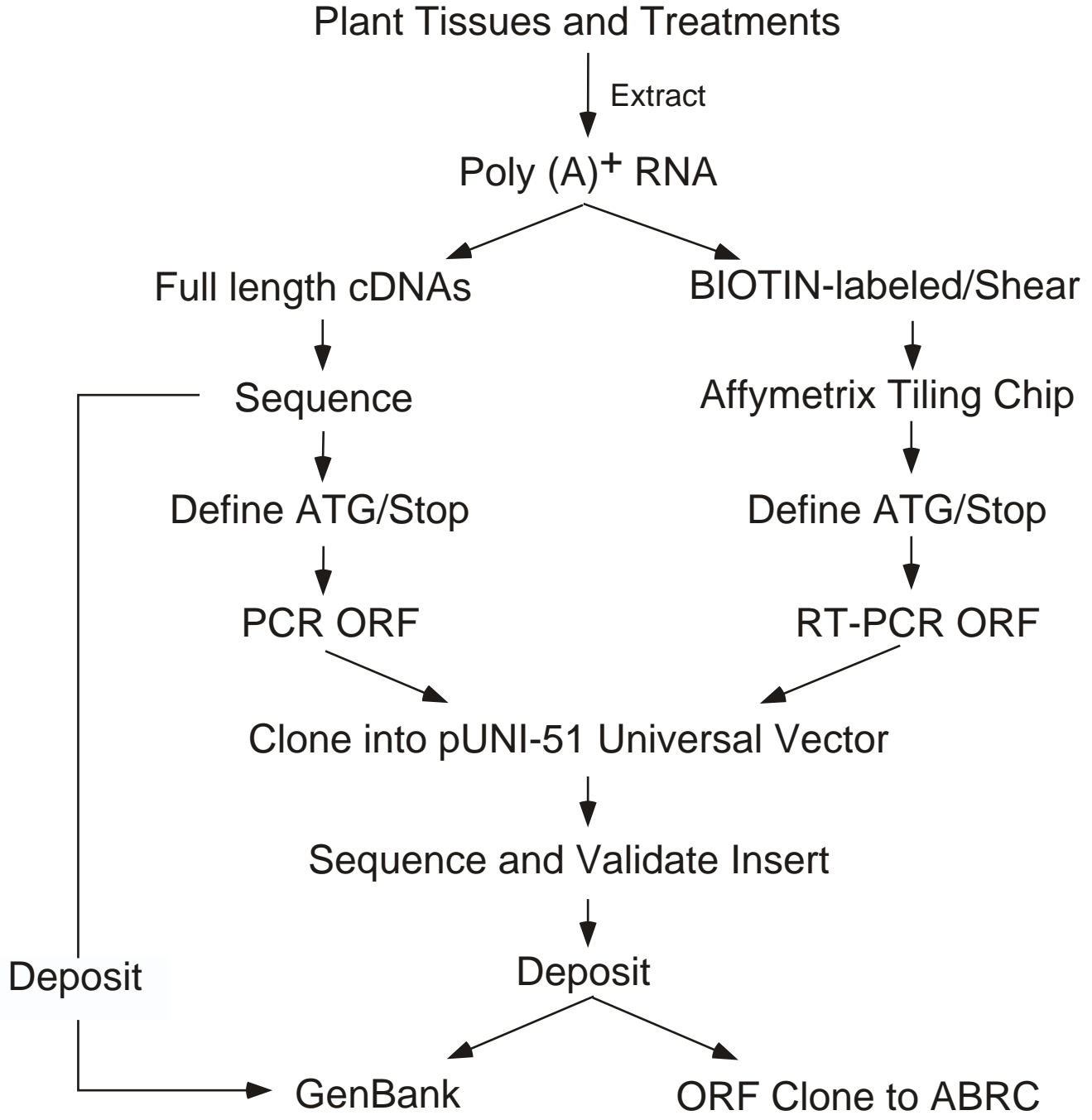


Fig S1

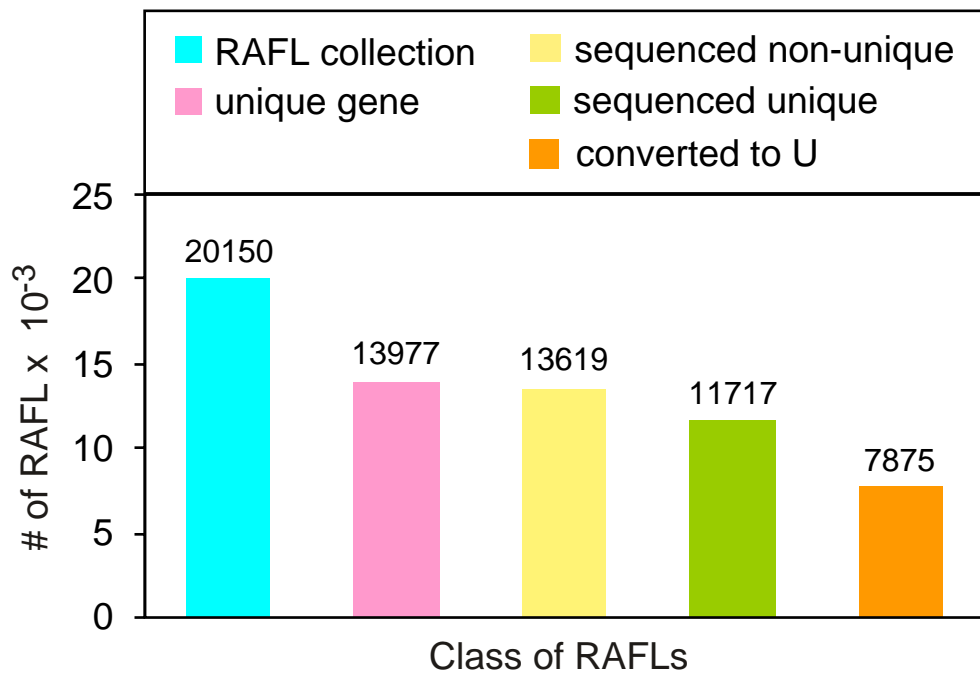
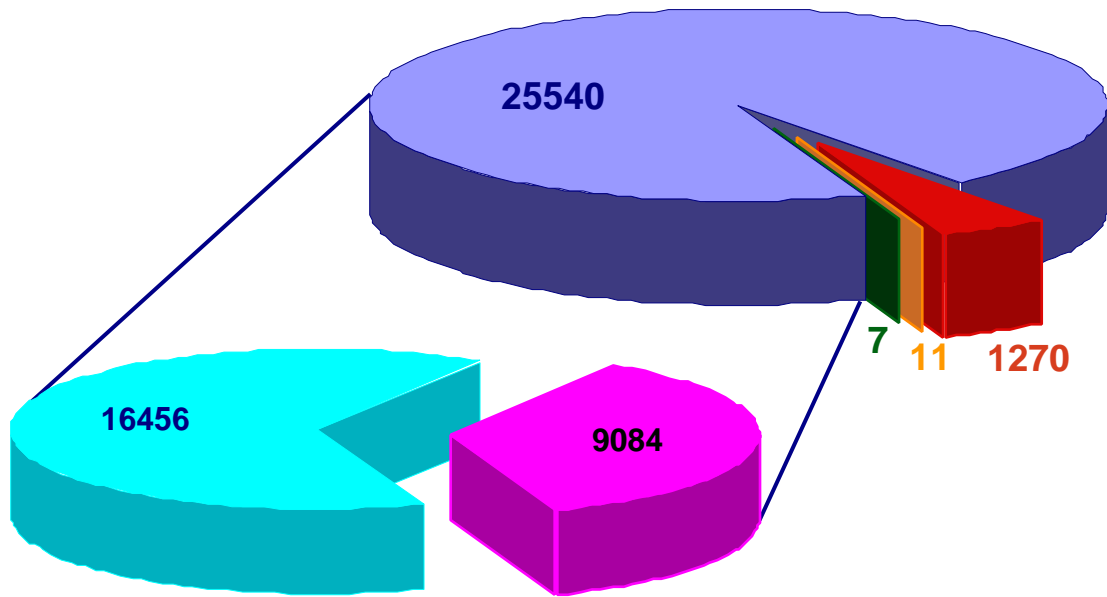
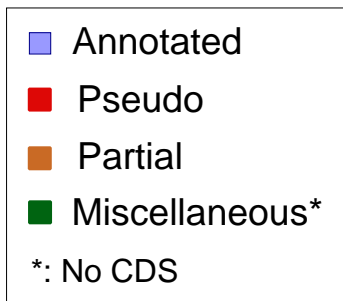


Fig S2



Total: 26,828 genes



Total: 25,540 Protein encoded annotated genes

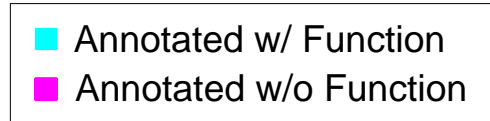


Fig S3

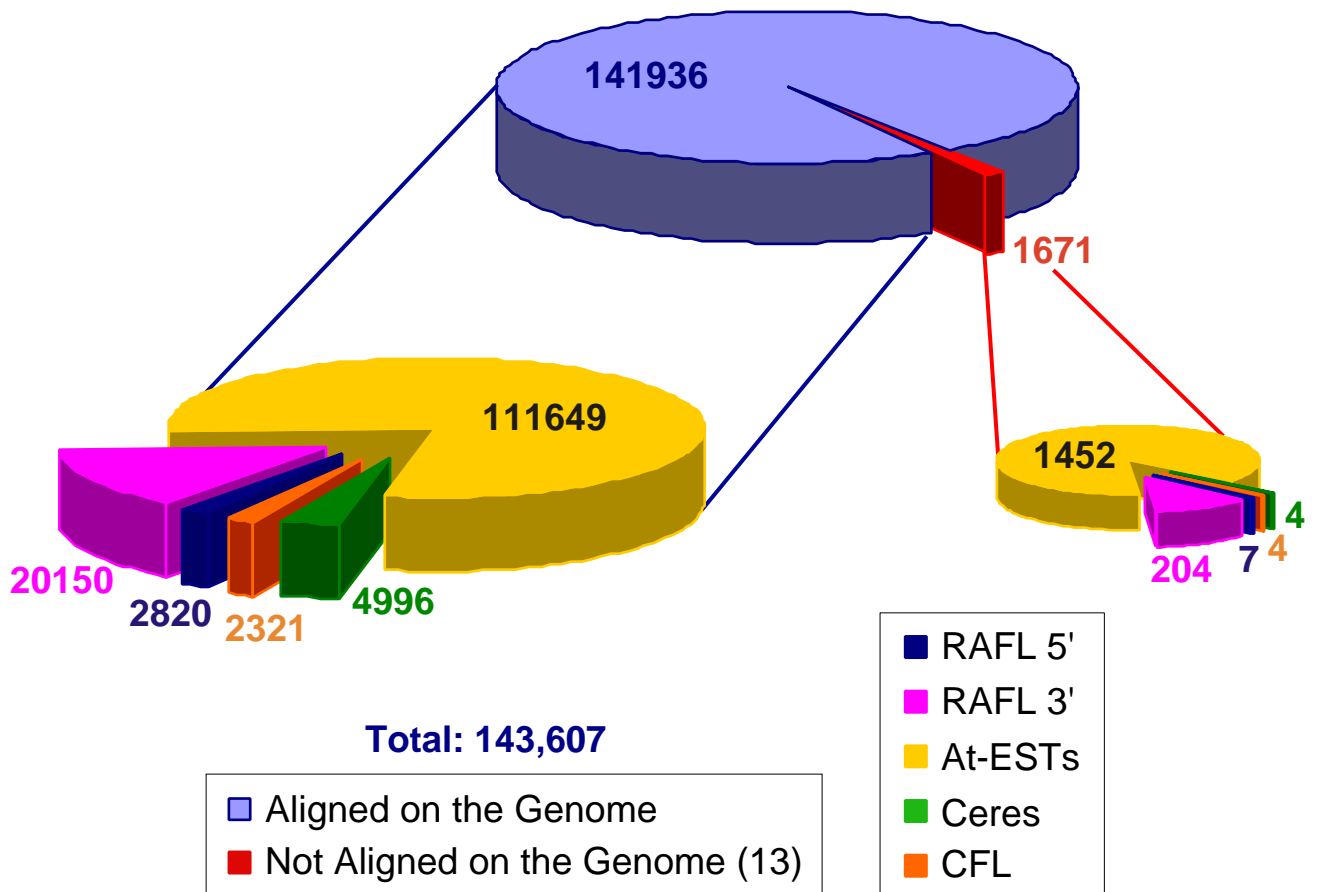
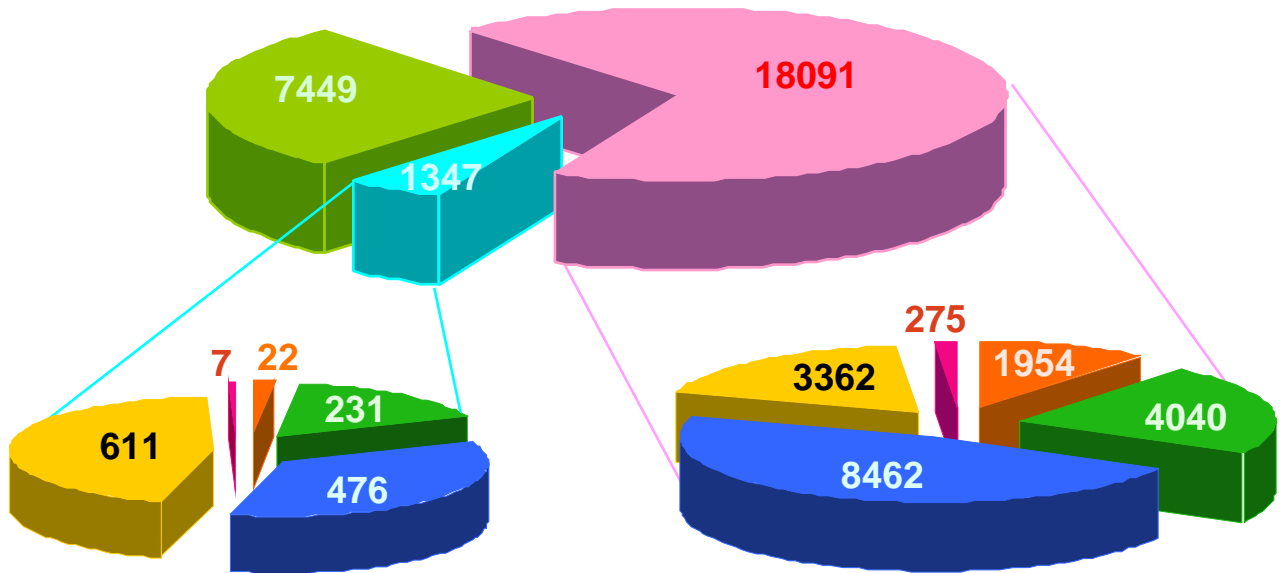


Fig S4



Total: 26,864 Annotated and Newly discovered genes



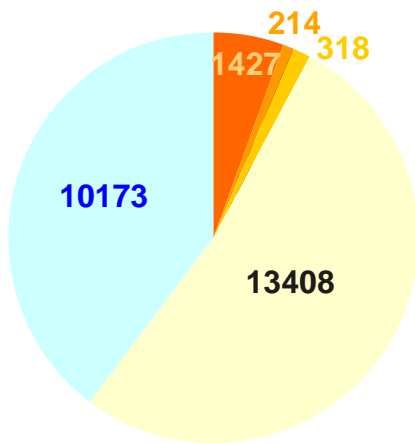
Fig S5

Annotated expressed genes

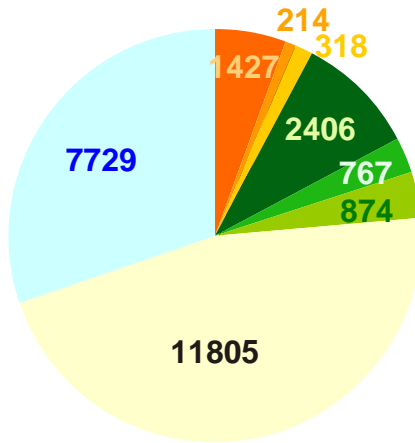
A. Total: 15,367

B. Total: 17,811

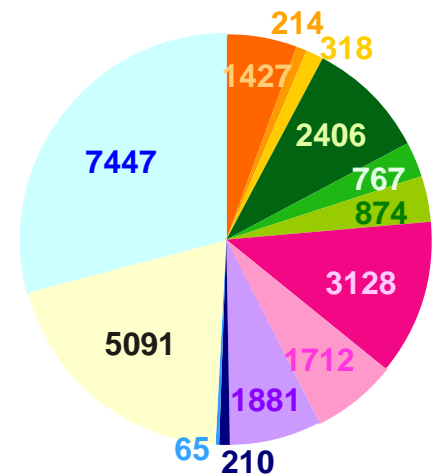
C. Total: 18,093



August 2001



September 2002



March 2003

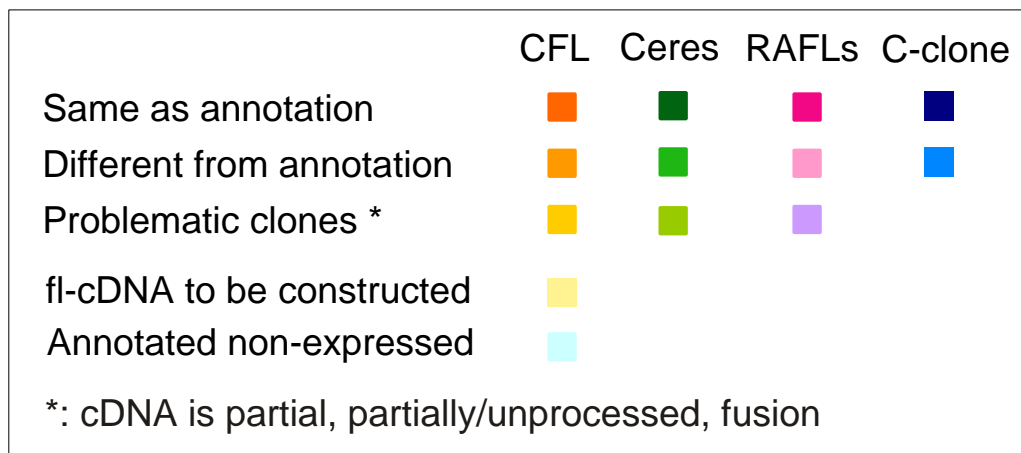


Fig S6

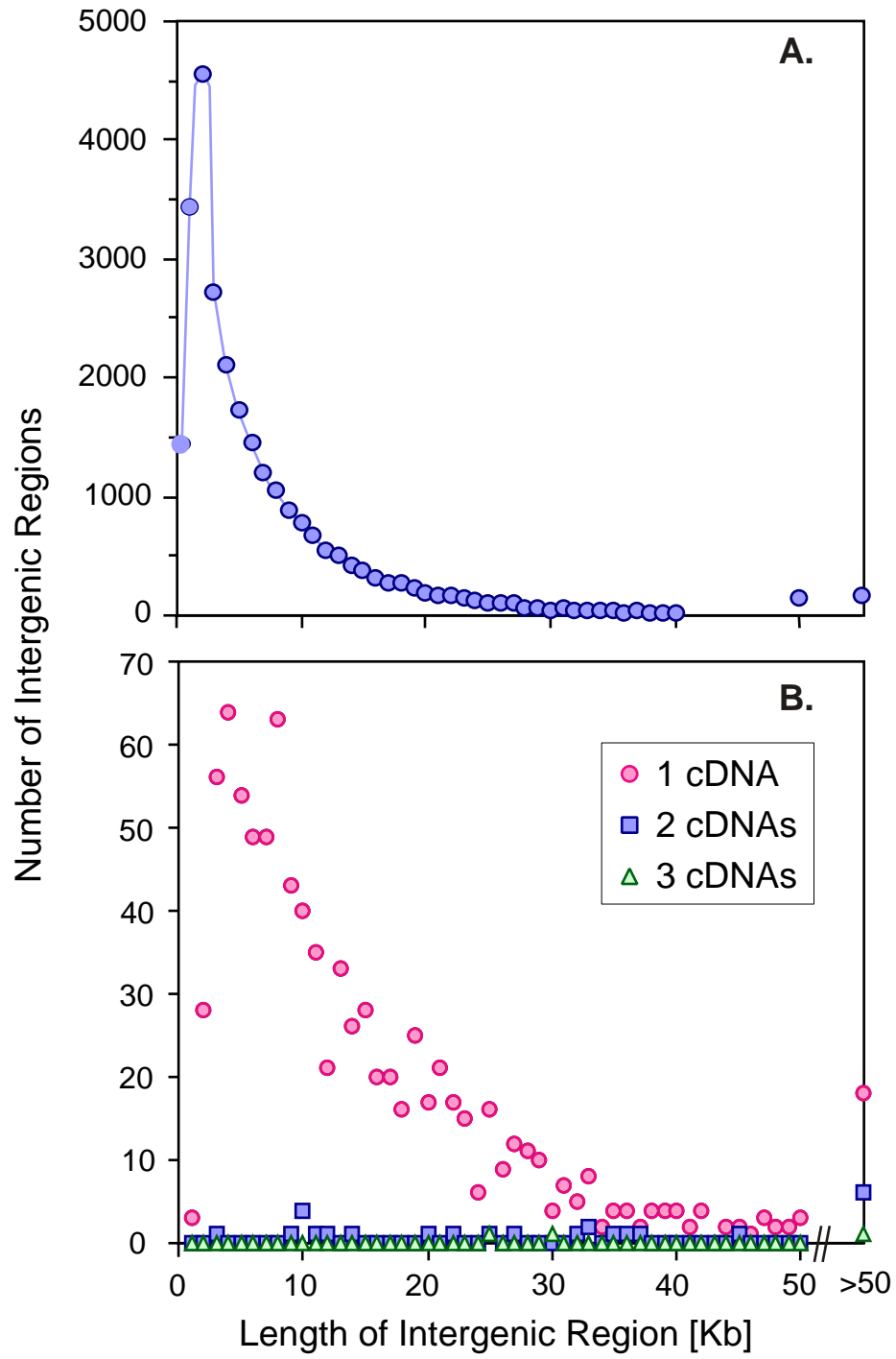


Fig S7

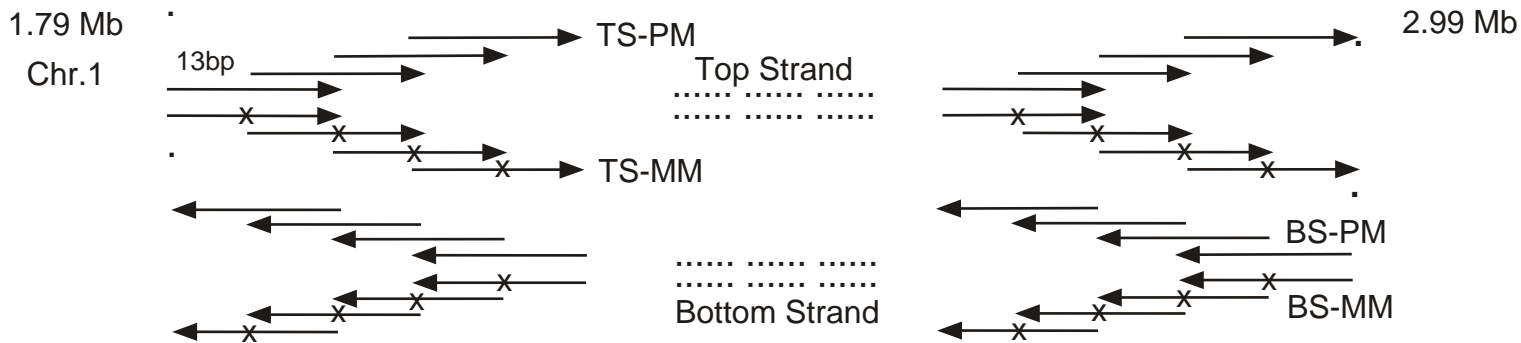
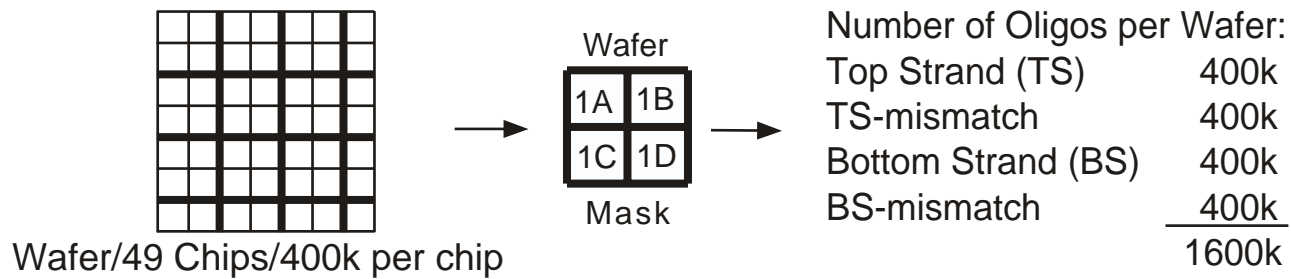


Fig S8

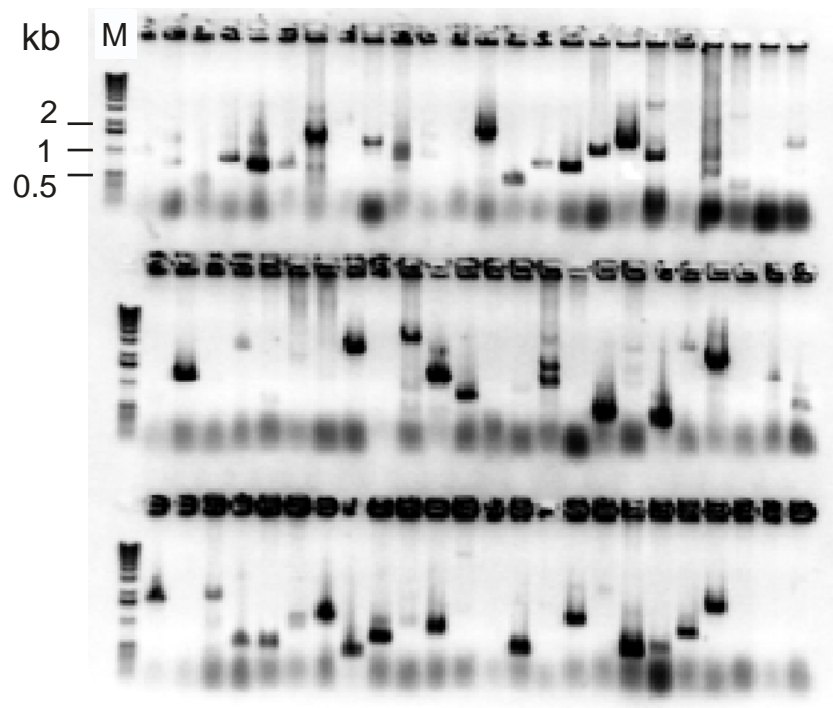
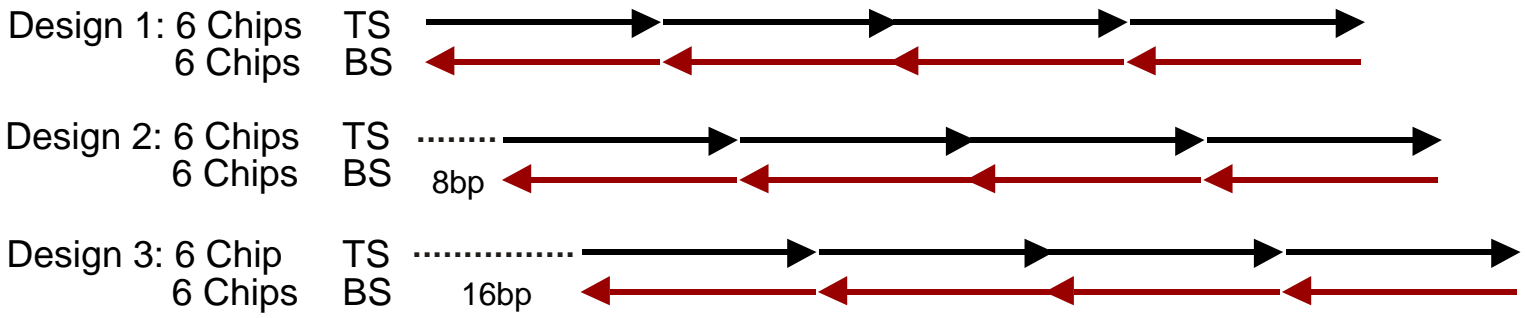


Fig S9



Wafer/49 Chips

37	1						} Design 1
38						12	
39	13						} Design 2
40						24	
41	25						} Design 3
42						36	
43	44	45	46	47	48	49	← Extra Chips

37-45: Expression Chips
46-47: Promoter Mapping Chips
48-49: Splice Junction Chips

Fig S10



Fig S11
36



Fig S12



Fig S13



Fig S14

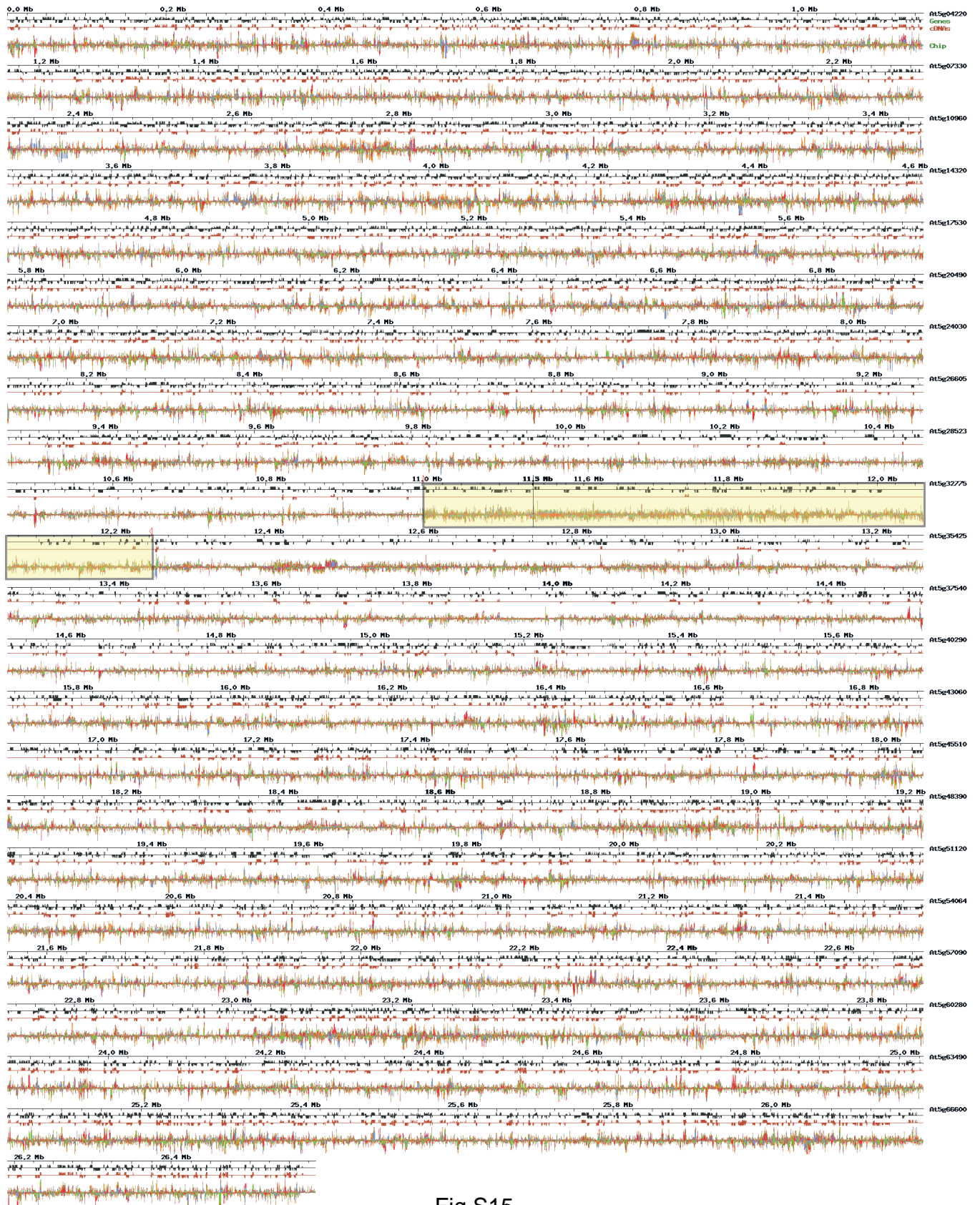


Fig S15

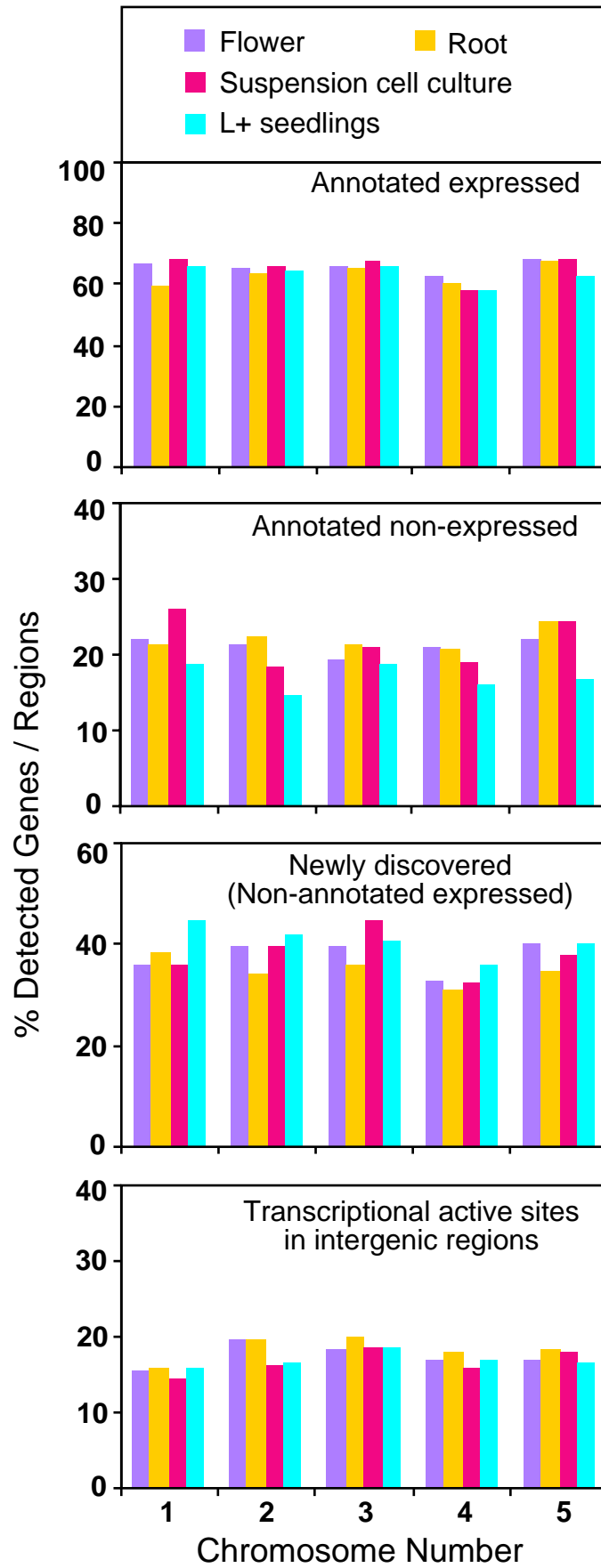
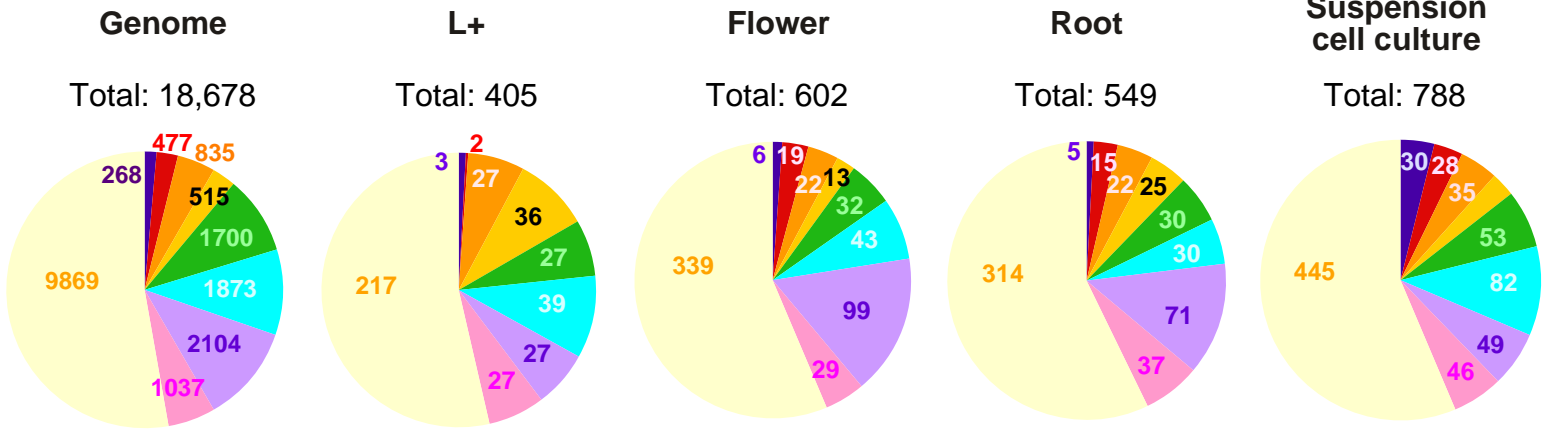


Fig S16

Annotated expressed



Annotated non-expressed

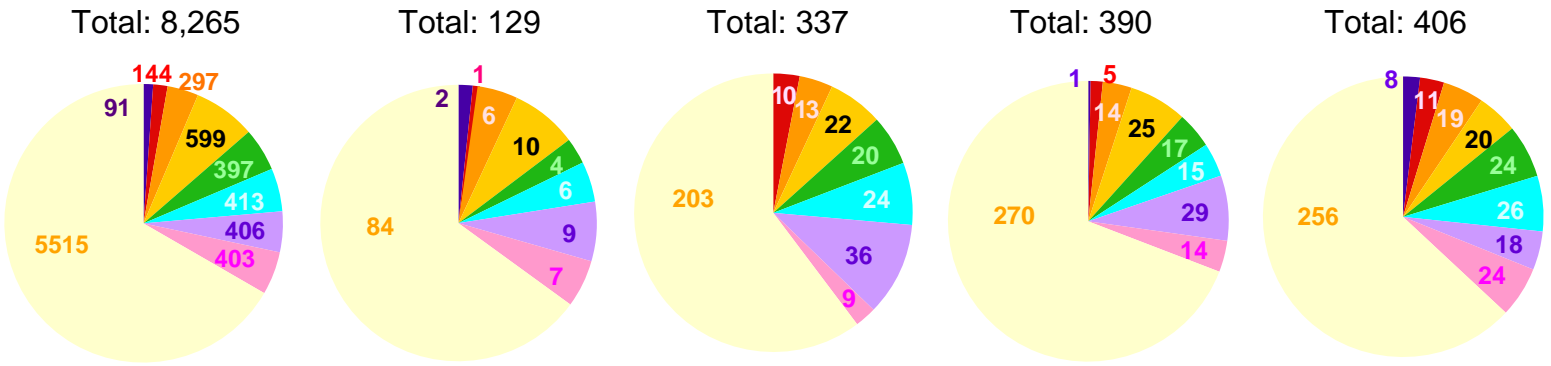


Fig S17

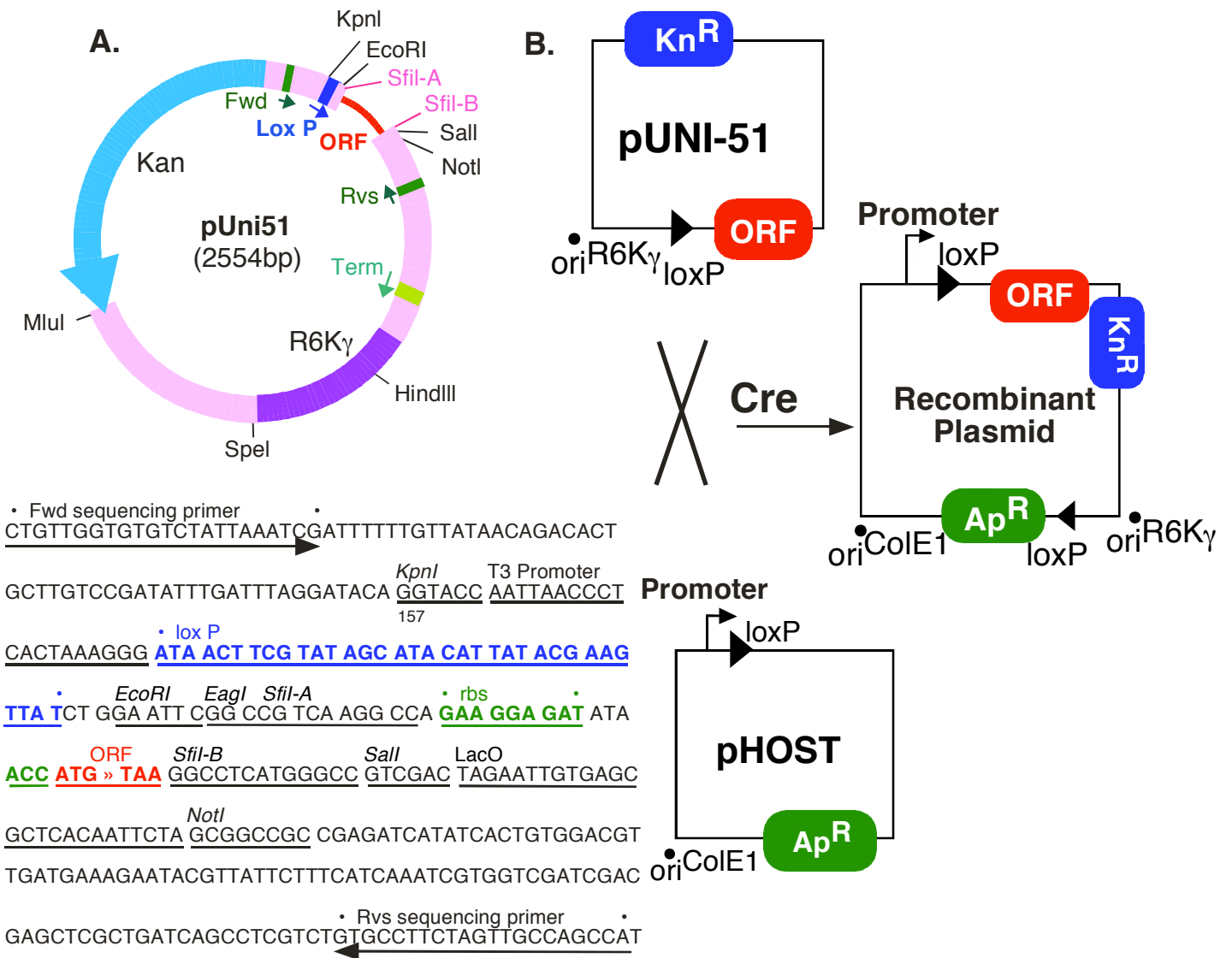


Fig S18

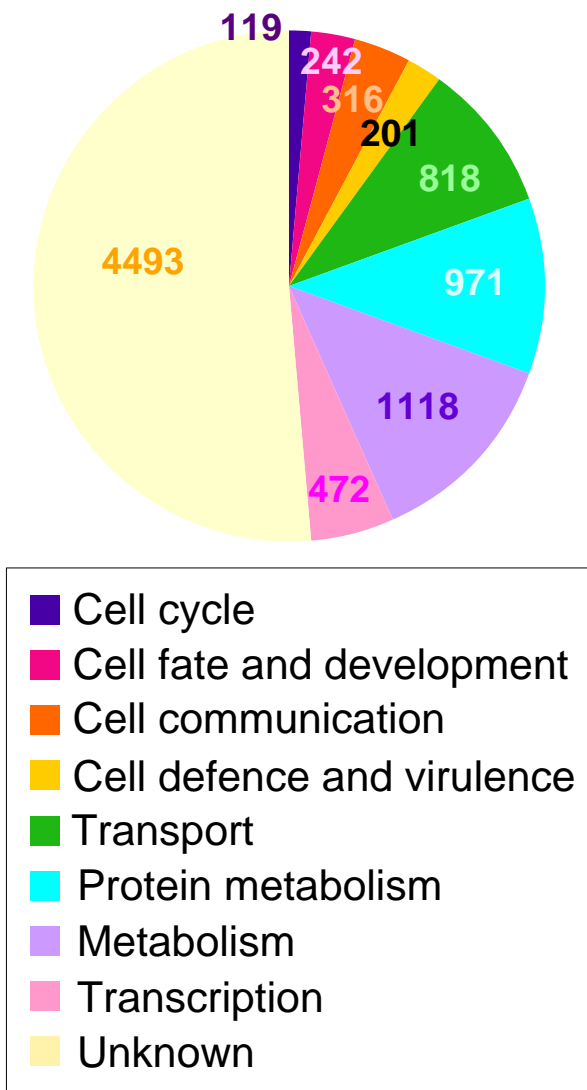
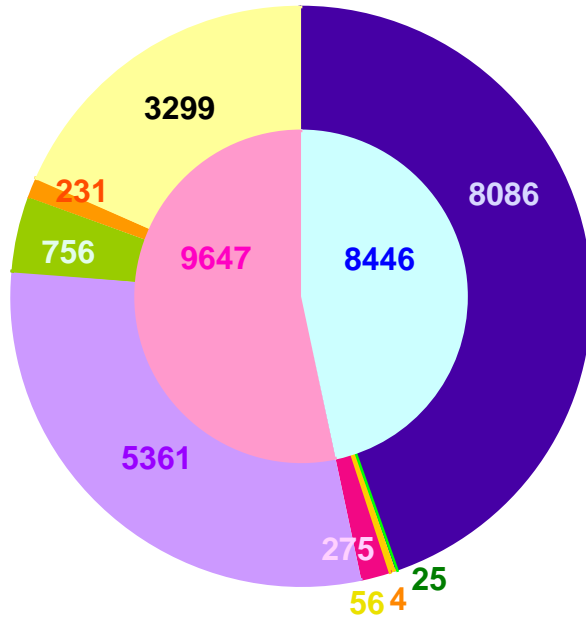


Fig S19

A. Annotated Expressed Genes
Total: 18,093



B. Newly Discovered Genes (Non-annotated expressed)
Total: 1,347

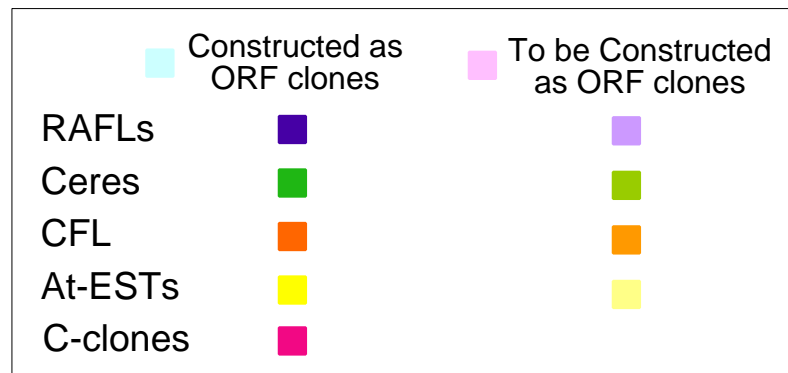
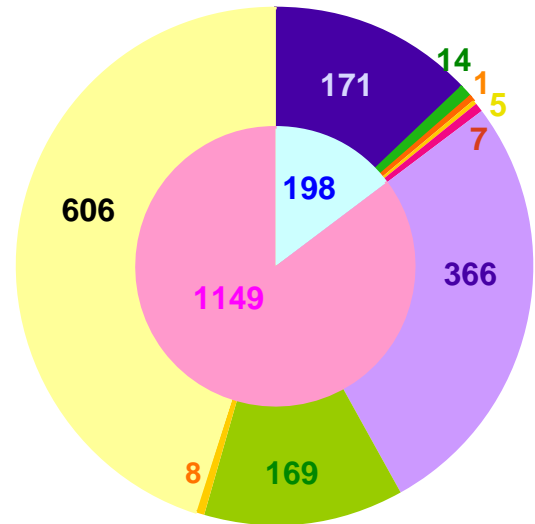
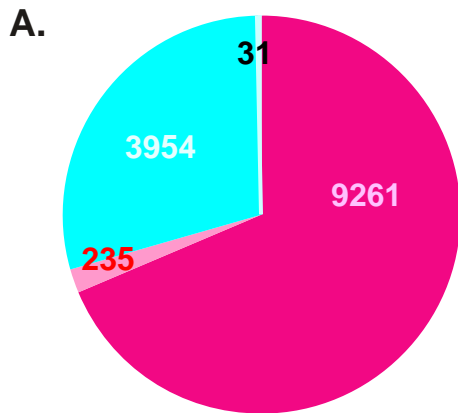
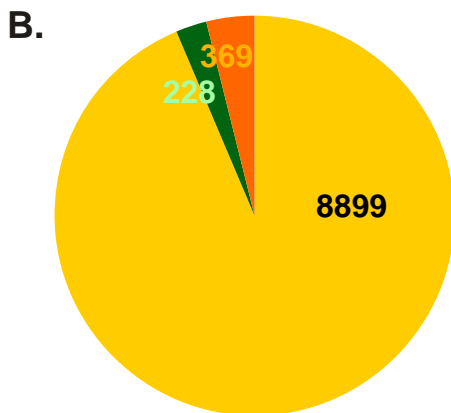


Fig S20



RAFLs Sequenced: 13,481 clones (Non Unique)

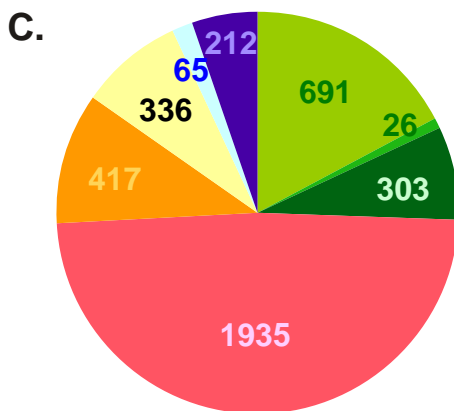
- Error free FI: Hit w/ annotated gene
- Error free FI: Newly discovered gene
- Problematic: Hit w/ annotated gene
- Problematic: Newly discovered gene



Non-Problematic RAFLs: 9,496 (70%)

- FI: Hit w/ annotated gene
- FI: Newly discovered gene
- potentially FI *

*: Upstream ATG found in genome inside of 300bp window



Problematic RAFLs: 3,985 (30%)

- 5' partial
- 5'/3' partial
- 3' partial
- Mutation
- partially/unprocessed
- Hit w/ pseudo etc
- Fusion
- Un-categorized *

*: Potentially genomic sequence error etc.

Fig S21

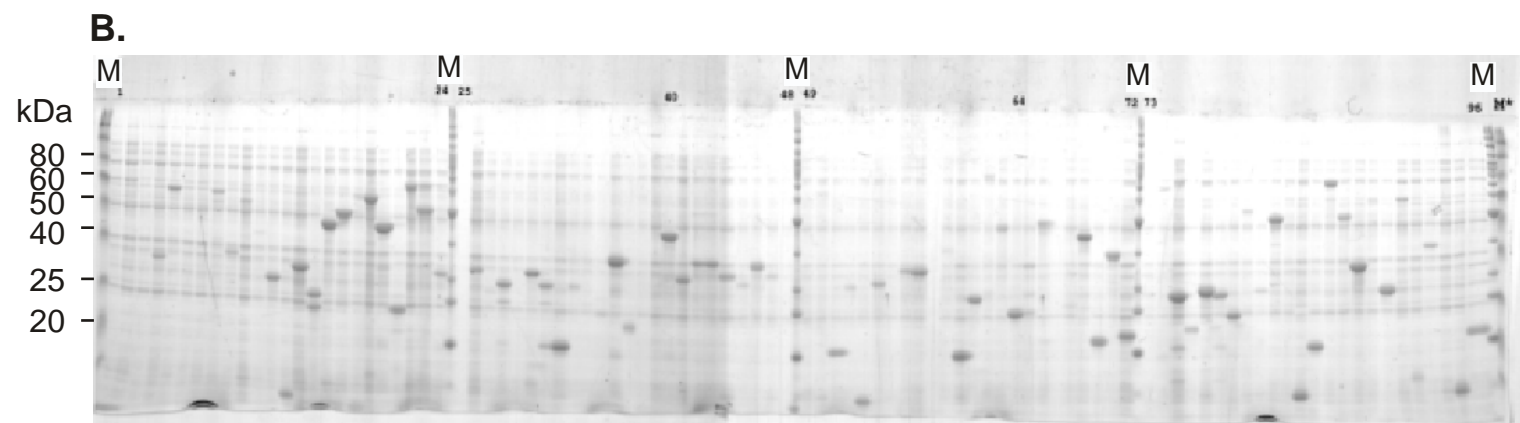
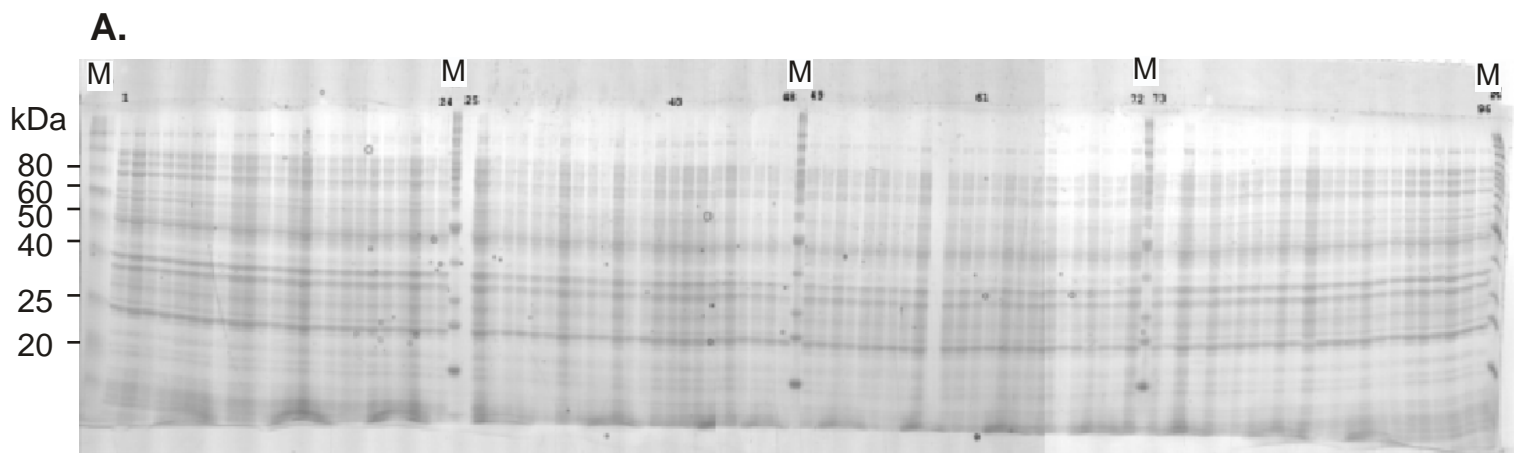


Fig S22

A.

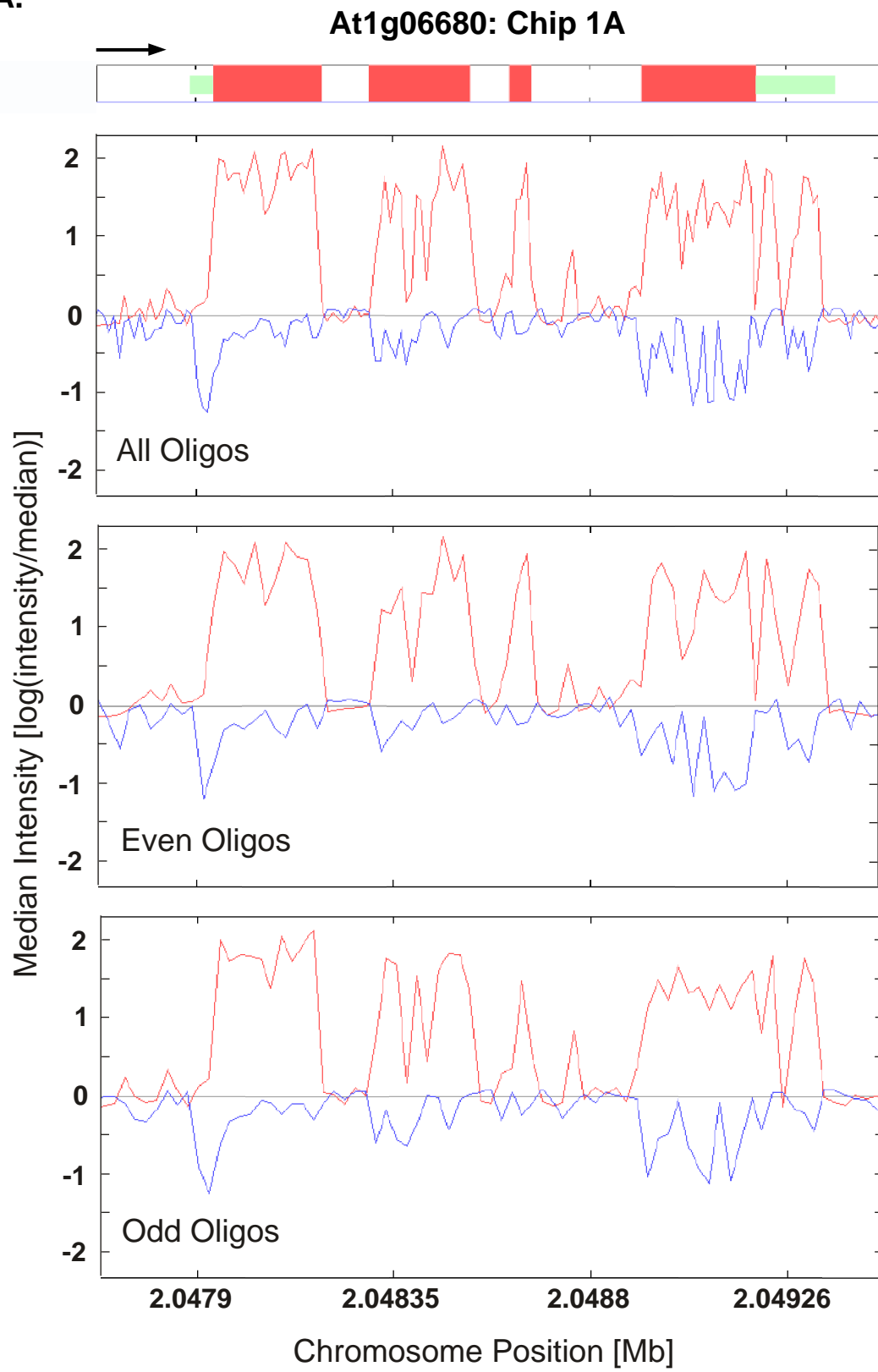
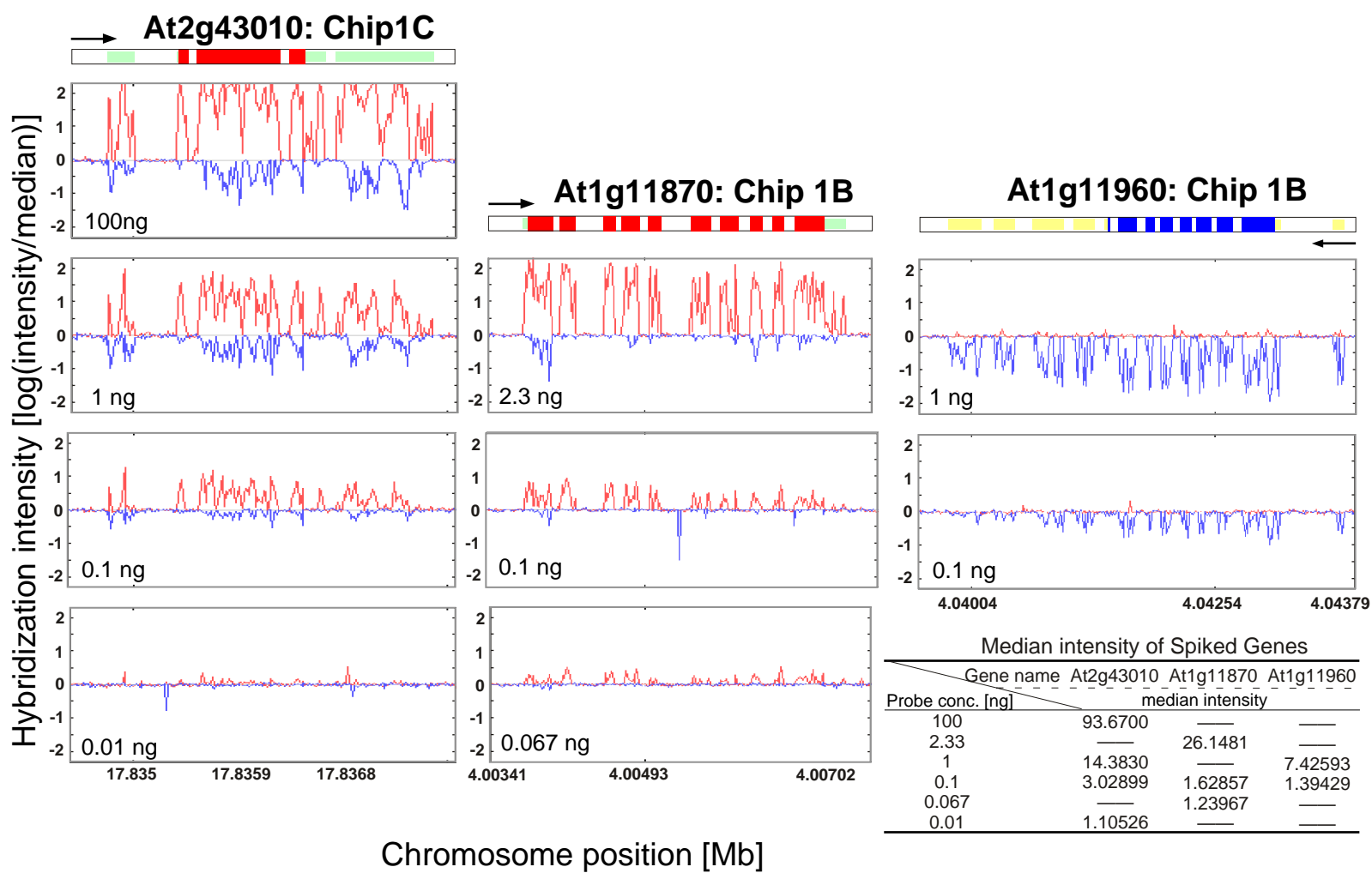


Fig S23



Median intensity of Spiked Genes			
Gene name	At2g43010	At1g11870	At1g11960
Probe conc. [ng]	median intensity		
100	93.6700	—	—
2.33	—	26.1481	—
1	14.3830	—	7.42593
0.1	3.02899	1.62857	1.39429
0.067	—	1.23967	—
0.01	1.10526	—	—

Fig S24

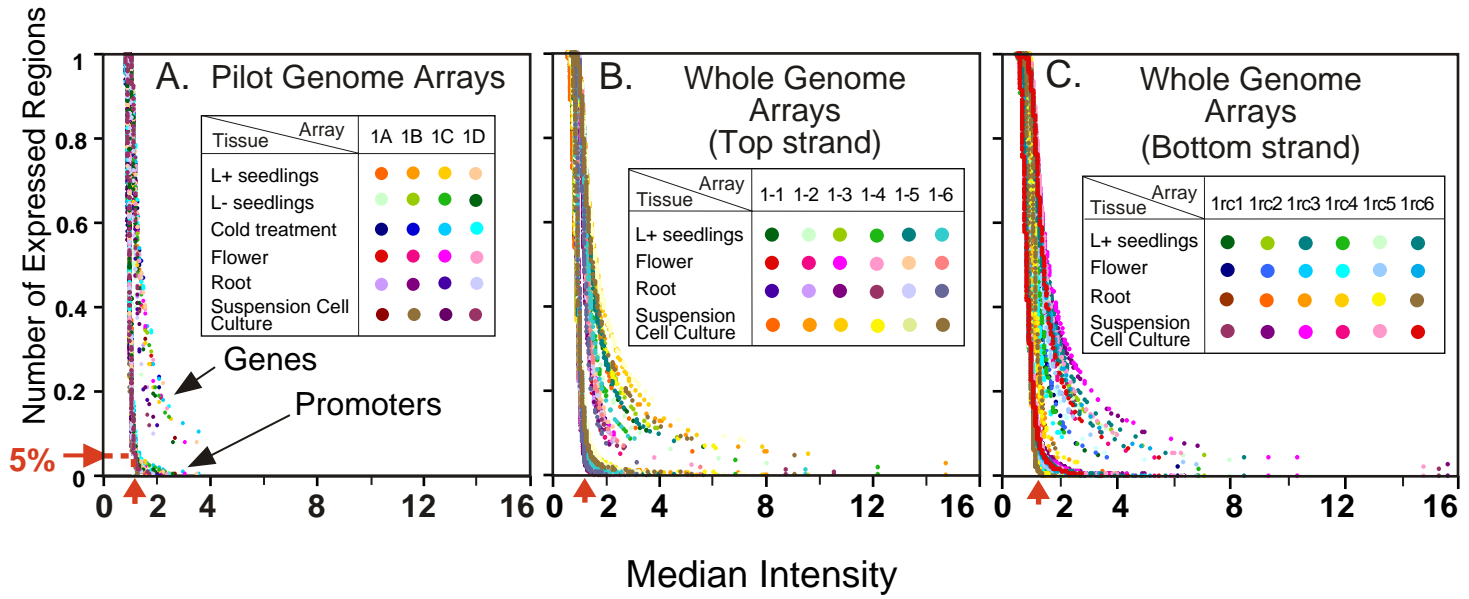


Fig S25

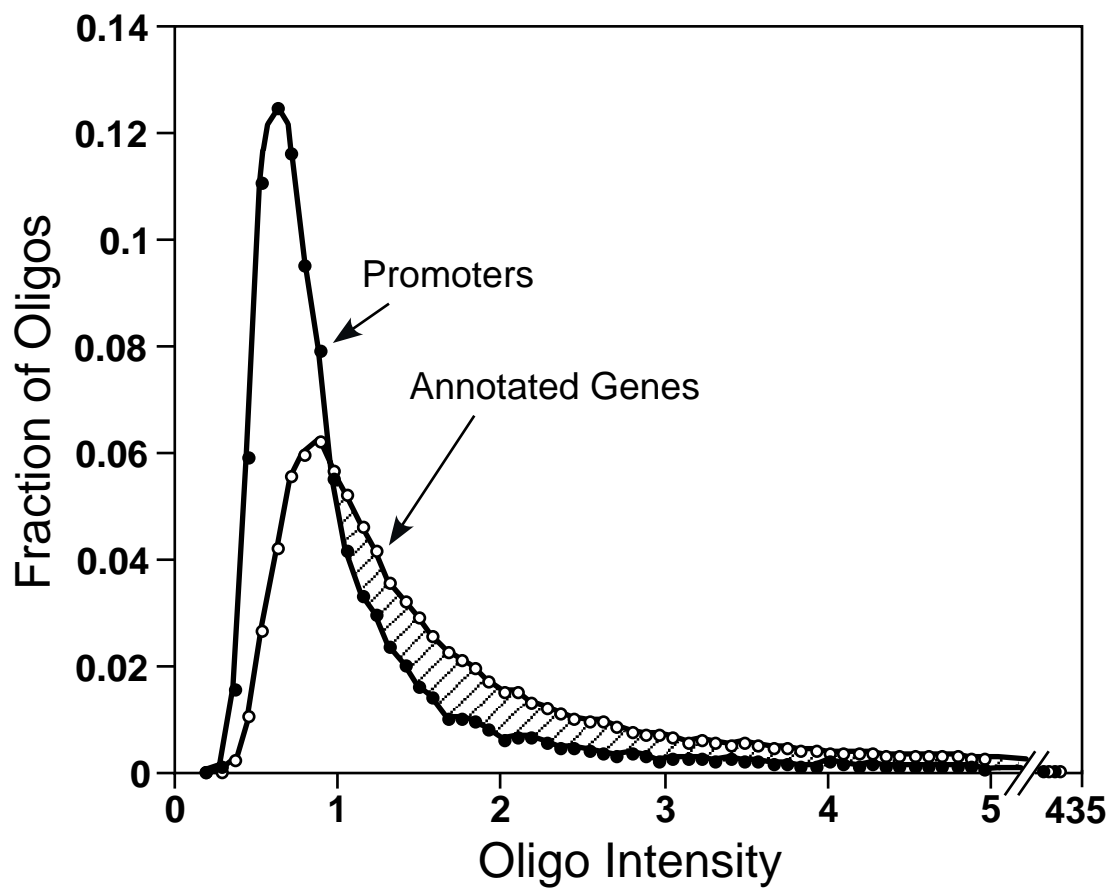


Fig S26

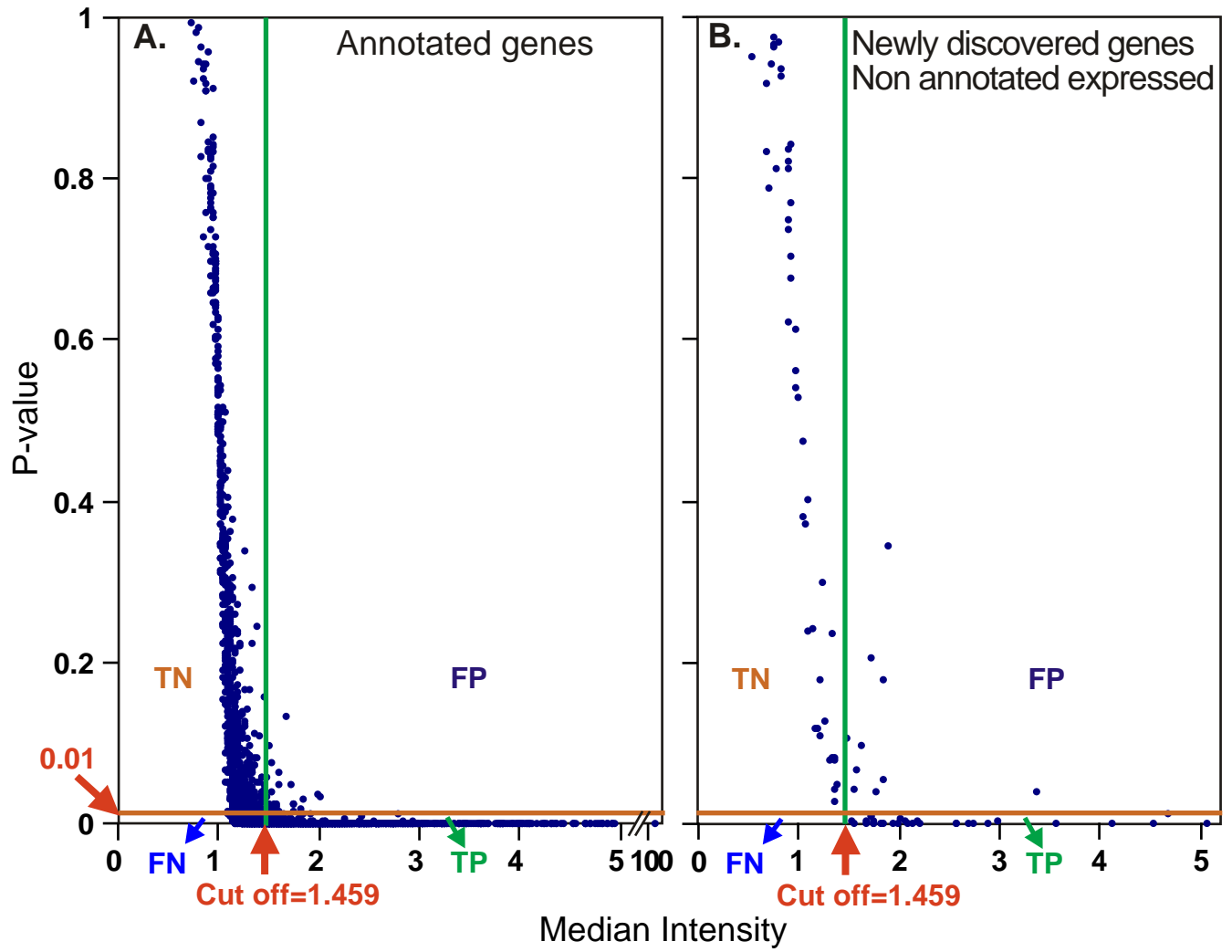


Fig S27

Table S1 Isolation of ORFs by RT-PCR using Chip hybridization data

Class of Genes	Attempted	Positive RT-PCR	Chip Clones (C)	
			w/ ORF	w/o ORF*
Annotated Expressed				
w/ Intron	67	55	28	27
w/o Intron	16	13	12	1
Annotated Non-expressed				
w/ Intron	97	71	34	37
w/o Intron	35	29	22	7
Total	215	168	96	72

* Stop in ORF

Table S2. Classes and Number of cDNAs Mapped on the *Arabidopsis* Genome

Class of cDNA	Number of cDNAs		
A. <i>Arabidopsis</i>			
Community Full Length (CFL)			2,325
Ceres			5,000
ESTs			113,101
RAFLs, 3' and 5'			61,172
R			13,619
U			8,841
C			954
B. Non <i>Arabidopsis</i>			
	EST	Proteins	mRNAs
<i>Brassica</i>	8,000	2,656	896
Rice	126,314	24,544	1,832
Wheat	415,592	2,185	715

Table S3. Values of Sensitivity and Specificity for the Pilot Genome Arrays

Tissue	Array 1A		Array 1B		Array 1C		Array 1D	
	sensitivity	specificity	sensitivity	specificity	sensitivity	specificity	sensitivity	specificity
L+	0.835	0.975	0.833	0.974	0.664	0.988	0.757	0.990
L-	0.747	0.982	0.861	0.971	0.774	0.990	0.728	0.983
L+, cold treated	0.833	0.986	0.773	0.984	0.656	0.989	0.764	0.979
Flower	0.916	0.964	0.823	0.976	0.814	0.987	0.790	0.990
Root	0.876	0.969	0.914	0.974	0.765	0.985	0.702	0.989
Suspension cell culture	0.862	0.983	0.923	0.976	0.703	0.990	0.756	0.986

Table S4. Values of sensitivity and specificity for the whole genome arrays

Tissue	sensitivity	specificity	sensitivity	specificity	sensitivity	specificity
<i>A. Top Strand</i>	Array 1-1		Array 1-2		Array 1-3	
L+	0.759	0.954	0.821	0.921	0.799	0.946
Flower	0.796	0.921	0.870	0.887	0.850	0.935
Root	0.851	0.913	0.859	0.899	0.858	0.910
Suspension cell culture	0.822	0.950	0.810	0.951	0.840	0.952
<i>B. Bottom Strand</i>	Array 1-rc-1		Array 1-rc-2		Array 1-rc-3	
L+	0.796	0.939	0.709	0.959	0.800	0.958
Flower	0.799	0.936	0.705	0.941	0.822	0.953
Root	0.770	0.893	0.779	0.897	0.824	0.930
Suspension cell culture	0.791	0.955	0.710	0.959	0.805	0.967
Tissue	sensitivity	specificity	sensitivity	specificity	sensitivity	specificity
<i>A. Top Strand</i>	Array 1-4		Array 1-5		Array 1-6	
L+	0.753	0.959	0.743	0.952	0.784	0.921
Flower	0.780	0.940	0.823	0.938	0.780	0.928
Root	0.815	0.929	0.846	0.943	0.840	0.911
Suspension cell culture	0.732	0.974	0.759	0.962	0.828	0.933
<i>B. Bottom Strand</i>	Array 1-rc-4		Array 1-rc-5		Array 1-rc-6	
L+	0.940	0.904	0.734	0.961	0.752	0.953
Flower	0.742	0.946	0.822	0.946	0.812	0.959
Root	0.786	0.905	0.806	0.908	0.837	0.903
Suspension cell culture	0.751	0.953	0.795	0.958	0.767	0.944

Supplemental Notes and References

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17. F. H. C. Marriot, *Applied Statistics* **28**, 75 (1979).
18. The non alignment of some ESTs and cDNAs on the genome is due to (a) bad sequencing quality; (b) the genome may be missing; or (c) the clones contain mitochondria or *E. coli* DNA, cloning vector DNA, or DNA of other organisms.
19. M. Seki et al., *Science* **296**, 141 (2002).

Table S5 Genes detected by the WGAs using the four mRNA samples

#	Gene	#	Gene	#	Gene	#	Gene
1	Atlg01010	44	Atlg01550	87	Atlg02065	130	Atlg02680
2	Atlg01020	45	Atlg01560	88	Atlg02070	131	Atlg02690
3	Atlg01030	46	Atlg01570	89	Atlg02080	132	Atlg02710
4	Atlg01050	47	Atlg01580	90	Atlg02100	133	Atlg02720
5	Atlg01060	48	Atlg01600	91	Atlg02110	134	Atlg02730
6	Atlg01070	49	Atlg01610	92	Atlg02120	135	Atlg02750
7	Atlg01080	50	Atlg01620	93	Atlg02130	136	Atlg02770
8	Atlg01090	51	Atlg01630	94	Atlg02140	137	Atlg02780
9	Atlg01110	52	Atlg01640	95	Atlg02150	138	Atlg02790
10	Atlg01120	53	Atlg01650	96	Atlg02160	139	Atlg02800
11	Atlg01130	54	Atlg01710	97	Atlg02170	140	Atlg02810
12	Atlg01140	55	Atlg01720	98	Atlg02180	141	Atlg02813
13	Atlg01160	56	Atlg01725	99	Atlg02190	142	Atlg02816
14	Atlg01170	57	Atlg01730	100	Atlg02200	143	Atlg02820
15	Atlg01180	58	Atlg01740	101	Atlg02205	144	Atlg02850
16	Atlg01190	59	Atlg01750	102	Atlg02220	145	Atlg02860
17	Atlg01200	60	Atlg01760	103	Atlg02260	146	Atlg02870
18	Atlg01210	61	Atlg01770	104	Atlg02270	147	Atlg02880
19	Atlg01220	62	Atlg01780	105	Atlg02280	148	Atlg02890
20	Atlg01225	63	Atlg01790	106	Atlg02305	149	Atlg02900
21	Atlg01230	64	Atlg01800	107	Atlg02310	150	Atlg02910
22	Atlg01240	65	Atlg01810	108	Atlg02330	151	Atlg02920
23	Atlg01250	66	Atlg01820	109	Atlg02340	152	Atlg02930
24	Atlg01260	67	Atlg01830	110	Atlg02350	153	Atlg03000
25	Atlg01290	68	Atlg01840	111	Atlg02360	154	Atlg03030
26	Atlg01300	69	Atlg01860	112	Atlg02370	155	Atlg03040
27	Atlg01310	70	Atlg01900	113	Atlg02380	156	Atlg03050
28	Atlg01320	71	Atlg01910	114	Atlg02390	157	Atlg03070
29	Atlg01330	72	Atlg01920	115	Atlg02400	158	Atlg03090
30	Atlg01350	73	Atlg01930	116	Atlg02405	159	Atlg03110
31	Atlg01360	74	Atlg01940	117	Atlg02410	160	Atlg03120
32	Atlg01370	75	Atlg01950	118	Atlg02450	161	Atlg03130
33	Atlg01390	76	Atlg01960	119	Atlg02470	162	Atlg03140
34	Atlg01400	77	Atlg01970	120	Atlg02475	163	Atlg03150
35	Atlg01420	78	Atlg01980	121	Atlg02490	164	Atlg03160
36	Atlg01430	79	Atlg01990	122	Atlg02520	165	Atlg03170
37	Atlg01440	80	Atlg02000	123	Atlg02550	166	Atlg03180
38	Atlg01470	81	Atlg02010	124	Atlg02560	167	Atlg03190
39	Atlg01480	82	Atlg02020	125	Atlg02570	168	Atlg03200
40	Atlg01490	83	Atlg02030	126	Atlg02610	169	Atlg03210
41	Atlg01500	84	Atlg02040	127	Atlg02630	170	Atlg03220
42	Atlg01510	85	Atlg02050	128	Atlg02640	171	Atlg03230
43	Atlg01540	86	Atlg02060	129	Atlg02660	172	Atlg03250

173	Atlg03260	219	Atlg04010	265	Atlg04590	311	Atlg05180
174	Atlg03290	220	Atlg04040	266	Atlg04610	312	Atlg05190
175	Atlg03320	221	Atlg04050	267	Atlg04630	313	Atlg05200
176	Atlg03330	222	Atlg04070	268	Atlg04640	314	Atlg05205
177	Atlg03350	223	Atlg04080	269	Atlg04660	315	Atlg05210
178	Atlg03360	224	Atlg04100	270	Atlg04670	316	Atlg05220
179	Atlg03370	225	Atlg04110	271	Atlg04680	317	Atlg05230
180	Atlg03380	226	Atlg04120	272	Atlg04690	318	Atlg05240
181	Atlg03400	227	Atlg04130	273	Atlg04710	319	Atlg05250
182	Atlg03410	228	Atlg04140	274	Atlg04750	320	Atlg05260
183	Atlg03420	229	Atlg04170	275	Atlg04760	321	Atlg05270
184	Atlg03430	230	Atlg04180	276	Atlg04770	322	Atlg05280
185	Atlg03440	231	Atlg04190	277	Atlg04780	323	Atlg05300
186	Atlg03457	232	Atlg04200	278	Atlg04800	324	Atlg05340
187	Atlg03475	233	Atlg04210	279	Atlg04810	325	Atlg05350
188	Atlg03495	234	Atlg04220	280	Atlg04820	326	Atlg05360
189	Atlg03520	235	Atlg04230	281	Atlg04830	327	Atlg05370
190	Atlg03530	236	Atlg04240	282	Atlg04850	328	Atlg05380
191	Atlg03540	237	Atlg04250	283	Atlg04860	329	Atlg05385
192	Atlg03590	238	Atlg04260	284	Atlg04870	330	Atlg05400
193	Atlg03600	239	Atlg04270	285	Atlg04880	331	Atlg05410
194	Atlg03610	240	Atlg04280	286	Atlg04900	332	Atlg05420
195	Atlg03620	241	Atlg04290	287	Atlg04910	333	Atlg05430
196	Atlg03630	242	Atlg04300	288	Atlg04930	334	Atlg05450
197	Atlg03660	243	Atlg04310	289	Atlg04940	335	Atlg05460
198	Atlg03675	244	Atlg04330	290	Atlg04950	336	Atlg05470
199	Atlg03687	245	Atlg04340	291	Atlg04960	337	Atlg05480
200	Atlg03700	246	Atlg04350	292	Atlg04970	338	Atlg05500
201	Atlg03710	247	Atlg04360	293	Atlg04980	339	Atlg05510
202	Atlg03730	248	Atlg04370	294	Atlg04985	340	Atlg05520
203	Atlg03740	249	Atlg04390	295	Atlg04990	341	Atlg05530
204	Atlg03790	250	Atlg04400	296	Atlg05000	342	Atlg05540
205	Atlg03800	251	Atlg04410	297	Atlg05010	343	Atlg05560
206	Atlg03820	252	Atlg04420	298	Atlg05020	344	Atlg05575
207	Atlg03850	253	Atlg04430	299	Atlg05030	345	Atlg05580
208	Atlg03860	254	Atlg04440	300	Atlg05050	346	Atlg05590
209	Atlg03870	255	Atlg04445	301	Atlg05055	347	Atlg05600
210	Atlg03880	256	Atlg04470	302	Atlg05060	348	Atlg05620
211	Atlg03890	257	Atlg04480	303	Atlg05070	349	Atlg05630
212	Atlg03900	258	Atlg04510	304	Atlg05080	350	Atlg05650
213	Atlg03905	259	Atlg04520	305	Atlg05090	351	Atlg05660
214	Atlg03910	260	Atlg04530	306	Atlg05100	352	Atlg05670
215	Atlg03940	261	Atlg04540	307	Atlg05120	353	Atlg05680
216	Atlg03970	262	Atlg04550	308	Atlg05130	354	Atlg05710
217	Atlg03990	263	Atlg04560	309	Atlg05140	355	Atlg05720
218	Atlg04000	264	Atlg04570	310	Atlg05150	356	Atlg05730

357	Atlg05740	403	Atlg06280	449	Atlg06870	495	Atlg07430
358	Atlg05750	404	Atlg06290	450	Atlg06890	496	Atlg07440
359	Atlg05760	405	Atlg06310	451	Atlg06900	497	Atlg07470
360	Atlg05770	406	Atlg06320	452	Atlg06925	498	Atlg07473
361	Atlg05780	407	Atlg06330	453	Atlg06930	499	Atlg07476
362	Atlg05785	408	Atlg06340	454	Atlg06950	500	Atlg07480
363	Atlg05790	409	Atlg06350	455	Atlg06960	501	Atlg07490
364	Atlg05805	410	Atlg06360	456	Atlg06970	502	Atlg07500
365	Atlg05810	411	Atlg06380	457	Atlg06980	503	Atlg07510
366	Atlg05820	412	Atlg06390	458	Atlg06990	504	Atlg07520
367	Atlg05830	413	Atlg06400	459	Atlg07000	505	Atlg07530
368	Atlg05840	414	Atlg06410	460	Atlg07010	506	Atlg07570
369	Atlg05850	415	Atlg06430	461	Atlg07020	507	Atlg07600
370	Atlg05860	416	Atlg06450	462	Atlg07030	508	Atlg07610
371	Atlg05870	417	Atlg06460	463	Atlg07040	509	Atlg07630
372	Atlg05890	418	Atlg06470	464	Atlg07050	510	Atlg07650
373	Atlg05900	419	Atlg06500	465	Atlg07070	511	Atlg07660
374	Atlg05910	420	Atlg06520	466	Atlg07080	512	Atlg07670
375	Atlg05930	421	Atlg06530	467	Atlg07090	513	Atlg07690
376	Atlg05940	422	Atlg06540	468	Atlg07110	514	Atlg07700
377	Atlg05960	423	Atlg06550	469	Atlg07130	515	Atlg07705
378	Atlg05970	424	Atlg06560	470	Atlg07135	516	Atlg07720
379	Atlg06000	425	Atlg06570	471	Atlg07140	517	Atlg07730
380	Atlg06010	426	Atlg06590	472	Atlg07150	518	Atlg07740
381	Atlg06020	427	Atlg06620	473	Atlg07160	519	Atlg07745
382	Atlg06030	428	Atlg06630	474	Atlg07170	520	Atlg07750
383	Atlg06040	429	Atlg06640	475	Atlg07180	521	Atlg07770
384	Atlg06050	430	Atlg06650	476	Atlg07200	522	Atlg07780
385	Atlg06060	431	Atlg06660	477	Atlg07210	523	Atlg07790
386	Atlg06070	432	Atlg06670	478	Atlg07220	524	Atlg07795
387	Atlg06080	433	Atlg06680	479	Atlg07230	525	Atlg07810
388	Atlg06090	434	Atlg06690	480	Atlg07240	526	Atlg07820
389	Atlg06110	435	Atlg06700	481	Atlg07250	527	Atlg07830
390	Atlg06120	436	Atlg06720	482	Atlg07260	528	Atlg07840
391	Atlg06130	437	Atlg06730	483	Atlg07280	529	Atlg07850
392	Atlg06150	438	Atlg06740	484	Atlg07290	530	Atlg07870
393	Atlg06160	439	Atlg06760	485	Atlg07300	531	Atlg07890
394	Atlg06190	440	Atlg06770	486	Atlg07310	532	Atlg07900
395	Atlg06200	441	Atlg06780	487	Atlg07320	533	Atlg07920
396	Atlg06210	442	Atlg06790	488	Atlg07340	534	Atlg07930
397	Atlg06220	443	Atlg06800	489	Atlg07360	535	Atlg07940
398	Atlg06230	444	Atlg06810	490	Atlg07370	536	Atlg07950
399	Atlg06240	445	Atlg06820	491	Atlg07380	537	Atlg07960
400	Atlg06250	446	Atlg06830	492	Atlg07400	538	Atlg07970
401	Atlg06260	447	Atlg06840	493	Atlg07410	539	Atlg07980
402	Atlg06270	448	Atlg06850	494	Atlg07420	540	Atlg07990

541	Atlg08000	587	Atlg08620	633	Atlg09270	679	Atlg09815
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544	Atlg08040	590	Atlg08650	636	Atlg09300	682	Atlg09850
545	Atlg08050	591	Atlg08660	637	Atlg09310	683	Atlg09860
546	Atlg08090	592	Atlg08680	638	Atlg09330	684	Atlg09870
547	Atlg08100	593	Atlg08690	639	Atlg09340	685	Atlg09900
548	Atlg08110	594	Atlg08700	640	Atlg09380	686	Atlg09910
549	Atlg08120	595	Atlg08710	641	Atlg09390	687	Atlg09920
550	Atlg08130	596	Atlg08720	642	Atlg09415	688	Atlg09930
551	Atlg08150	597	Atlg08750	643	Atlg09430	689	Atlg09940
552	Atlg08180	598	Atlg08760	644	Atlg09450	690	Atlg09950
553	Atlg08190	599	Atlg08770	645	Atlg09460	691	Atlg09960
554	Atlg08200	600	Atlg08780	646	Atlg09480	692	Atlg09970
555	Atlg08210	601	Atlg08790	647	Atlg09486	693	Atlg09990
556	Atlg08220	602	Atlg08800	648	Atlg09490	694	Atlg10000
557	Atlg08230	603	Atlg08810	649	Atlg09500	695	Atlg10010
558	Atlg08250	604	Atlg08820	650	Atlg09520	696	Atlg10020
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566	Atlg08370	612	Atlg08940	658	Atlg09610	704	Atlg10100
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575	Atlg08470	621	Atlg09070	667	Atlg09710	713	Atlg10200
576	Atlg08480	622	Atlg09090	668	Atlg09730	714	Atlg10210
577	Atlg08490	623	Atlg09100	669	Atlg09740	715	Atlg10220
578	Atlg08500	624	Atlg09130	670	Atlg09750	716	Atlg10230
579	Atlg08510	625	Atlg09150	671	Atlg09760	717	Atlg10240
580	Atlg08520	626	Atlg09160	672	Atlg09770	718	Atlg10250
581	Atlg08540	627	Atlg09180	673	Atlg09780	719	Atlg10270
582	Atlg08550	628	Atlg09200	674	Atlg09790	720	Atlg10280
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584	Atlg08570	630	Atlg09230	676	Atlg09800	722	Atlg10310
585	Atlg08580	631	Atlg09240	677	Atlg09810	723	Atlg10320
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726	Atlg10350	772	Atlg10940	818	Atlg11670	864	Atlg12380
727	Atlg10360	773	Atlg10950	819	Atlg11680	865	Atlg12390
728	Atlg10370	774	Atlg10960	820	Atlg11700	866	Atlg12400
729	Atlg10380	775	Atlg10970	821	Atlg11750	867	Atlg12410
730	Atlg10385	776	Atlg10990	822	Atlg11760	868	Atlg12420
731	Atlg10390	777	Atlg11000	823	Atlg11770	869	Atlg12440
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733	Atlg10410	779	Atlg11050	825	Atlg11790	871	Atlg12470
734	Atlg10430	780	Atlg11060	826	Atlg11800	872	Atlg12490
735	Atlg10460	781	Atlg11080	827	Atlg11820	873	Atlg12500
736	Atlg10470	782	Atlg11090	828	Atlg11840	874	Atlg12520
737	Atlg10480	783	Atlg11120	829	Atlg11850	875	Atlg12530
738	Atlg10490	784	Atlg11140	830	Atlg11860	876	Atlg12550
739	Atlg10500	785	Atlg11145	831	Atlg11870	877	Atlg12560
740	Atlg10510	786	Atlg11180	832	Atlg11880	878	Atlg12570
741	Atlg10520	787	Atlg11190	833	Atlg11890	879	Atlg12580
742	Atlg10522	788	Atlg11200	834	Atlg11910	880	Atlg12600
743	Atlg10530	789	Atlg11210	835	Atlg11925	881	Atlg12610
744	Atlg10540	790	Atlg11220	836	Atlg11930	882	Atlg12630
745	Atlg10550	791	Atlg11240	837	Atlg11940	883	Atlg12640
746	Atlg10560	792	Atlg11260	838	Atlg11960	884	Atlg12660
747	Atlg10580	793	Atlg11270	839	Atlg12000	885	Atlg12670
748	Atlg10590	794	Atlg11280	840	Atlg12010	886	Atlg12680
749	Atlg10600	795	Atlg11310	841	Atlg12020	887	Atlg12710
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755	Atlg10690	801	Atlg11400	847	Atlg12090	893	Atlg12770
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765	Atlg10810	811	Atlg11560	857	Atlg12250	903	Atlg12890
766	Atlg10820	812	Atlg11570	858	Atlg12270	904	Atlg12900
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912	Atlg13000	958	Atlg13700	1004	Atlg14310	1050	Atlg14860
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915	Atlg13060	961	Atlg13740	1007	Atlg14340	1053	Atlg14890
916	Atlg13080	962	Atlg13750	1008	Atlg14345	1054	Atlg14900
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918	Atlg13100	964	Atlg13770	1010	Atlg14370	1056	Atlg14920
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920	Atlg13120	966	Atlg13820	1012	Atlg14390	1058	Atlg14940
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922	Atlg13150	968	Atlg13860	1014	Atlg14410	1060	Atlg14960
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924	Atlg13170	970	Atlg13880	1016	Atlg14430	1062	Atlg14980
925	Atlg13190	971	Atlg13900	1017	Atlg14440	1063	Atlg14990
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944	Atlg13440	990	Atlg14160	1036	Atlg14685	1082	Atlg15190
945	Atlg13450	991	Atlg14170	1037	Atlg14687	1083	Atlg15200
946	Atlg13480	992	Atlg14180	1038	Atlg14700	1084	Atlg15210
947	Atlg13520	993	Atlg14185	1039	Atlg14710	1085	Atlg15220
948	Atlg13530	994	Atlg14200	1040	Atlg14720	1086	Atlg15230
949	Atlg13560	995	Atlg14210	1041	Atlg14730	1087	Atlg15240
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951	Atlg13580	997	Atlg14230	1043	Atlg14770	1089	Atlg15260
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1093	Atlg15300	1139	Atlg15880	1185	Atlg16570	1231	Atlg17210
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1095	Atlg15320	1141	Atlg15910	1187	Atlg16610	1233	Atlg17270
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1097	Atlg15340	1143	Atlg15950	1189	Atlg16650	1235	Atlg17290
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1107	Atlg15430	1153	Atlg16080	1199	Atlg16780	1245	Atlg17440
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1116	Atlg15550	1162	Atlg16220	1208	Atlg16890	1254	Atlg17540
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1122	Atlg15690	1168	Atlg16290	1214	Atlg16970	1260	Atlg17650
1123	Atlg15700	1169	Atlg16300	1215	Atlg17050	1261	Atlg17680
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1126	Atlg15730	1172	Atlg16340	1218	Atlg17080	1264	Atlg17720
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1128	Atlg15750	1174	Atlg16370	1220	Atlg17100	1266	Atlg17740
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1836	Atlg26280	1882	Atlg26940	1928	Atlg27560	1974	Atlg28210
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2016	Atlg28700	2062	Atlg29550	2108	Atlg30270	2154	Atlg30845
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2018	Atlg28760	2064	Atlg29640	2110	Atlg30300	2156	Atlg30870
2019	Atlg28960	2065	Atlg29660	2111	Atlg30320	2157	Atlg30880
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2203	Atlg31630	2249	Atlg32250	2295	Atlg33055	2341	Atlg33790
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2205	Atlg31660	2251	Atlg32290	2297	Atlg33080	2343	Atlg33810
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2214	Atlg31800	2260	Atlg32400	2306	Atlg33220	2352	Atlg34010
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2219	Atlg31850	2265	Atlg32460	2311	Atlg33265	2357	Atlg34110
2220	Atlg31860	2266	Atlg32470	2312	Atlg33270	2358	Atlg34130
2221	Atlg31870	2267	Atlg32500	2313	Atlg33280	2359	Atlg34160
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2223	Atlg31885	2269	Atlg32540	2315	Atlg33330	2361	Atlg34190
2224	Atlg31910	2270	Atlg32550	2316	Atlg33340	2362	Atlg34200
2225	Atlg31920	2271	Atlg32560	2317	Atlg33350	2363	Atlg34210
2226	Atlg31930	2272	Atlg32570	2318	Atlg33360	2364	Atlg34220
2227	Atlg31940	2273	Atlg32580	2319	Atlg33410	2365	Atlg34245
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2237	Atlg32090	2283	Atlg32780	2329	Atlg33590	2375	Atlg34360
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3143	Atlg54990	3189	Atlg55580	3235	Atlg56210	3281	Atlg57760
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3146	Atlg55020	3192	Atlg55620	3238	Atlg56240	3284	Atlg57820
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3154	Atlg55160	3200	Atlg55730	3246	Atlg56345	3292	Atlg58032
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