A Maize Map Standard With Sequenced Core Markers, Grass Genome Reference Points and 932 Expressed Sequence Tagged Sites (ESTs) in a 1736-Locus Map

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ABSTRACT

We have constructed a 1736-locus maize genome map containing1156 loci probed by cDNAs, 545 probed by random genomic clones, 16 by simple sequence repeats (SSRs), 14 by isozymes, and 5 by anonymous clones. Sequence information is available for 56% of the loci with 66% of the sequenced loci assigned functions. A total of 596 new ESTs were mapped from a B73 library of 5-wk-old shoots. The map contains 237 loci probed by barley, oat, wheat, rice, or tripsacum clones, which serve as grass genome reference points in comparisons between maize and other grass maps. Ninety core markers selected for low copy number, high polymorphism, and even spacing along the chromosome delineate the 100 bins on the map. The average bin size is 17 cM. Use of bin assignments enables comparison among different maize mapping populations and experiments including those involving cytogenetic stocks, mutants, or quantitative trait loci. Integration of nonmaize markers in the map extends the resources available for gene discovery beyond the boundaries of maize mapping information into the expanse of map, sequence, and phenotype information from other grass species. This map provides a foundation for numerous basic and applied investigations including studies of gene organization, gene and genome evolution, targeted cloning, and dissection of complex traits.

MAIZE research has had a long tradition in the area of gene mapping. The first published genetic map compiled by Emerson *et al.* (1935) contained 62 loci based on morphological variants. Refinement of this map progressed on the basis of accumulated recombination data for the next 60 years. A cytological map based on B-A translocations (Roman and Ullstrup 1951) and phenotypic markers is also available (Beckett 1991). The use of B-A and reciprocal A-A translocations permitted the physical map to be oriented and aligned with the genetic map. The first molecular-marker maize map was published by Helentjaris *et al.* (1986). It contained 116 loci and used cDNA and random genomic clones as probes. Maps based on publicly available maize restriction fragment length polymorphism (RFLP) probes were presented by Coe *et al.* (1987) and Burr *et al.* (1988) using random genomic clones on an F_2 population and on a set of recombinant inbred lines, respectively. Gardiner *et al.* (1993) published an updated version of the earlier F_2 map on the basis of an immortalized version of the same F_2 population. It contained 214 loci and the first group of "core" markers. Weber and Helentjaris (1989) used RFLP analysis of progeny from crosses of B-A translocation lines with inbreds to link the cytological map information with the molecular map. Beavis *et al.* (1992) developed a mapping population based on random mating that provided improved resolution compared to F_2 or recombinant inbred populations of similar size. More recently, a composite map based on four mapping populations, containing 275 loci representing both expressed sequence tagged sites (ESTs) and anonymous sequences was published (Causse *et al.* 1996). A number of other groups have produced RFLP maps in maize, most with the intent of mapping quantitative traits relative to the molecular markers (Beavis and Grant 1991; Edwards *et al.* 1992; Pe *et al.* 1993; Ajmone-Marsan *et al.* 1994; Damerval *et al.* 1994; Frova and Sari-Gorla 1994; Quarrie *et al.* 1994; Sari-Gorla *et al.* 1994; Veldboom and Lee 1994; Veldboom *et al.* 1994; Causse *et al.* 1995;

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Lebreton *et al.* 1995; Agrama and Moussa 1996; Austin and Lee 1996a,b; Bohn *et al.* 1996; Byrne *et al.* 1996; Lubberstedt *et al.* 1997). PCR-based DNA markers composed of tandemly repeated short di- or trinucleotide repeats known as simple sequence repeat (SSR) markers have also been utilized to map genes in maize (Senior and Heun 1993; Taramino and Tingey 1996). These markers are more amenable to high-throughput mapping but are not yet available in sufficient number to provide even coverage of the maize genome.

We present here a linkage map containing a large number of ESTs and sequence-tagged sites (STSs), a set of 90 core markers, and 237 loci probed by clones from other grass species. These three features allow the information from this map to be combined with other maize and grass species map data to facilitate a variety of gene discovery experiments.

MATERIALS AND METHODS

Laboratory procedures: DNA was prepared using the mixed alkyltrimethyl-ammonium bromide (CTAB) extraction method (Saghai-Maroof *et al.* 1984) from 54 immortalized F_2 individuals from a cross of Tx303 × CO159, the inbred parents and their F_1 hybrid (Gardiner *et al.* 1993). Restriction digestions were performed using *Eco*RI, *Hin*dIII, *Eco*RV, *Bam*HI, *Dra*I, *Xba*I, *Bgl*II, or *Sst*I. DNA was electrophoresed in 0.8% agarose gels at 50 V for a distance of ~10 cm. Gels were denatured for 30 min in 0.4 n NaOH, 0.6 m NaCl followed by a 30-min neutralization in 0.5 m Tris, pH 7.5, 1.5 m NaCl. DNA was transferred to Magnacharge membrane using 25 mm $NaPO_4$, pH 6.5. Membranes were baked and cross-linked according to manufacturer recommendations (MSI, Westborough, MA).

Probes used in this study included cDNA and genomic clones from maize and other related grasses. They included *agr* maize clones (Mycogen Plant Sciences), *asg* maize clones (Asgrow Seed), *bnl* maize clones (Brookhaven National Laboratory), *csu* maize clones (Chris Baysdorfer, California State University-Hayward), *npi* maize clones (Native Plants & Pioneer Hi-Bred International), *php* maize clones (Pioneer Hi-Bred International), *uaz* maize clones (Tim Helentjaris, University of Arizona), *umc* maize clones (University of Missouri-Columbia), *rgp* rice clones (Rice Genome Research Project, Tsukuba, Japan), *bcd* barley clones (Susan McCouch, Cornell University), *cdo* oat clones (Susan McCouch, Cornell University), *rz* rice clones (Susan McCouch, Cornell University), *umn* oat clones (Ronald Phillips, University of Minnesota), *tda* tripsacum clones (Ann Blakey, Ball State University), and numerous genes from targeted cloning experiments supplied by individual investigators.

Membranes were prehybridized a minimum of 6 hr in a solution of 0.05 m Tris, pH 8.0, 0.01 m EDTA, pH 8.0, 5× SSC, 0.2% SDS, 1× Denhardt's solution, 0.1 mg/ml denatured salmon sperm DNA. All hybridizations were carried out using [α-^{32}P]dCTP oligo-labeled probes at 65° overnight in a hybridization solution containing the above ingredients plus 10% dextran sulfate. Washing protocol was as follows: three 5-min room temperature washes in 2× SSC, 0.5% SDS, one 20-min room temperature wash in 0.1× SSC, 0.1% SDS, and two 30-min 65° washes in 0.1× SSC, 0.1% SDS. Membranes were patted dry with toweling, placed in plastic sheet protectors, and exposed to Kodak X-OMAT film in the presence of a CRONEX-type intensifying screen for 1 to 7 days at −80° depending on the counts per minute as determined with a Ludlum-III monitor (Sweetwater, TX).

The enzyme with the best fragment separation between the two parental lines, CO159 and Tx303, was chosen for mapping. In some cases, for multiple copy probes, more than one enzyme was used to map additional loci.

The polymerase chain reaction (PCR) conditions and cycling profiles for SSR analysis were based on the protocol established by M. Lynn Senior (personal communication) but included slight modifications, mainly to accommodate the specific polymerase used for the experiment. Final concentrations of reaction components were as follows: Perkin-Elmer Buffer, 1×; $MgCl_2$, 2.5 mm; dATP, dCTP, dGTP, dTTP, 0.1 mm each, SSR primers-forward and reverse, 50 ng each (Research Genetics, Huntsville, AL); AmpliTaq Gold polymerase, 0.3 units (Perkin-Elmer, Norwalk, CT); genomic DNA, 50 ng; sterile water to a total volume of 15 μl.

All thermocycling was performed in a 96-well thin-walled microtiter-style plate [Costar (Cambridge, MA) 6509] with an oil overlay in an Amplitron II thermocycler (Barnstead/Thermolyne, Dubuque, IA). The cycling profile included a preliminary 8- to 10-min dwell at 95° to activate the polymerase. This was followed by two cycles of 1 min at 95°, 1 min at 65°, and 90 sec at 72°. Subsequently, single cycles of a 1° decrement for the annealing temperature were done until an annealing temperature of 55° was achieved. The final phase of amplification included 29 additional cycles at the 55° annealing temperature. Following amplification, PCR products were resolved in a 3.5% Super Fine Resolution agarose (Amresco Inc., Solon, OH), 1× TBE gel containing ~2 μg/ml ethidium bromide.

Data collection and map construction: All autoradiograms were scored independently by two readers. SSR gel images were captured with a CCD camera system (Stratagene, La Jolla, CA) and genotypes were recorded from either computer monitor images or thermal prints. Markers with missing data for three or more individuals were typically discarded.

Linkage groups were constructed using MAPMAKER for UNIX, version 3 (Whitehead Institute, Cambridge, MA) on a Sun SPARC Server 1000 (Sun Systems, Palo Alto, CA). The 10 maize linkage groups were defined with the "make chromosomes" function and the 90 core markers were anchored to linkage groups. Initial framework orders were assigned for the core markers for each linkage group on the basis of previous map constructions at LOD 5 for chromosomes 1 and 3–10 and LOD 4 for chromosome 2 (Coe *et al.* 1995). The remaining markers were attached to linkage groups with the "assign" command. Additional markers were three-point ordered into the framework, first at LOD 3 and then at LOD 2, 10–15 markers at a time with the "build" command. Remaining markers assigned to each linkage group were positioned relative to the framework loci with the "place" command. Loci with unique positions were inserted into the framework while those lacking sufficient recombination events to provide three-point order were positioned on the basis of two-point analysis. The "together" command was used to further resolve the position of the "placed" loci in the framework. The remaining markers were then positioned against the new framework with the "place" command. Marker loci with more than three double crossovers based on the "genotype" function were deleted. Three-point local ordering was assessed using the ripple command in 5-marker intervals with a threshold LOD of 3.0. Significantly better alternate orders were identified for two intervals tested. Ten additional regions were identified where alternate orders were available at LOD 3.0. For these 10 regions, numbers of single and double crossovers for each alternate order were assessed. In 6 of the 10 cases, double crossovers were minimized by one of the alternate orders and map orders

were set to reflect the order that minimized double crossovers. In the 4 remaining cases, two three-point orders were equally likely. These regions are *asg29b-csu2a-csu850-umc8g vs. asg29b-umc8g-csu850-csu2a* (bin 2.05), *csu587b-csu26a-umc108-asg84b vs. csu587b-umc108-csu26a-asg84b* (bin 5.07), *csu835-csu481-csu360-csu116a vs. csu835-csu360-csu481-csu116a* (bin 6.02), and *umc238a-idh2-csu291-mdh2 vs. umc238a-csu291-idh2-mdh2* (bin 6.07). Chromosome maps were drawn to postscript files, exported, translated to Macintosh format, and edited with Adobe Illustrator 6.0.1 (Adobe Systems, Mountainview, CA).

The core marker set: Markers that had simple fragment patterns and were distributed along the chromosome approximately every 20 cM were selected as potential core markers. Markers not among the previous core set identified by Gardiner *et al.* (1993) were screened against inbreds A619, A632, B73, Mo17, CO159, and Tx303 using *Eco*RI, *Hin*dIII, *Eco*RV, *Bam*HI, *Dra*I, *Xba*I, *Bgl*II, and *Sst*I restriction endonucleases to determine whether they were polymorphic enough to be designated as core markers. A marker was deemed to be acceptable if it was polymorphic with a minimum of three of the eight enzymes with the majority of inbred lines. Subsequently, all the previous core markers were screened in the same manner. Final choices were made on the basis of even-spacing, simple-fragment patterns, high degree of polymorphism, and public availability. Markers meeting these criteria that had insert sizes <1000 bp were given preference to facilitate more complete single-pass sequencing of the clones.

The *csu* clones: Sequencing of *csu* clones through number 173 was reported previously (Keith *et al.* 1993). The 5′-ends of clones *csu174* through *csu1196* were dideoxy-sequenced according to the protocol of Keith *et al.* (1993). These clones were selected from a B73 library of 5-wk-old shoots. Sixty-six clones that were duplicates of other *csu* clones in this group on the basis of sequence comparisons among group members were removed from the clone set prior to screening and mapping. DNA sequence data were submitted to GenBank for all nonduplicate clones.

Core marker sequencing: Core marker insert DNA maintained in plasmids was prepared for sequencing by the alkaline lysis method (Birnboim 1983). DNA quality was determined using a 0.8% agarose gel containing cut and uncut DNA. The quantity of DNA was determined using a spectrophotometer for samples with acceptable quality. Sequencing was performed one of two ways. In the first case, dideoxy-termination reactions labeled with [α-^{35}S]dCTP were performed according to manufacturer recommendations using the T7 Sequenase Kit (U.S. Biochem, Cleveland). Depending upon the vector the cloned RFLP was ligated into, M13 forward and reverse or T7 and SP6 primers were used to sequence the DNA. For each direction, 2 μg of dsDNA was annealed to the appropriate primer. Reactions were run on a 6% polyacrylamide gel for 2 hr for short runs to read sequence close to the primer or 6 hr for long runs. Gels were fixed in 10% acetic acid/5% methanol and thoroughly dried under vacuum. Dried gels were exposed to Kodak X-OMAT AR film for 1 to 2 days. Sequence data were double checked. In the second case, sequencing was done by PCR incorporation of fluorescently labeled bases followed by data generation on the ABI 373 sequencing machine (PE Applied Biosystems, Foster City, CA).

Homology searching: Sequence similarity data were provided by individual investigators with each cDNA or genomic clone from targeted cloning experiments submitted for mapping at the Maize RFLP Laboratory. Following map construction and refinement, all noncore sequences that were not received from targeted cloning experiments were analyzed for homology using the NCBI blast server or the dbEST neighbors algorithm (www.ncbi.nlm.nih.gov/BLAST; Altschul *et al.* 1990; http://www.ncbi.nlm.nih.gov/irx/dbST/dbest_query.html; http://www.ncbi.nlm.nih.gov/Entrez/entrezhelp.html#Special; Boguski *et al.* 1993). Following BLASTX searching, sequences with *P* values of $<10^{-8}$ against the EST database, 10^{-10} against the nonredundant nucleotide or nonredundant peptide databases, or 10^{-10} using the neighbors algorithm were assigned putative functions. Mnemonics were derived for the loci associated with those clones that were consistent with the maize nomenclature guidelines (www.agron.missouri.edu/maize_nomenclature.html) and using plantwide nomenclature (http://jiio6.jic.bbsrc.ac.uk) whenever possible. In assignments both strands of genomic sequences were considered, while only the positive strand of directionally cloned cDNAs was considered. At the time the comparisons were conducted, the nonredundant nucleotide database did not include EST or STS sequences but did include GenBank, DDBJ, EMBL, and Protein Data Bank (PDB) sequences; the nonredundant peptide database included translations of the GenBank coding sequences and sequences in SwissProt, PDB, and Protein Information Resource (PIR).

Core marker sequences were analyzed using the e-mail version of BLAST1.4.11 (Altschul *et al.* 1990; blast@ncbi.nlm.nih.gov). Homology searches against the NCBI nr and dbEST databases were made using, respectively, the BLASTX and TBLASTX algorithms. Identity was declared at $P(N) < 10^{-6}$. In some cases, although a gene name is given, it was clear that the reported match is only to a motif, not to the entire gene.

RESULTS

EST Map: A map containing 1736 loci was produced (Figure 1). This represents an increase of 1427 loci over the previously published map (Chao *et al.* 1994). The total maize map length was 1727.4 cM, with one crossover equal to 0.9 cM. Chromosome 1 had the longest map distance at 245.2 cM and chromosome 10, the shortest at 138.6 cM (Table 1). In general, chromosome length as measured genetically decreased with decreasing physical length from chromosome 1 through 10. Chromosome 7 was a noticeable exception to this trend. The largest remaining gap (22.8 cM) in the maize map occurs in the telomere region of chromosome 7. Eleven other gaps of >10 cM occur in telomeric regions. Twelve additional gaps of >10 cM occur throughout the internal regions of the chromosomes.

Of the 1736 loci, 1156 (67%) were probed by cDNAs, 545 (31%) were probed by genomic clones, 14 (1%) corresponded to isozymes, 16 (1%) were mapped using SSRs, and 5 represented anonymous clones. Of the probes screened 19% were single copy, 58% medium copy (2–5 copies), and 23% high copy number (>5 copies). A total of 590 new ESTs from the *csu* clone set were mapped. The total number of loci per chromosome decreased from longest to shortest chromosome with the exception of chromosomes 2, 6, and 7, which had fewer markers than expected (Table 1).

Sequence homology: Table 2 lists the loci for which sequence homology has been determined, the database entry they matched, and maize bin location. GenBank numbers are provided for *csu* clones sequenced and mapped as part of this study. The data indicate that 637 (36.7%) of all loci corresponded to genes of known

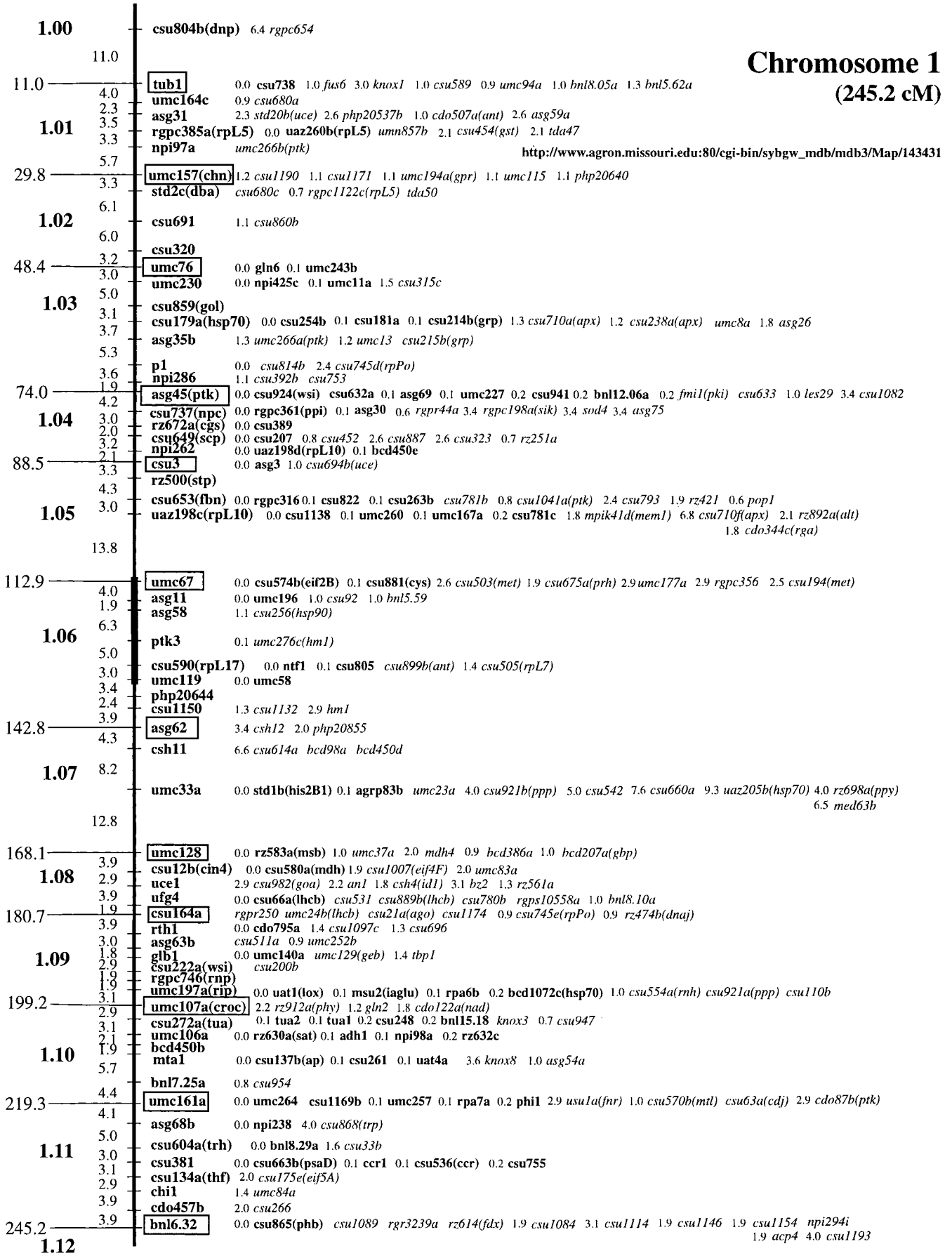

Chromosome 1
(245.2 cM)
http://www.agron.missouri.edu:80/cgi-bin/sybgw_mdb/mdb3/Map/143431
1.00
csu804b(dnp) 6.4 rgpc654
11.0
tub1 0.0 csu738 1.0 fus6 3.0 knox1 1.0 csu589 0.9 umc94a 1.0 bnl8.05a 1.3 bnl5.62a
4.0
umc164c 0.9 csu680a
2.3
asg31 2.3 std20b(uce) 2.6 php20537b 1.0 cdo507a(ant) 2.6 asg59a
1.01
3.5
rgpc385a(rpL5) 0.0 uaz260b(rpL5) umn857b 2.1 csu454(gst) 2.1 tda47
3.3
npi97a umc266b(ptk)
5.7
29.8
umc157(chn) 1.2 csu1190 1.1 csu1171 1.1 umc194a(gpr) 1.1 umc115 1.1 php20640
3.3
std2c(dba) csu680c 0.7 rgpc1122c(rpL5) tda50
6.1
1.02
csu691 1.1 csu860b
6.0
csu320
3.2
48.4
umc76 0.0 gln6 0.1 umc243b
3.0
umc230 0.0 npi425c 0.1 umc11a 1.5 csu315c
5.0
1.03
csu859(gol)
3.1
csu179a(hsp70) 0.0 csu254b 0.1 csu181a 0.1 csu214b(grp) 1.3 csu710a(apx) 1.2 csu238a(apx) umc8a 1.8 asg26
3.7
asg35b 1.3 umc266a(ptk) 1.2 umc13 csu215b(grp)
5.3
p1 0.0 csu814b 2.4 csu745d(rpPo)
3.6
npi286 1.1 csu392b csu753
1.9
74.0
asg45(ptk) 0.0 csu924(wsi) csu632a 0.1 asg69 0.1 umc227 0.2 csu941 0.2 bnl12.06a 0.2 fmi1(pki) csu633 1.0 les29 3.4 csu1082
4.2
csu737(npc) 0.0 rgpc361(ppi) 0.1 asg30 0.6 rgpr44a 3.4 rgpc198a(sik) 3.4 sod4 3.4 asg75
1.04
3.0
rz672a(cgs) 0.0 csu389
2.0
csu649(scp) 0.0 csu207 0.8 csu452 2.6 csu887 2.6 csu323 0.7 rz251a
3.2
npi262 0.0 uaz198d(rpL10) 0.1 bcd450e
2.1
88.5
csu3 0.0 asg3 1.0 csu694b(uce)
3.3
rz500(stp)
4.3
csu653(fbn) 0.0 rgpc316 0.1 csu822 0.1 csu263b csu781b 0.8 csu1041a(ptk) 2.4 csu793 1.9 rz421 0.6 pop1
1.05
3.0
uaz198c(rpL10) 0.0 csu1138 0.1 umc260 0.1 umc167a 0.2 csu781c 1.8 mpik41d(mem1) 6.8 csu710f(apx) 2.1 rz892a(alt) 1.8 cdo344c(rga)
13.8
112.9
umc67 0.0 csu574b(eif2B) 0.1 csu881(cys) 2.6 csu503(met) 1.9 csu675a(prh) 2.9 umc177a 2.9 rgpc356 2.5 csu194(met)
4.0
asg11 0.0 umc196 1.0 csu92 1.0 bnl5.59
1.9
asg58 1.1 csu256(hsp90)
6.3
1.06
ptk3 0.1 umc276c(hm1)
5.0
csu590(rpL17) 0.0 ntf1 0.1 csu805 csu899b(ant) 1.4 csu505(rpL7)
3.0
umc119 0.0 umc58
3.4
php20644
2.4
csu1150 1.3 csu1132 2.9 hm1
3.9
142.8
asg62 3.4 csh12 2.0 php20855
4.3
csh11 6.6 csu614a bcd98a bcd450d
8.2
1.07
umc33a 0.0 std1b(his2B1) 0.1 agrp83b umc23a 4.0 csu921b(ppp) 5.0 csu542 7.6 csu660a 9.3 uaz205b(hsp70) 4.0 rz698a(ppy) 6.5 med63b
12.8
168.1
umc128 0.0 rz583a(msb) 1.0 umc37a 2.0 mdh4 0.9 bcd386a 1.0 bcd207a(gbp)
3.9
csu12b(cin4) 0.0 csu580a(mdh) 1.9 csu1007(eif4F) 2.0 umc83a
1.08
2.9
uce1 2.9 csu982(goa) 2.2 an1 1.8 csh4(id1) 3.1 bz2 1.3 rz561a
3.9
ufg4 0.0 csu66a(lhcb) csu531 csu889b(lhcb) csu780b rgps10558a 1.0 bnl8.10a
1.9
180.7
csu164a rgpr250 umc24b(lhcb) csu21a(ago) csu1174 0.9 csu745e(rpPo) 0.9 rz474b(dnaj)
3.9
rth1 0.0 cdo795a 1.4 csu1097c 1.3 csu696
3.0
asg63b csu511a 0.9 umc252b
1.8
glb1 0.0 umc140a umc129(geb) 1.4 tbp1
1.09
2.9
csu222a(wsi) csu200b
1.9
rgpc746(rnp)
1.9
umc197a(rip) 0.0 uat1(lox) 0.1 msu2(iaglu) 0.1 rpa6b 0.2 bcd1072c(hsp70) 1.0 csu554a(rnh) csu921a(ppp) csu110b
3.1
199.2
umc107a(croc) 2.2 rz912a(phy) 1.2 gln2 1.8 cdo122a(nad)
2.9
csu272a(tua) 0.1 tua2 0.1 tua1 0.2 csu248 0.2 bnl15.18 knox3 0.7 csu947
3.1
umc106a 0.0 rz630a(sat) 0.1 adh1 0.1 npi98a 0.2 rz632c
2.1
1.10
1.9
bcd450b
mta1 0.0 csu137b(ap) 0.1 csu261 0.1 uat4a 3.6 knox8 1.0 asg54a
5.7
bnl7.25a 0.8 csu954
4.4
219.3
umc161a 0.0 umc264 csu1169b 0.1 umc257 0.1 rpa7a 0.2 phi1 2.9 usu1a(fnr) 1.0 csu570b(mtl) csu63a(cdj) 2.9 cdo87b(ptk)
4.1
asg68b 0.0 npi238 4.0 csu868(trp)
5.0
1.11
csu604a(trh) 0.0 bnl8.29a 1.6 csu33b
3.0
csu381 0.0 csu663b(psaD) 0.1 ccr1 0.1 csu536(ccr) 0.2 csu755
3.1
csu134a(thf) 2.0 csu175e(eif5A)
2.9
chi1 1.4 umc84a
3.9
cdo457b 2.0 csu266
3.9
245.2
bnl6.32 0.0 csu865(phb) csu1089 rgr3239a rz614(fdx) 1.9 csu1084 3.1 csu1114 1.9 csu1146 1.9 csu1154 npi294i 1.9 acp4 4.0 csu1193
1.12

Figure 1.

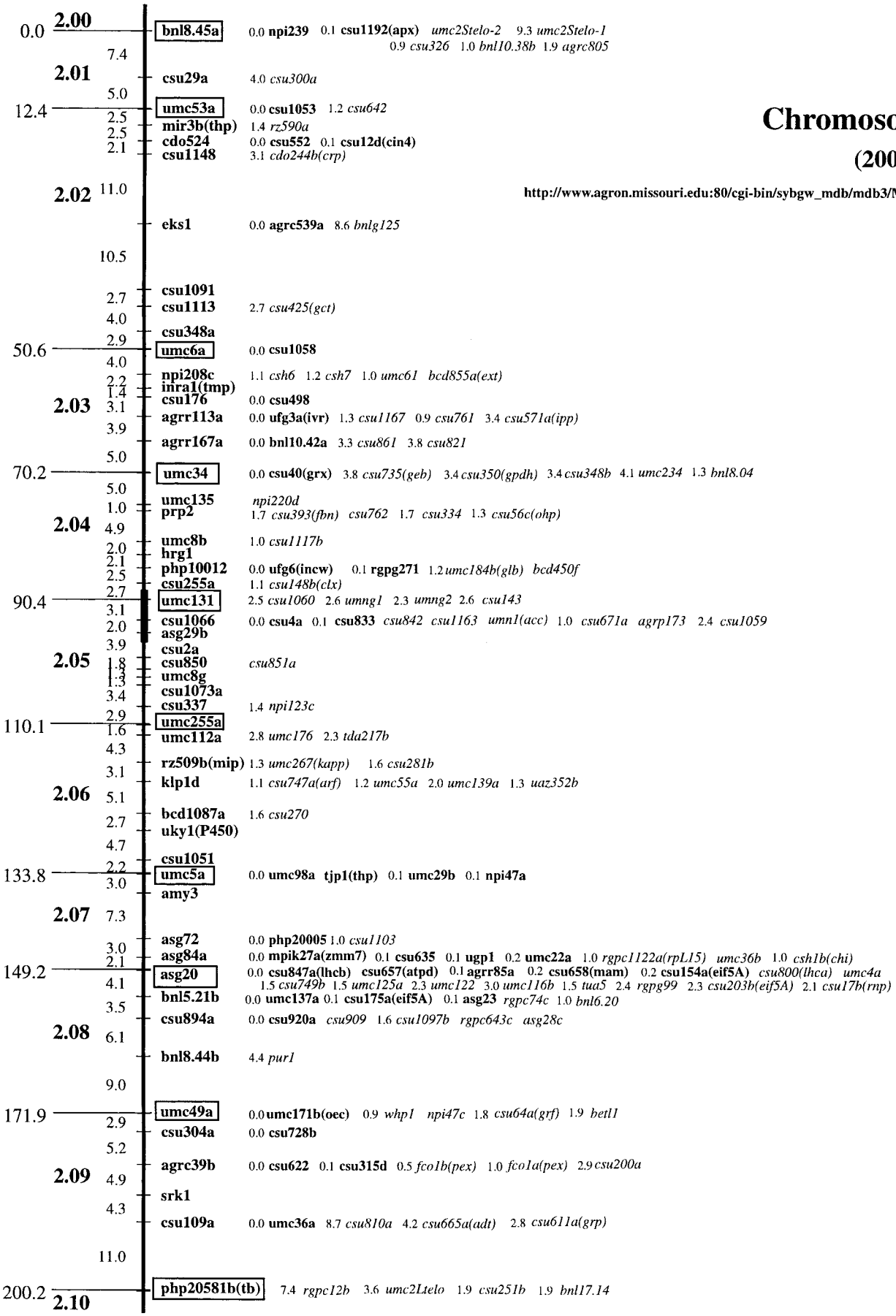


Figure 1.—*Continued.*

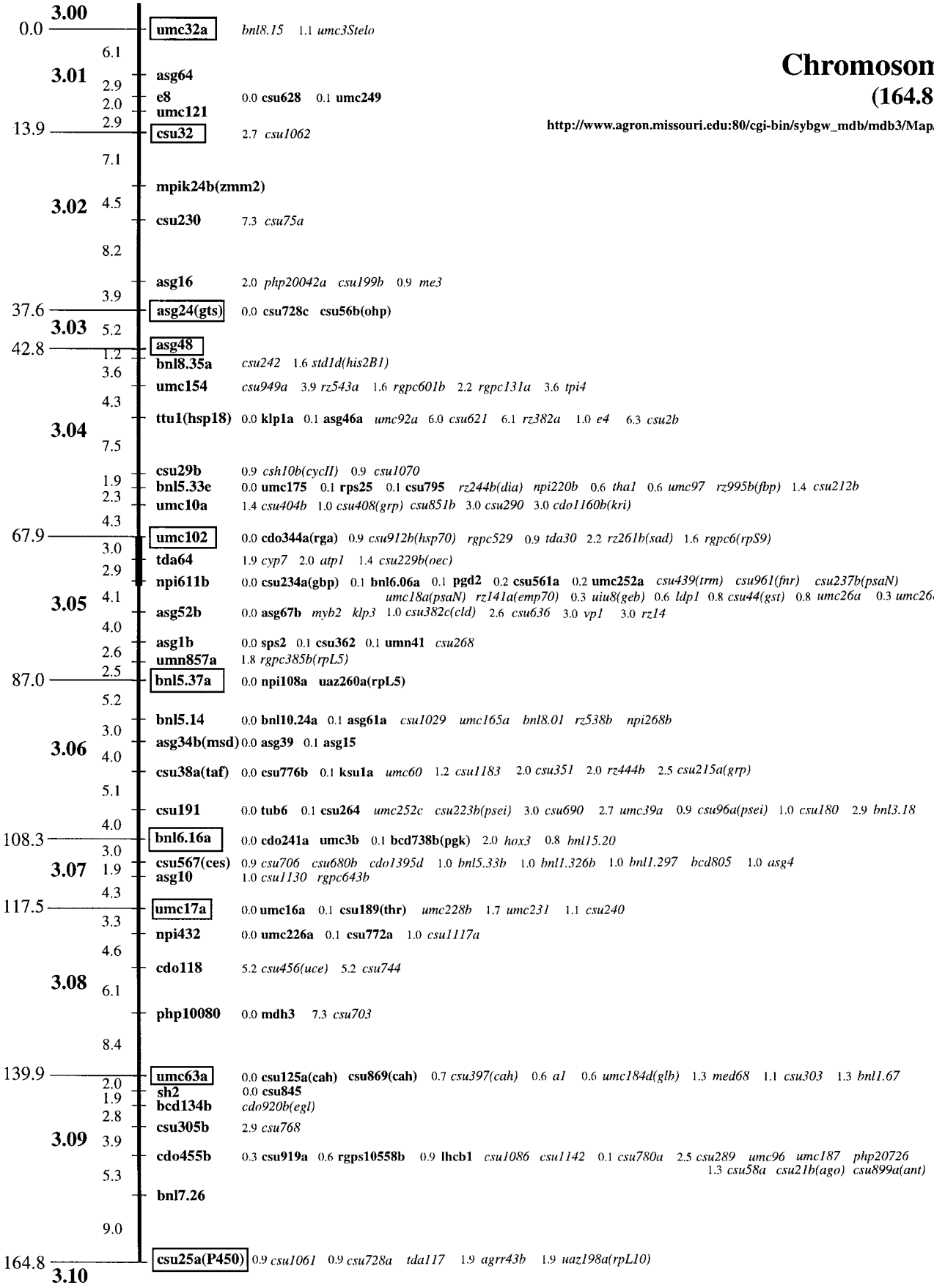
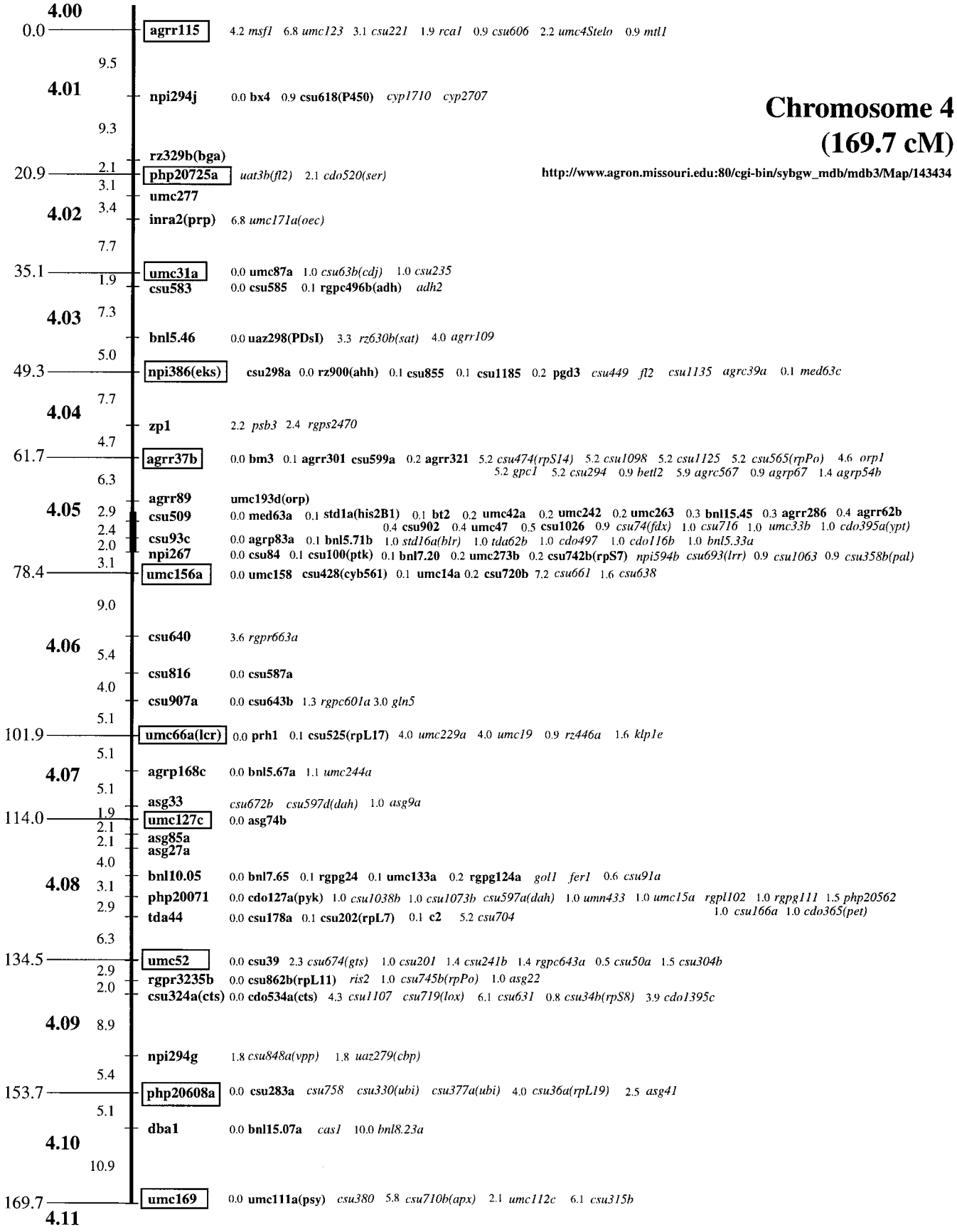


Figure 1.—*Continued.*



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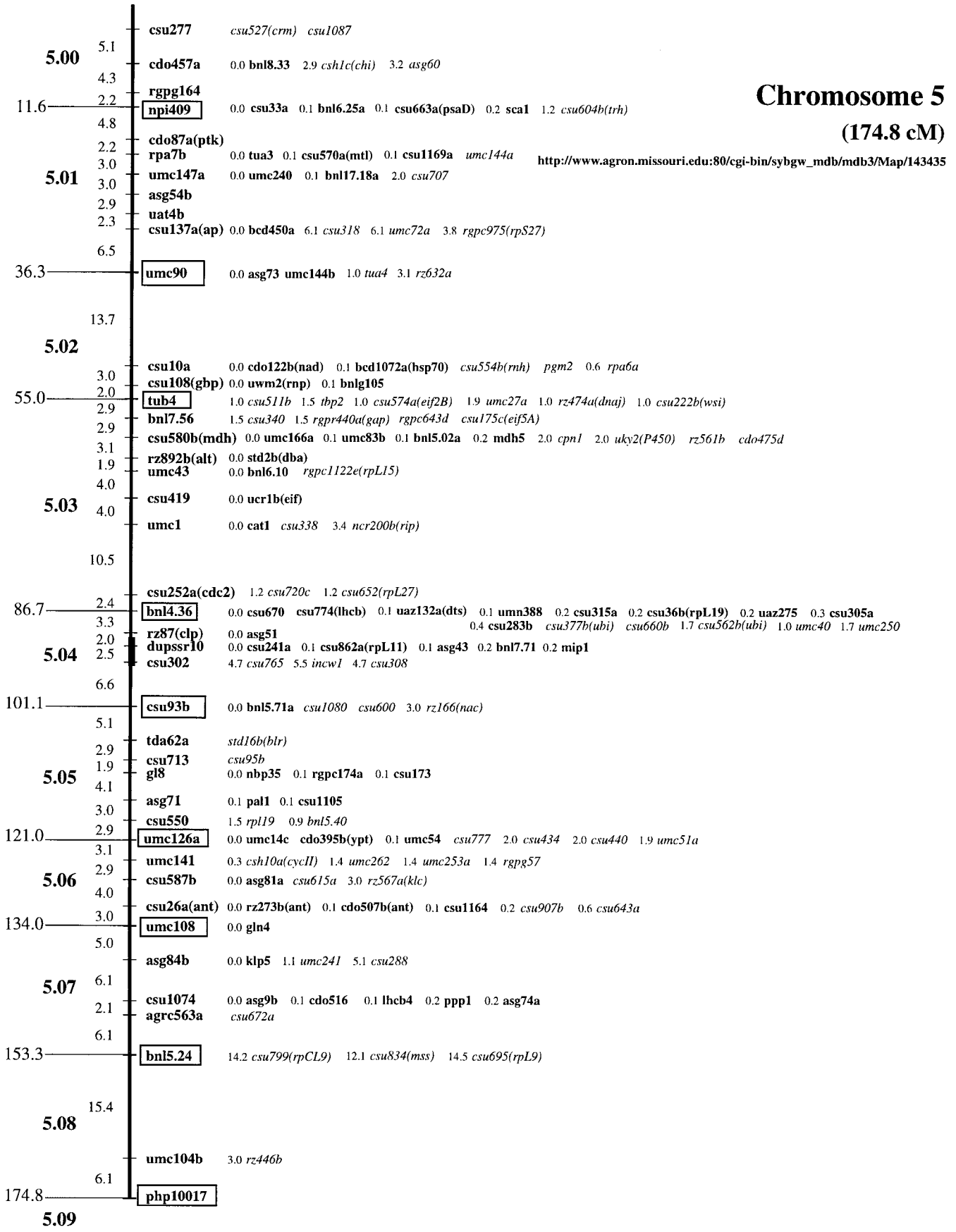

Figure 1.—*Continued.*

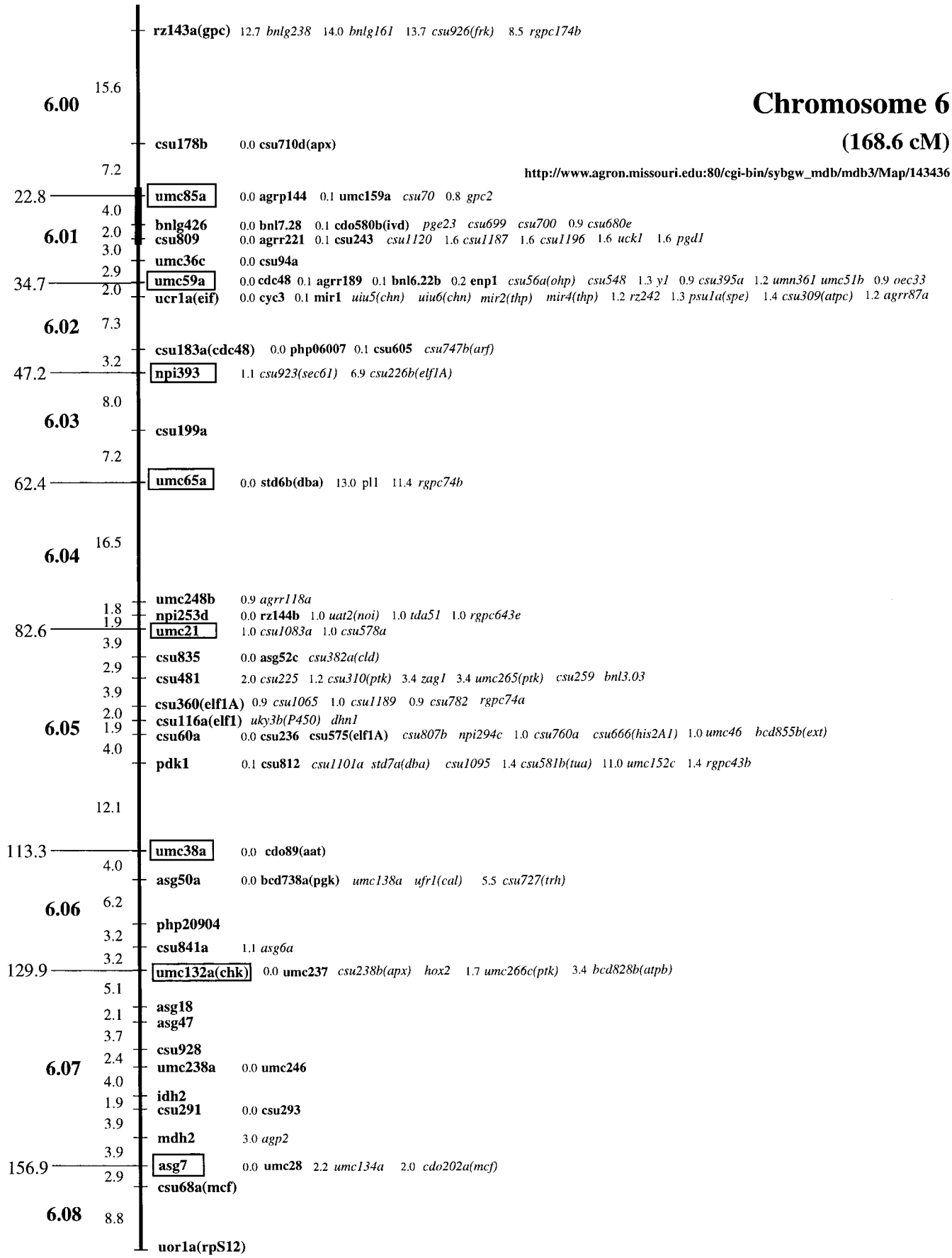

Figure 1.—*Continued.*

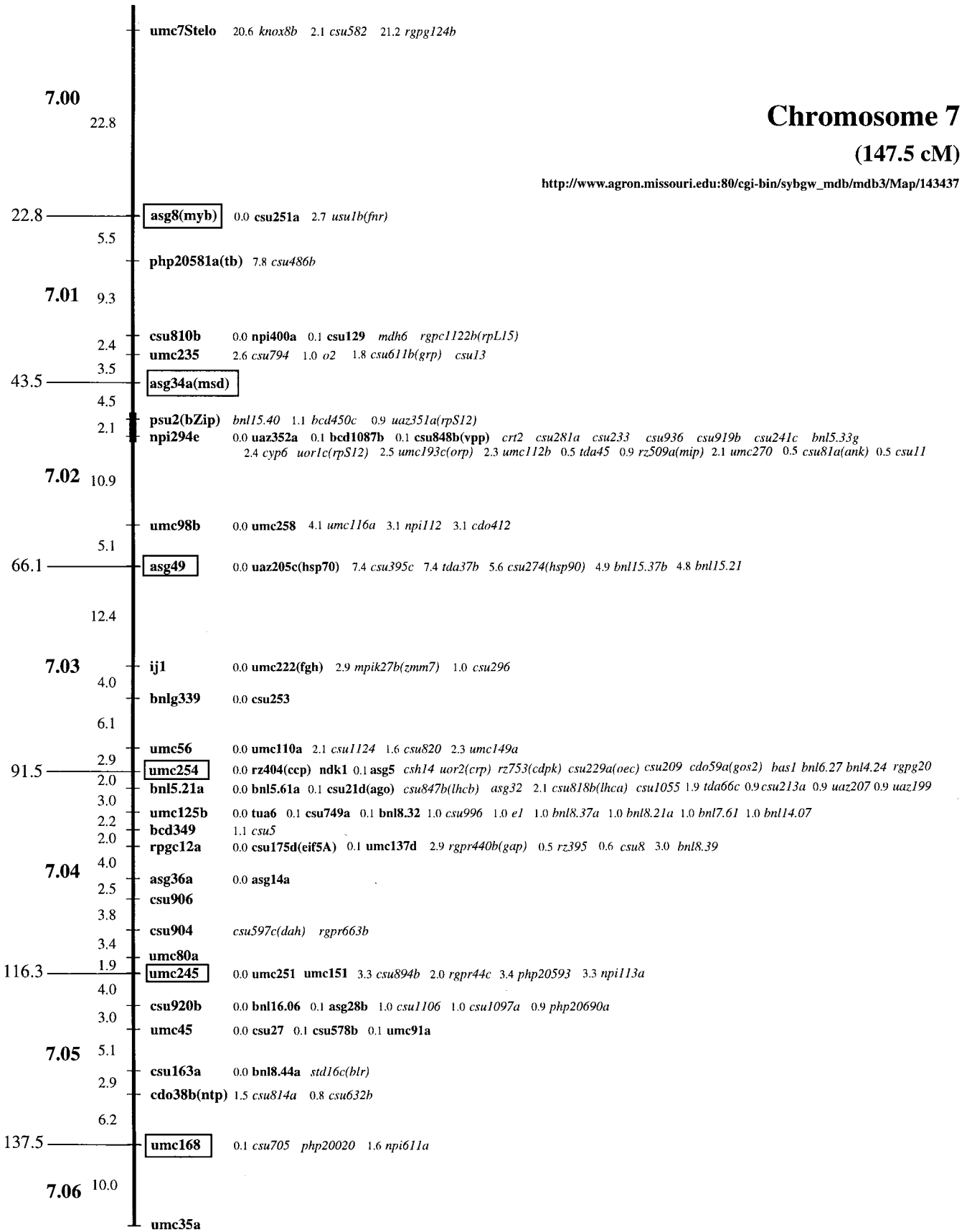

Figure 1.—*Continued.*

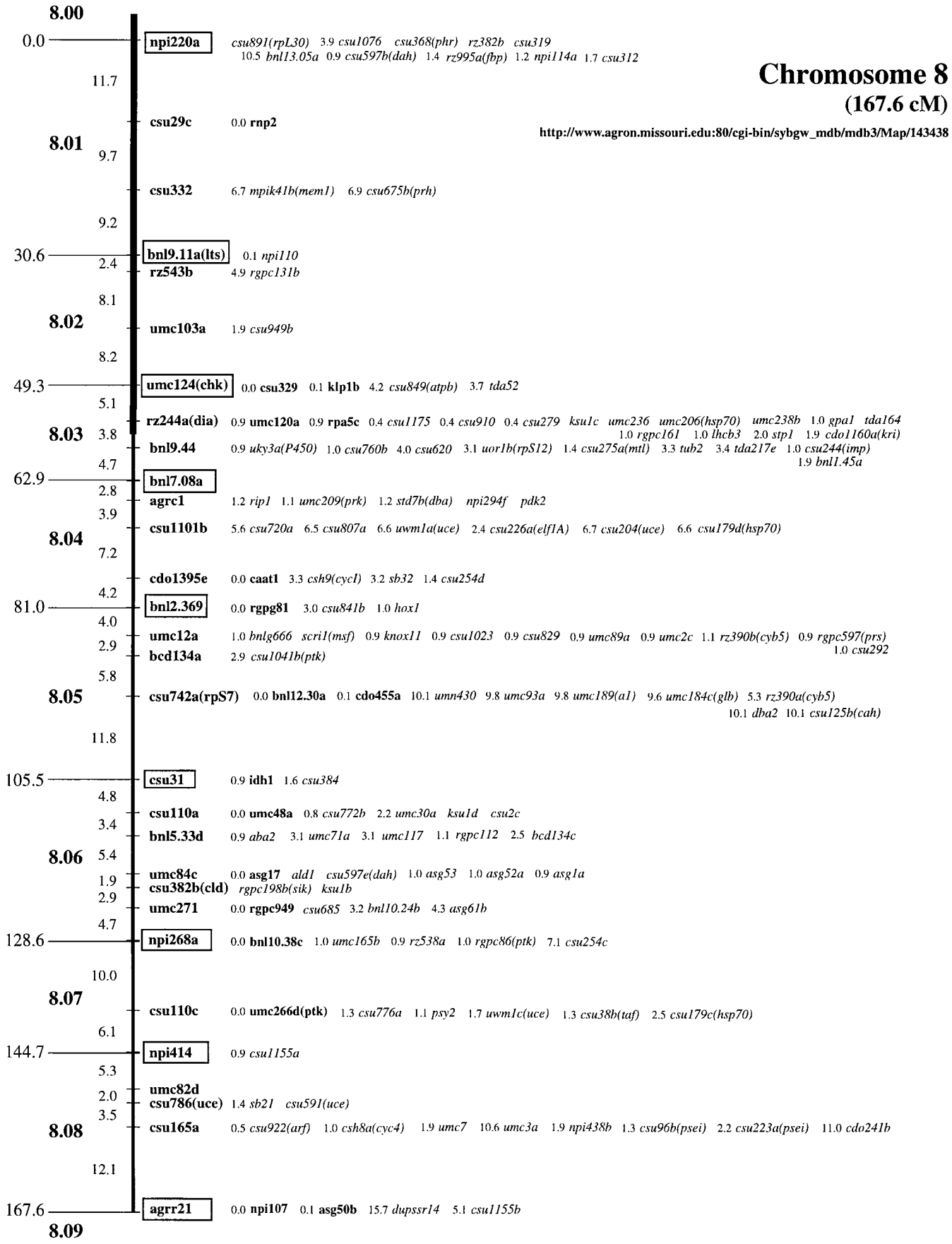

Figure 1.—*Continued.*

Figure 1.—*Continued.*

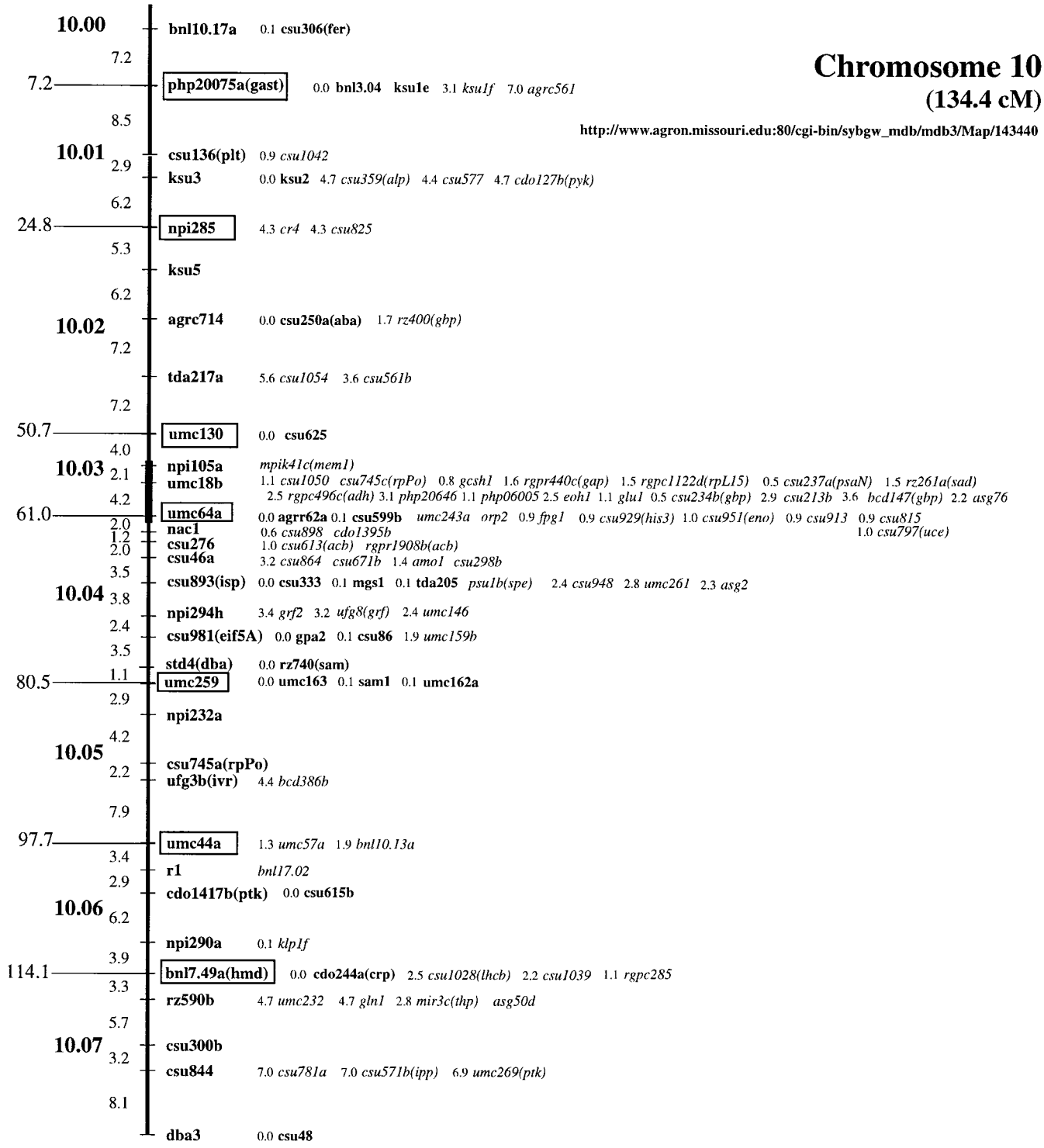

Figure 1.—UMC EST map of *Zea mays* L. The map was constructed using 54 immortalized F_2 individuals derived from Tx303 × CO159. Markers are listed to the right of the map line. Large numbers (chromosome number, bin number, *i.e.*, 1.01) to the left of the chromosome indicate the chromosome bins. Core marker loci are shown in boxes immediately to the right of each hash line on the chromosome and represent the first marker in the bin below. Interval support for these markers is LOD 5 for all but chromosome 2, which is LOD 4. Numbers to the left of the hash line are coordinates. Small numbers immediately to the left of the chromosome indicate centimorgan distances between the markers using Haldane's correction. Loci in bold are set to the framework and order assured at LOD 2.0. Italics indicates loci that are placed by two-point association to the boldfaced loci on the same line; order for these loci is uncertain but placement can be considered to be at or below the framework mark at which they are shown, on the basis of tests using alternative orders of frameworked markers. Estimated centromere locations are represented by a wider line, on the basis of composite judgment of mapping data for genes and molecular markers, as well as B-A translocations and other cytogenetic information contained in MaizeDB (http://www.agron.missouri.edu). Acronyms for loci probed by nonmaize clones are indicated as follows: *bcd* (barley), *cdo* (oat), *rgp* (rice), *rz* (rice), *tda* (tripsacum), and *umn* (oat). URLs for tabular versions of each linkage group are provided below the total centimorgan values.

TABLE 1

Distribution of sequenced, known-function, and unknown-function loci by chromosome (chromosome lengths in centimorgans were derived using Haldane's correction)

Chromosome	No. of known function loci	No. of loci without known function[a]	Total number of loci	Chromosome length (cM)	Loci that are identified genes (%)	Loci with sequence (%)
1	118	154	272	245.2	43.4	61.4
2	52	130	182	200.2	28.6	48.5
3	63	138	201	164.8	31.3	53.7
4	70	130	200	169.7	35.0	51.0
5	67	103	170	174.8	39.4	52.9
6	63	77	140	168.6	45.0	59.3
7	41	105	146	147.5	28.1	50.0
8	63	98	161	167.6	39.1	56.5
9	49	94	143	150.4	34.3	58.7
10	52	69	121	138.6	43.0	62.1
All	638	1098	1736	1727.4	36.8	55.4

[a] Loci without function include those with sequence but no known function and those with no sequence information.

function. Of the loci on the map 56% (962) have sequence information available. The designated genes and loci with sequence information are fairly evenly distributed among the chromosomes (Table 1). Of the loci with sequence information, 66% have been assigned putative functions with only 34% having no known function at this time. Nucleotide matches were identified to regulatory factors as well as structural genes and included such diverse processes as membrane transport, signal transduction, cell cycle regulation, carbon metabolism, floral development, stress response, DNA synthesis, and fatty acid metabolism.

Of the loci corresponding to previously unpublished *csu* sequences 41% (242) had homology to known genes. Among the new *csu* clones, 41 were single copy and were given gene designations. Several of the new *csu* sequences corresponded to isozymes previously mapped using protein gels: p-csu262, corresponding to *pgd1* and *pgd2*, which encodes 6-phosphogluconate dehydrogenase; p-csu892, encoding ADP-glucose pyrophosphorylase (*agp2*); p-csu249, encoding malate dehydrogenase (*mdh5*); p-csu182, encoding superoxide dismutase (*sod4*); and p-csu301, encoding triose phosphate isomerase (*tpi4*). No recombinants were detected between the isozyme and cDNA mapscores for *pgd1* in this population. *pgd2*, *mdh5*, and *tpi4* were previously mapped as isozymes on the Brookhaven National Laboratory (BNL) map. Common flanking markers between the two maps were used to confirm the common positions of the isozymes and cDNAs. Relative map positions of isozymes and cDNAs were determined for *agp2* and *sod4* on the basis of alignment of this map with the classical genetic map using common RFLP and isozyme markers as a bridge.

Core markers: Ninety core markers were identified that best met the selection criteria of low copy number, high rate of polymorphism, even spacing, and public availability. Core marker interval support was LOD 5 for all but maize chromosome 2, which had interval support of LOD 4. The lower LOD support for chromosome 2 is a reflection of the larger size of bin 2.02. Forty of the previous core markers were retained but several substitutions were made to the previous core marker set (Table 3). The core markers delineate 100 bins with the average bin size equaling 17 cM. Polymorphism information for the inbreds and enzymes screened is available in the Maize Genome Database (MaizeDB, http://www.agron.missouri.edu). Core marker sets are available via the probe request hotlink in MaizeDB or by contacting the University of Missouri–Columbia Maize RFLP Laboratory c/o Theresa Musket.

Sequence data were obtained for 84 of the core markers. Table 3 contains the sequence similarity information and GenBank numbers for the core markers. Homology to genes of known function was identified for 14 of the core markers by BLASTX searching of the nonredundant database. Matches to functionally uncharacterized ESTs or unknown proteins were identified for 7 additional core markers. Functionality of four of the clones had been identified by targeted cloning experiments. Seventeen percent of the genomic cores and 11% of the cDNA cores derived by nontargeted cloning had matches to genes of known functions.

Grass genome reference points: The map contains 25 loci probed by barley clones, 56 by oat clones, 136 by rice clones, 19 by tripsacum clones, and 1 by a wheat clone, for a total of 237 loci probed by nonmaize clones. The majority of the clones are anchor markers from the Cornell grass maps or from the Japanese Rice Genome Project (RGP) map. There are 221 loci probed by maize or rice clones shared between this map and the RGP rice map (Harushima *et al.* 1998).

TABLE 2

Bin assignments, gene functions, accession numbers, and organism matches for loci mapped on Tx303 × CO159 Immortalized F_2 population

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
1,3-β-Glucan	csu735	AA143913	*csu735(geb)*	2.03–2.04	−13	*Arabidopsis thaliana*
1,4-α-Glucan branching enzyme	p1-3sbe10		*psu1a(spe), psu1b(spe)*	6.02, 10.04		
24-kD zein	pcc518		*fl2, uat3b(fl2)*	4.04, 4.02		
26S proteasome ATPase	csu834	W21752	*csu834(mss)*	5.07–5.08	−46	*Spinacia oleracea*
26S proteasome regulatory subunit S12	rgp c597		*rgpc597(prs)*	8.05	−31	*Arabidopsis thaliana*
3-Deoxy *d*-arabino-heptulosonate 7-phosphate synthase	csu597	AA661448	*csu597a(dah), csu597b(dah), csu597c(dah), csu597d(dah), csu597e(dah)*	4.08, 8.00–8.01, 7.04, 4.07, 8.06		
6-Phosphogluconate dehydrogenase	csu262	T18824	*pgd1, pgd2*	6.01, 3.05		*Medicago sativa*
6-phosphogluconate dehydrogenase	csu843	W21760	*pgd3*	4.03–4.04	−28	*Medicago sativa*
α-Amylase	AS-5		*amy3*	2.07		
α-Tubulin	csu272	T18832	*csu272a(tua), tua4*	1.10, 5.01–5.02	−48	*Zea mays*
α-Tubulin	csu399	W49910	*csu399a(tua), tua4*	1.10, 5.01–5.02	−29	*Picea abies*
α-Tubulin	csu581	AA051892	*tua6, csu581b (tua)*	7.04, 6.05	−29	*Plasmodium falciparum*
α-Tubulin	csu662	AA072439	*tua4*	5.01–5.02	−50	*Pisum sativum*
α-Tubulin	tua1		*tua1*	1.10		
α-Tubulin	tua2		*tua2*	1.10		
α-Tubulin	tua3		*tua3*	5.01		
α-Tubulin	tua4		*tua4*	5.01–5.02		
α-Tubulin	tua5		*tua5*	2.07–2.08		
α-Tubulin	tua6		*tua6*	7.04		
ABA-ripening-inducible protein	csu725	AA661453	*aba2*	8.06	−25	*Oryza sativa*
Acetyl-CoA carboxylase	22J		*umn1(acc)*	2.05		
Acid phosphatase	Isozyme		*acp1**	9.03		
Acid phosphatase	Isozyme		*acp4**	1.11–1.12		
Acyl-CoA binding protein	rgp r1908		*rgpr1908a(acb), rgpr1908b(acb)*	9.02–9.03, 10.04	−38	*Ricinus communis*
Acyl-CoA binding protein	csu613	AA054794	*csu613(acb)*	10.04	−29	*Ricinus communis*
ADP-glucose pyrophos-phorylase	csu897	W21619	*agp2*	6.07	−16	*Triticum aestivum*
ADP-glucose pyrophos-phorylase, endosperm-60-kD subunit	sh2850		*sh2*	3.09		
ADP-glucose pyrophos-phorylase, endosperm-55-kD subunit	bt2		*bt2*	4.05		
ADP-ribosylation factor	csu747	AA143922	*csu747a(arf), csu747b(arf)*	2.06, 6.02	−38	*Histoplasma capsulatum*
ADP-ribosylation factor	csu922	W21636	*csu922(arf)*	8.08	−56	*Oryza sativa*
Alanine aminotransferase	rz892		*rz892a(alt), rz892b(alt)*	1.05, 5.03	−17	*Panicum miliaceum*
Alcohol dehydrogenase	rgp c496		*adh1, rgpc496b(adh), rgpc496c(adh)*	1.10, 4.03, 10.03	−51	*Zea mays*
Alcohol dehydrogenase	umc200		*ald2*	4.03		
Aldehyde dehydrogenase	prf2a		*rf2*	9.03		
Aldolase	umc216		*ald1*	8.06		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Aluminum-induced protein	csu359	T27554	*csu359(alp)*	10.01	−16	*Triticum aestivum*
Ankyrin	csu81		*csu81a(ank)*	7.02	−12	*Arabidopsis thaliana*
Apetala	csu137 U:		*csu137a(ap), csu137b(ap)*	5.01, 1.10	−35	*Arabidopsis thaliana*
Apetala 2	H1100.43		*gl15*	9.03		
Argonaute protein	csu21		*csu21a(ago), csu21b(ago) csu21d(ago)*	1.09, 3.09, 7.04	−11	*Arabidopsis thaliana*
Ascorbate peroxidase	csu710	AA143901	*csu710a(apx), csu710b(apx), csu238b(apx), csu710d(apx), csu710e(apx), csu710f(apx)*	1.03, 4.10–4.11, 6.06–6.07, 6.00, 9.05, 1.05	−39	*Oryza sativa*
Ascorbate peroxidase	csu1192	W49455	*csu1192(apx)*	2.00–2.01	−40	*Brassica napus*
Ascorbate peroxidase	csu238	T26938	*csu238a(apx), csu238b(apx)*	1.03, 6.07	−25	*Oryza sativa*
Aspartyl-tRNA synthetase	5CO1B12		*uaz132a(dts)*	5.03–5.04	−41	*Rattus norvegicus*
ATP-dependent transporter	csu665	AA072441	*csu665a(adt), csu665b(adt)*	2.09, 9.01–9.02	−13	*Saccharomyces cerevisiae*
ATP synthase β-subunit	bcd828		*bcd828b(atpb)*	6.06–6.07	−32	*Triticum aestivum*
ATP synthase γ-subunit	csu309	W49894	*csu309(atpc)*	6.02	−16	*Pisum sativum*
ATP/ADP translocator	cdo507		*cdo507a(ant), cdo507b(ant)*	1.01, 5.06	−25	*Oryza sativa*
ATP/ADP translocator	csu26		*csu26a(ant)*	5.06	−27	*Zea mays*
ATP/ADP translocator	csu899	W21620	*csu899a(ant), csu899b(ant)*	3.09, 1.06	−59	*Zea mays*
ATP/ADP translocator	rz273		*rz273b(ant)*	5.06	−74	*Oryza sativa*
ATPase F1-subunit	csu849	W21766	*csu849(atpb)*	8.02–8.03	−58	*Actinidia deliciosa*
β-Alanine pyruvate aminotransferase	cdo89		*cdo89(aat)*	6.06	−34	*Rattus norvegicus*
β-Alanine synthase	cdo385		*bas1*	7.04	−12	*Caenorhabditis elegans*
β-Fructokinase	csu926	W21640	*csu926(frk)*	6.00	−15	*Beta vulgaris*
β-Galactosidase	rz329		*rz329b(bga)*	4.01	−21	*Asparagus officinalis*
β-Glucosidase	Isozyme		*glu1**	10.03		
β-Ketoacyl CoA reductase	gl8.08 cDNA		*gl8*	5.05		
β-Tubulin	tub1		*tub1*	1.01		
β-Tubulin	tub2		*tub2*	8.03		
β-Tubulin	tub4		*tub4*	5.03		
β-Tubulin	tub6		*tub6*	3.06		
Basal endosperm transferase protein	bet-1		*betl1*	2.08–2.09		
Basal endosperm transferase protein	bet2		*betl2*	4.04–4.05		
Blue light photoreceptor	pAS16		*std16a(blr), std16b(blr), std16c(blr)*	4.05, 5.05, 7.05		
bZip protein	mEMBP1		*psu2(bZip)*	7.02		
Caffeic *O*-methyl-transferase	mc1		*bm3*	4.05		
Calcium-dependent protein kinase	rz753		*rz753(cdpk)*	7.04	−69	*Oryza sativa*
Calmodulin	pZmCAL M1		*ufr1(cal)*	6.06		
Calmodulin-binding protein	5C04D02		*uaz279(cbp)*	4.09	−63	*Zea mays*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Calnexin	csu148		*csu148b(clx)*	2.04	−20	*Arabidopsis thaliana*
Calreticulin	csu1140	W49439	*crt2*	7.02	−70	*Zea mays*
CaMB-channel protein	rz404		*rz404(ccp)*	7.04	−23	*Nicotiana tabacum*
Cap-binding protein	csu1007U	W49482	*csu1007(eif4F)*	1.08	−37	*Oryza sativa*
Carbonic anhydrase	csu397	W49908	*csu397(cah)*	3.08–3.09	−8	*Zea mays*
Carbonic anhydrase	csu869	W21715	*csu869(cah)*	3.09	−28	*Zea mays*
Carbonic anhydrase	csu125		*csu125a(cah), csu125b(cah)*	3.09, 8.05	−46	Hordeum
Catalase isozyme B	rz508		*cat1*	5.03	−55	*Oryza sativa*
cDNA J homolog	csu63		*csu63a(cdj), csu63b(cdj)*	1.11, 4.02–4.03	−48	*Allium porrum*
Cell division protein 48	csu146		*cdc48*	6.02	−26	*Capsicum annuum*
Cell division protein 48	csu183	T18843	*csu183a(cdc48), csu183b(cdc48)*	6.02, 9.04	−23	*Synechocystis* sp.
Cell wall protein	rz574		*rz574b(cwp)*	9.05–9.06	−18	*Arabidopsis thaliana*
Cellulose synthase	csu567U	AA051881	*csu567(ces)*	3.07	−48	*Gossypium hirsutum*
Cf2.2 and Erecta	csu693	AA072468	*csu693(lrr)*	4.05	−9	*Cf2-Solanum pimpinellifolium, Erecta-Arabidopsis thaliana*
Chalcone isomerase	CHI		*chi1, csh1b(chi), csh1c(csh)*	1.11, 2.07, 5.00		
Chalcone synthase	umc198		*c2, whp1*	4.08, 2.08–2.09		
Choline kinase	umc124		*umc124(chk)*	8.03	−23	*Homo sapiens*
Choline kinase	umc132		*umc132a(chk)*	6.07	−12	*Oryza sativa*
Chitinase	pCh11		*uiu6(chn)*	6.02		
Chitinase	pCh2		*uiu5(chn)*	6.02		
Chitinase	umc157		*umc157(chn)*	1.02		
Chloroplast RNA processing	pCrp1-2		*uor2(crp)*	7.04		
Chromosome region maintenance protein	csu527	AA030709	*csu527(crm)*	5.00	−14	*Saccharomyces cerevisiae*
Cin4 retroelement	csu12		*csu12b(cin4), csu12d(cin4)*	1.08, 2.02		
Citrate synthase	cdo534		*cdo534a(cts)*	4.09	−61	*Populus* sp.
Citrate synthase	csu324	W49861	*csu324a(cts)*	4.09	−36	*Populus* sp.
Cold-induced protein	csu382	T27570	*csu382a(cld), csu382b(cld), csu382c(cld)*	6.05, 8.06, 3.05	−19	*Brassica napus*
Copper amide oxidase	rz69		*amo1*	10.04	−11	*Pisum sativum*
crinkly	pCR4c5H		*cr4*	10.01–10.02		
CRINKLY precursor	cdo244		*cdo244a(crp), cdo244b(crp)*	10.07, 2.02	−12	*Zea mays*
Cyclin	Ia		*csh8a(cyc4)*	8.08		
Cyclin	Ib		*csh9(cycl)*	8.04		
Cyclin	III		*cyc3*	6.02		
Cyclin	p10		*csh10a(cycll), csh10b(cycll)*	5.06, 3.04		
Cycloartenol synthase	csu265	T18827	*cas1*	4.10	−24	*Arabidopsis thaliana*
Cystathionine γ-synthase	rz672		*rz672a(cgs)*	1.04	−58	*Zea mays*
Cystatin	csu223	T18803	*csu223a(psei), csu223b(psei)*	8.08, 3.06	−17	*Zea mays*
Cysteine synthase	csu881U	W21609	*csu881(cys)*	1.05–1.06	−23	*Zea mays*
Cytochrome b5	rz390U:		*rz390a(cyb5), rz390b(cyb5)*	8.05, 8.05	−38	*Oryza sativa*
Cytochrome b561	csu428	W59826	*csu428(cyb561)*	4.06	−16	*Bos taurus*
Cytochrome C-reductase	csu576	AA051888	*ccr1*	1.11	−35	*Solanum tuberosum*
Cytochrome P450	np1703		*cyp7*	3.05		
Cytochrome P450	np1710		*cyp1710*	4.01		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Cytochrome P450	np2707		*cyp2707*	4.01		
Cytochrome P450	pCYP71C1U		*bx4*	4.01		
Cytochrome P450	csu618	AA054799	*csu618(P450)*	4.01	−19	*Zea mays*
Cytochrome P450	np2611		*uky1(P450)*	2.06		
Cytochrome P450	np2708		*uky2(P450)*	5.03		
Cytochrome P450	np3712		*uky3a(P450), uky3b(P450)*	8.03, 6.05		
Cytochrome P450	phi034		*cyp6***	7.02		
Cytoplasmic malate dehydrogenase	csu580	AA051891	*csu580a(mdh), csu580b(mdh)*	1.08, 5.03	−41	*Zea mays*
Dehydrin	umc170		*dhn1*	6.05		
Dihydrodipoamide dehydrogenase	rz244		*rz244a(dia), rz244b(dia)*	8.03, 3.04	−43	*Pisum sativum*
DNA-binding activity	pAS10		*dba1*	4.10		
DNA-binding activity	pAS11		*std7a(dba), std7b(dba)*	6.05, 8.04		
DNA-binding activity	pAS12 U:		*dba2*	8.05		
DNA-binding activity	pAS13 U:		*dba3*	10.07		
DNA-binding activity	pAS14		*dba4*	9.06		
DNA-binding activity	pAS7		*std4(dba)*	10.05		
DNA-binding activity	pAS8		*std6a(dba), std6b(dba)*	9.03, 6.04		
DNA-binding activity	pAS9		*std2a(dba), std2b(dba), std2c(dba)*	9.06–9.07, 5.03, 1.02		
DNA-binding protein	umc107		*umc107a(croc)*	1.10	−39	*Picea*
DNA polymerase	csu804	W21728	*csu804a(dnp), csu804b(dnp)*	9.08, 1.00	−6	Human herpes virus
DNA J protein	rz474		*rz474a(dnaj), rz474b(dnaj)*	5.02–5.03, 1.08–1.09	−44	*Solanum tuberosum*
Dormancy-regulatory protein	vp1		*vp1*	3.05		
dTDP glucose dehydratase	csu219	T18799	*csu219(tgd)*	9.05	−25	*Arabidopsis thaliana*
E. coli origin of replication	pAS3		*eoh1*	10.03		
eg1, protein kinase stage I oogenesis specific	cdo920		*cdo920(egl)*	3.09	−16	*Drosophila melanogaster*
Elongation factor 1A	csu226	T18806	*csu226a(elf1A), csu226b(elf1A), csu360(elf1A)*	8.04, 6.02–6.03, 6.05	−22	*Malus domestica*
Elongation factor 1A	csu116		*csu116a(elf1A)*	6.05	−25	*Zea mays*
Elongation factor 1A	csu360	T27555	*csu360(elf1A)*	6.05	−46	*Forsythia* sp.
Elongation factor 1A	csu575	AA051887	*csu575(elf1A)*	6.05	−131	*Zea mays*
Endomenbrane protein EMP70 precursor	rz141		*rz141a(emp70)*	3.05	−55	*Arabidopsis thaliana*
Endopeptidase	Isozyme		*enp1**	6.01–6.02		
Enolase	csu951	W21657	*csu951(eno)*	10.03–10.04	−58	*Ricinus communis*
Ent-kaurene synthase B	csu186	T18845	*eks1*	2.02	−8	*Cucurbita maxima*
Ent-kaurene synthase, A-activity	An1		*an1*	1.08		
Ent-kaurene synthase, A-activity	npi386		*npi386(eks2)*	4.04	−12	*Arabidopsis thaliana*
Esterase	Isozyme		*e8**	3.01		
Esterase	Isozyme		*e4**	3.04		
Esterase	Isozyme		*e1**	7.04		
Eucaryotic initiation factor 5A	csu175	T18836	*csu175a(eif5A), csu175c (eif5A), csu175d (eif5A), csu175e(eif5A)*	2.07–2.08, 5.03, 7.04, 1.11	−10	*Zea mays*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Eucaryotic initiation factor	plif4a		*ucr1a(eif), ucr1b(eif)*	6.02, 5.03		
Eucaryotic initiation factor 5A	csu154		*csu154a(eif5A)*	2.08	−29	*Phaseolus vulgaris*
Eucaryotic initiation factor 5A	csu203	T18787	*csu175d(eif5A), csu203b (eif5A),*	7.04, 2.08	−32	*Zea mays*
Eucaryotic initiation factor 5A	csu702	AA143899	*csu203b(eif5A)*	2.07–2.08	−27	*Zea mays*
Eucaryotic initiation factor 5A	csu981	W21687	*csu981(eif5A)*	10.04	−8	*Phaseolus vulgaris*
Extensin	csu355	T27552	*csu355(ext)*	9.05	−8	*Solanum lycopersicum*
Extensin, class 1	bcd855		*bcd855a(ext), bcd855b(ext)*	2.03, 6.05	−17	*Arabidosis thaliana*
Ferredoxin	csu74		*csu74(fdx)*	4.05	−16	*Zea mays*
Ferredoxin III precursor	rz614		*rz614(fdx)*	1.12	−46	*Zea mays*
Ferredoxin NADP-reductase	csu961	W21667	*csu961(fnr)*	3.05	−56	*Oryza sativa*
Ferredoxin NADP-reductase	Zm prn1L		*usu1a(fnr), usu1b(fnr)*	1.10–1.11, 7.00–7.01		
Ferripyochelin binding protein	rz995		*rz995a(fbp) rz995b(fbp)*	8.00–8.01, 3.04	−17	*Methanococcus jannaschii*
Ferritin	FM1		*fer1*	4.08		
Ferritin	csu306	W49892	*csu306(fer)*	10.00	−18	*Vigna unguiculata*
Fibrillin	csu393	W49905	*csu393(fbn)*	2.04	−30	*Capsicum annum*
Fibrillin	csu653	AA072431	*csu653(fbn)*	1.05	−25	*Capsicum annum*
Flavonol 3-*O*-glucosyl-transferase	umc192		*bz1*	9.02		
Folylpolyglutamate synthetase	csu969	W21675	*fpg1*	10.03–10.04	−10	*Mus musculus*
Fusca 6, signal-transduction pathway gene	csu896	W21618	*fus6*	1.00–1.01	−11	*Arabidopsis thaliana*
G-protein subunit	umc194		*umc194a(gpr)*	1.01–1.02		
General regulatory factor	GRF1-GR14-12		*ufg8 (grf)*	10.04		
General regulatory factor, 14-3-3 protein	GRF2-GR14-6		*grf2*	10.04		
General regulatory factor, 14-3-3 protein	csu64		*csu64a(grf)*	2.08–2.09	−19	*Zea mays*
Gibberellin and auxin stimulated protein	php20075		*php20075a(gast)*	10.01	−36	*Lycopersicum esculentum*
Globulin	umc184		*glb1, umc184b(glb), umc184c(glb), umc184d(glb)*	1.09, 2.04, 8.05, 3.08–3.09		
Glucan endo-1,3-β-glucosidase	pGlu		*uiu8(geb)*	3.05		
Glucan endo-1,3-β-glucosidase	umc129		*umc129(geb)*	1.09		
Glucose-6-phosphate dehydrogenase	csu350	T27548	*csu350(gpdh)*	2.03–2.04	−31	*Medicago sativa*
Glutamine synthetase	pDP1		*gln6*	1.03		
Glutamine synthetase	pGS1535		*gln4*	5.07		
Glutamine synthetase	pGS1931		*gln2*	1.09–1.10		
Glutamine synthetase	pGS691		*gln5*	4.06		
Glutamine synthetase	pMS5		*gln1*	10.07		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Glutaminyl-tRNA synthetase	csu674	AA072448	*csu674(gts)*	4.08–4.09	−22	*Homo sapiens*
Glutaminyl-tRNA synthetase	asg24		*asg24(gts)*	3.03	−17	Lupinus
Glutaredoxin	csu40		*csu40(grx)*	2.04	−23	*Oryza sativa*
Glutathione *S*-transferase	umc181		*bz2*	1.08		
Glutathione *S*-transferase	csu44		*csu44(gst)*	3.05	−40	*Zea mays*
Glutathione *S*-transferase	csu454	AA011860	*csu454(gst)*	1.01	−12	*Zea mays*
Glyceraldehyde-3-phosphate dehydrogenase	csu1047	W49424	*gpa2*	10.04	−12	*Sinapis alba*
Glyceraldehyde-3-phosphate dehydrogenase	csu140		*gpa2*	10.04	−31	*Sinapis alba*
Glyceraldehyde-3-phosphate dehydrogenase	csu610	AA054791	*gpa2*	10.04	−25	*Zea mays*
Glyceraldehyde-3-phosphate dehydrogenase	rz143		*rz143a(gpc)*	6.00	−30	*Oryza sativa*
Glyceraldehyde-3-phosphate dehydrogenase, C, cytosolic	umc191		*gpc1*	4.04–4.05		
Glyceraldehyde-3-phosphate dehydrogenase, C, cytosolic	umc203		*gpc2*	6.00–6.01		
Glyceraldehyde-3-phosphate dehydrogenase, NADP+ phosphorylating	umc188		*gpa1*	8.03		
Glycine-rich protein	csu408	W59808	*csu408(grp)*	3.04	−22	*Zea mays*
Glycine-rich protein	csu214	T18795	*csu214a(grp), csu214b(grp)*	9.03–9.04, 1.03		
Glycine-rich protein	csu215	T18796	*csu215a(grp), csu215b(grp)*	3.06, 1.03		
Glycine-rich RNA binding protein	csu611	AA054792	*csu611a(grp), csu611b(grp)*	2.09, 7.01	−31	*Oryza sativa*
Glycine decarboxylase-H protein	csu681	AA072454	*gcsh1*	10.03	−15	*Mesembryanthemum crystallinum*
Glycosyl transferase	csu425	W59825	*csu425(gct)*	2.02	−9	*Saccharomyces cerevisiae*
Golgi-associated protein	csu982	W21688	*csu982(goa)*	1.08	−52	*Zea mays*
Golgi-associated protein se-wap41	rgp r440		*rgpr440a(gap), rgpr440b(gap), rgpr440c(gap)*	5.03, 7.04, 10.03	−47	*Zea mays*
Goliath protein	csu216	T18797	*gol1*	4.08	−9	*Drosophila melanogaster*
Goliath protein	csu859	W21775	*csu859(gol)*	1.03	−8	*Drosophila melanogaster*
gos2, protein translation factor SUI1	cdo59		*cdo59a(gos2)*	7.04	−37	*Oryza sativa*
GTP-binding protein	cdo395		*cdo395a(ypt), cdo395b(ypt)*	4.05, 5.06	−21	*Arabidopsis thaliana*
GTP-binding protein	csu108		*csu108(gbp)*	5.02		
GTP-binding protein	bcd147L:		*bcd147(gbp)*	10.03	−19	*Saccharomyces cerevisiae*
GTP-binding protein	rz400		*rz400(gbp)*	10.02	−67	*Lotus japonicus*
GTP-binding protein, small	csu234	T18813	*csu234a(gbp), csu234b(gbp)*	3.05, 10.03	−22	*Pisum sativum*
Heat shock protein 18	pZmhsp 17.2M		*ttu1(hsp18)*	3.04		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Heat shock protein 70	5C04D01		*uaz205b(hsp70), uaz205c(hsp70)*	1.07, 7.03	−83	*Phaseolus vulgaris*
Heat shock protein 70	bcd1072		*bcd1072a(hsp70), bcd1072c(hsp70)*	5.02, 1.09	−39	*Spinacia oleracea*
Heat shock protein 70	csu179	T18839	*csu179a(hsp70), csu179b(hsp70), csu179c(hsp70), csu179d(hsp70)*	1.03, 9.03–9.04, 8.07, 8.04	−33	*Pisum sativum*
Heat shock protein 70	csu912U	W21630	*csu179a(hsp70), csu912b(hsp70), csu179c(hsp70)*	1.03, 3.04–3.05, 8.07	−32	*Zea mays*
Heat shock protein 70	umc206		*umc206(hsp70)*	8.03		
Heat shock protein 82	csu256	T26943	*csu256(hsp90)*	1.06	−30	*Arabidopsis thaliana*
Heat shock protein 82	csu274	T18833	*csu274(hsp90)*	7.02–7.03	−37	*Oryza sativa*
heat shock protein ClpB	rz87L:		*rz87(clp)*	5.04	−11	*Synechoccus* sp.
Histone 2B1	CH2B1 L:		*std1a(his2B1), std1b(his2B1), std1d(his2B1)*	4.05, 1.07, 3.04		
Histone 3	csu929	W21643	*csu929(his3)*	10.03–10.04	−31	*Glycine max*
Histone H2A1	csu666	AA072442	*csu666(his2A1)*	6.05	−27	*Petroselinum crispum*
Histone H2B	csu285	T18835	*csu285(his2B)*	9.07	−18	*Triticum aestivum*
Homeobox, transcription factor	pBK6		*hox3*	3.06–3.07		
Homeobox, transcription factor	pRB43		*hox2*	6.07		
Homeobox, transcription factor	pRB53		*hox1*	8.04–8.05		
Homeodomain protein	bnl7.49		*bnl7.49a(hmd)*	10.07	−43	Orchid
Hydroxyproline-rich glycoprotein	umc145		*hrg1*	2.04		
Importin	csu244	T18817	*csu244(imp)*	8.03	−16	*Arabidopsis thaliana*
Indeterminate, zinc-finger protein	p850		*csh4(id1)*	1.08		
Indol-3-ylacetyl glucosyl transferase	iaglu		*msu2(iaglu)*	1.09		
Inorganic H-pyrophosphatase	csu921	W21635	*csu921a(ppp), csu921b(ppp)*	1.09, 1.07	−49	*Hordeum vulgare*
Integral membrane protein	csu142		*stp1*	8.03	−28	*Beta vulgaris*
Invertase	lvRI genomic		*ufg3a(ivr), ufg3b(ivr)*	2.03, 10.05		
Invertase, cell wall	IJ6		*ufg6(incw)*	2.04		
Invertase, cell wall	IKS#46		*incw1*	5.04		
Iojap1	cDNA(ij)		*ij1*	7.03		
Isocitrate dehydrogenase	Isozyme		*idh2**	6.07		
Isocitrate dehydrogenase	Isozyme		*idh1**	8.05–8.06		
Isovaleryl CoA dehydrogenase precursor	cdo580		*cdo580b(ivd)*	6.01	−30	*Rattus norvegicus*
Ketol-acid reductoisomerase	cdo1160		*cdo1160a(kri), cdo1160b(kri)*	8.03, 3.04	−44	*Spinacia oleracea*
Kinase-associated acid phosphatase	ZmKAPP		*umc267(kapp)*	2.06		
Kinesin, light chain	rz567		*rz567a(klc)*	5.06	−33	*Arabidopsis thaliana*
Knotted-related homeobox	Knox1		*knox1*	1.00–1.01		
Knotted-related homeobox	Knox11		*knox11*	8.05		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Knotted-related homeobox	Knox3		*knox3*	1.10		
Knotted-related homeobox	Knox8		*knox8a, knox8b*	1.10, 7.00		
Lectin receptor	umc66		*umc66a(lcr)*	4.07	−18	*Oryza sativa*
Leucine tRNA synthase	bnl9.11		*bnl9.11a(lts)*	8.02	−10	*Bacillus subtillus*
Light harvesting chlorophyll a/b binding protein	csu1028	W49418	*csu1028(lhcb)*	10.06–10.07	−9	*Chlamydomonas reinhardtii*
Light harvesting chlorophyll a/b binding protein	csu460	AA011865	*lhcb1*	3.09	−24	*Arabidopsis thaliana*
Light harvesting chlorophyll a/b binding protein	csu466	AA011871	*csu466(lhcb)*	9.01–9.02	−35	*Petunia* sp.
Light harvesting chlorophyll a/b binding protein	csu774	AA143929	*csu774(lhcb)*	5.04	−35	*Pinus sylvestris*
Light harvesting chlorophyll a/b binding protein	csu778	AA143930	*csu778(lhcb)*	9.04	−18	*Pisum sativum*
Light harvesting chlorophyll a/b binding protein	csu847	W21764	*csu847a(lhcb), csu847b(lhcb)*	2.08, 7.04	−37	*Zea mays*
Light harvesting chlorophyll a/b binding protein	csu889U	W21615	*lhcb1, csu889b(lhcb)*	3.09, 1.08	−31	*Petunia* sp.
Light harvesting chlorophyll a/b binding protein	csu224	T18804	*lhcb3*	8.03	−27	*Petunia* sp.
Light harvesting chlorophyll a/b binding protein	csu227	T18807	*lhcb4*	5.07	−7	*Zea mays*
Light harvesting chlorophyll a/b binding protein	umc24		*lhcb1, umc24b(lhcb)*	3.09, 1.09		
Light harvesting chlorophyll a/b binding protein	csu66		*csu66a(lhcb)*	1.08		
Light harvesting complex I, photosystem I antenna protein	csu800	W21725	*csu800(lhca)*	2.08	−54	*Hordeum vulgare*
Light harvesting complex I, photosystem I antenna protein	csu818	W21738	*csu818a(lhca), csu818b(lhca)*	2.07–2.08, 7.04	−23	*Hordeum vulgare*
Lipoxygenase	csu719	AA143907	*csu719(lox)*	4.09	−13	*Phaseolus vulgaris*
Lipoxygenase isoenzyme 1	6C02F07L		*uat1(lox)*	1.09	−26	*Hordeum vulgare*
LUMINIDEPENDENS protein	csu838	W21755	*ldp1*	3.05	−21	*Arabidopsis thaliana*
MADS-box transcription factor	BRACE 9-1		*mpik24b(zmm2)*	3.02		
MADS-box transcription factor	BRACE 9-22		*mpik28(zmm8)*	9.06		
MADS-box transcription factor	BRACE 9-37		*mpik25(zmm3)*	9.02		
MADS-box transcription factor	BRACE 9-60		*mpik27a(zmm7), mpik27b(zmm7)*	2.07, 7.03		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
MADS-box transcription factor	zag1		*zag1*	6.05		
Major allergen ml protein	csu658	AA072435	*csu658(mam)*	2.07–2.08	−19	*Zea mays*
Major intrinsic protein	csu177	T18838	*mip1*	5.04	−6	*Oryza sativa*
Malate dehydrogenase	csu249	T18819	*mdh5*	5.03	−19	*Zea mays*
Malate dehydrogenase	csu374	T27564	*mdh6*	7.01	−25	*Zea mays*
Malate dehydrogenase	csu77		*mdh4*	1.07–1.08	−32	*Zea mays*
Malate dehydrogenase	Isozyme		*mdh3**	3.08		
Malate dehydrogenase	Isozyme		*mdh2**	6.07		
Male gametophyte-specific protein	Msb 8		*mgs1*	10.04		
Malic enzyme	csu16		*me3*	3.02	−69	*Flaveria trinervia*
Metallothionein-like protein	csu206	T18790	*mtl1*	4.00–4.01	−9	*Solanum tuberosum*
Metallothionein-like protein	csu275	W49888	*csu275a(mtl)*	8.03	−12	*Solanum lycopersicum*
Metallothionein-like protein	csu570	AA051883	*csu570a(mtl), csu570b(mtl)*	5.01, 1.10–1.11	−13	*Solanum lycopersicum*
Methionine synthase	csu194	T18851	*csu194(met)*	1.05–1.06	−33	*Solenostemon scutellarioides*
Methionine synthase	csu503	AA030695	*csu503(met)*	1.05–1.06	−35	*Catharanthus roseus*
Methylenetetrahydrofolate reductase	csu134		*csu134a(thf)*	1.11	−12	*Saccharomyces cerevisiae*
Methylmalonate semialdehyde dehydrogenase (acylating)	asg34		*asg34a(msd), asg34b(msd)*	7.02, 3.06	−18	*Pseudomonas aeruginosa*
Mitochondrial carrier family	cdo202		*cdo202a(mcf)*	6.07–6.08	−50	*Arabidopsis thaliana*
Mitochondrial carrier family	csu68		*csu68a(mcf)*	6.08	−38	*Arabidopsis thaliana*
Mitochondrial chaperonin hsp60	csu396	W49907	*cpn1*	5.03	−15	*Zea mays*
Mitochondrial F1-ATPase delta subunit	csu657	AA072434	*csu657(atpd)*	2.08	−39	Ipomea
Mitochondrial Rieske Iron Sulfur protein	csu893L	W21617	*csu893(isp)*	10.04	−17	*Zea mays*
Mitogen-activated protein kinase	csu252	T18821	*csu252a(cdc2), csu252b(cdc2)*	5.03, 9.03–9.04	−42	*Nicotiana tabacum*
Mouse transplantation antigen	5C04D09		*mta1*	1.10	−48	*Mus musculus*
mRNA-splicing factor	csu363	T27557	*msf1*	4.00–4.01	−26	*Drosophila melanogaster*
mRNA-splicing factor	PRP8-7		*scri1(msf)*	8.05		
Multprotein-bridging factor	5C01C06		*uaz246b(mbf)*	9.03	−32	*Bombyx mori*
Multispanning membrane protein	cdo1387		*cdo1387a(emp70)*	9.06	−30	*Homo sapiens*
myb-like protein	csu184	T18844	*myb2*	3.05	−34	*Arabidopsis thaliana*
myb protein	umc185		*p1*	1.03		
myb protein	umc205		*pl1*	6.03–6.04		
myb protein	asg8		*asg8(myb)*	7.01	−13	*Homo sapiens*
myc protein	umc182		*r1*	10.06		
NaCl stress protein	5C01G10		*nac1*	10.04	−15	*Hordeum vulgare*
NADH dehydrogenase (ubiquinone) complex I subunit	cdo122		*cdo122a(nad), cdo122b(nad)*	1.09–1.10, 5.02	−42	*Solanum tuberosum*
NADPH dihydroflavonol reductase	umc199		*a1*	3.08–3.09		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
NADPH HC-toxin reductase	hm1a		*hm1, hm2, umc276c(hm1)*	1.06, 9.04, 1.06		
Nascent-polypeptide associated complex, alpha subunit	csu737	AA143915	*csu737(npc)*	1.04	−33	*Mus musculus*
NDP-glucose-starch glucosyltransferase, starch granule bound	umc25		*wx1*	9.03		
NDP-glucose-starch glucosyltransferase, starch granule bound	phi061		*phi061(wx)***	9.02		
NDP-glucose-starch glucosyltransferase, starch granule bound	phi022		*phi022(wx)***	9.02		
NF-YB, CAAT-box binding protein subunit B	5C05F12		*caat1*	8.04	−34	*Zea mays*
Nitric oxide synthase	csu250	T18820	*csu250a(aba), csu250b(aba)*	10.02, 9.01	−4	*Bos taurus*
Nitrogen upregulated	Noi1		*uat2(noi)*	6.04		
Nuclear binding protein 35	csu598	AA051902	*nbp35*	5.05	−23	*Saccharomyces cerevisiae*
Nuclear transport factor	csu608	AA054789	*ntf1*	1.06	−21	*Saccharomyces cerevisiae*
Nucleoside triphosphatase	cdo38		*cdo38b(ntp)*	7.05	−21	*Arabidopsis thaliana*
Nucleotide diphosphate kinase	csu269	T18831	*ndk1*	7.04	−25	*Oryza sativa*
o2 protein	phi057		*o2***	7.01		
Obtusifoliol 14-α-demethylase cyp51	csu25		*csu25a(P450)*	3.10	−36	*Sorghum bicolor*
Opaque-2 heterodimerizing protein, transcriptional activator	csu56		*csu56a(ohp), csu56b(ohp), csu56c(ohp) csu56d(ohp)*	6.02, 3.03, 2.04, 9.04	−6	*Zea mays*
Organellar permease	5C02H10		*pop1*	1.05	−9	*Saccharomyces cerevisiae*
Oxygen-evolving complex 17-kD protein, ferredoxin NADP reductase binding protein	csu229	T18809	*csu229a(oec) csu229b(oec)*	7.04, 3.05	−26	*Pisum sativum*
Oxygen-evolving complex, 23-kD subunit	umc171		*umc171a(oec), umc171b(oec)*	4.02, 2.09		
Oxygen-evolving complex, 33-kD subunit	umc172		*oec33*	6.01–6.02		
Pathogenesis-related protein	5C04F07		*prp2*	2.04	−7	*Phaseolus vulgaris*
Pathogenesis-related protein	pZSS2		*inra2(prp)*	4.02		
Pathogenesis-related protein	phi083		*prp2***	2.04		
Peptidyl prolyl isomerase	rgp c361		*rgpc361(ppi)*	1.04	−11	*Triticum aestivum*
Pet112 protein, probable mitochondrial translation factor	cdo365		*cdo365(pet)*	4.08		*Synechocystis* sp.
Phenylalanine ammonia lyase	csu156		*pal1*	5.05	−24	*Oryza sativa*
Phenylalanine ammonia lyase	csu358	T27553	*csu358b(pal)*	4.05	−14	*Oryza sativa*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[a]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Phosphate phosphoenol-pyruvate translocator precursor	rz698		*rz698a(ppy)*	1.07		*Zea mays*
Phosphoenolpyruvate carboxykinase	csu145		*csu145a(pck)*	9.05–9.06	−11	*Urochloa panicoides*
Phosphoglucomutase (glucose-cofactor)	Isozyme		*pgm2**	5.02		
Phosphoglycerate kinase	bcd738		*bcd738a(pgk), bcd738b(pgk)*	6.06, 3.06–3.07	−28	*Triticum aestivum*
Phosphohexose isomerase	Isozyme		*phi1**	1.10–1.11		
Phospholipid transfer protein	csu136		*csu136(plt)*	10.01		
Phosphoprotein phospha-tase pp2A regulatory subunit	cdo590		*cdo590(ppr)*	9.03	−25	*Pisum sativum*
Phosphoribulokinase	umc209		*umc209(prk)*	8.04		
Photosystem I chain D precursor	csu663	AA072440	*csu663a(psaD), csu663b(psaD)*	5.00–5.01, 1.11	−39	Ipomea
Photosystem I subunit N	csu237	T18816	*csu237a(psaN), csu237b(psaN)*	10.03, 3.05	−23	*Hordeum vulgare*
Photosystem I subunit N	umc18		*umc18a(psaN)*	3.05		
Photosystem II, 10-kD peptide	csu754	AA143923	*psb3*	4.04	−32	*Spinacia oleracea*
Phytochrome A	rz912		*rz912a(phy)*	1.09–1.10	−56	*Oryza sativa*
Phytochrome-regulated gene	csu368	T27562	*csu368(phr)*	8.00–8.01	−23	*Ipomea, Arabidopsis*
Phytoene synthase	csu572	AA051885	*psy2*	8.07	−58	*Lycopersicum esculentum*
Phytoene synthase	umc111		*umc111(psy)*	4.11		
Phytoene synthase	plQ60–6M3500		*y1*	6.01–6.02		
Plasma membrane major intrinsic protein	rz509		*rz509a(mip), rz509b(mip)*	7.02, 2.06	−20	*Beta vulgaris*
Pollen ubiquitin regulator	Isozyme		*pur1**	2.08		
Pollen, extensin-like	pSS1		*fco1a(pex), fco1b(pex)*	2.09, 2.09		
Polyubiquitin	csu330	T26953	*csu330(ubi)*	4.10	−69	*Zea mays*
PPi-dependent phospho-fructo-1-kinase	csu228	T18808	*csu228(pfk)*	9.02	−14	*Entamoeba histolytica*
Prohibitin, B-cell receptor-associated protein	csu865	W21711	*csu865(phb)*	1.12	−23	*Mus musculus*
Proteasome C9	5C02A05		*prc1*	9.02	−55	*Spinacia oleracea*
Protein disulfide isomerase	5C11B04		*uaz298(PDI)*	4.03	−71	*Zea mays*
Protein kinase	3B1		*wsu1(ptk)*	9.04		
Protein kinase	cdo1417		*cdo1417b(ptk)*	10.06	−10	*Saccharomyces cerevisiae*
Protein kinase	csu310	W49895	*csu310(ptk)*	6.05	−10	*Oryza sativa*
Protein kinase	pKICAT		*umc265(ptk)*	6.05		
Protein kinase	pZmPK4		*umc269(ptk)*	10.07		
Protein kinase	ZmPK3		*umc266a(ptk), umc266b(ptk), umc266c(ptk), umc266d(ptk)*	1.03, 1.01, 6.06–6.07, 8.07		
Protein kinase	csu100		*csu100(ptk)*	4.05	−9	Ipomea
Protein kinase	pZmPRK1-11		*ptk3*	1.06		
Protein kinase	rgp c86		*rgpc86(ptk)*	8.06–8.07	−21	*Glycine max*
Protein kinase inhibitor	mZ2-12		*fmi1(pki)*	1.03–1.04		

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Protein kinase (endosperm)	csu1041L	W49420	*csu1041a(ptk), csu1041b(ptk)*	1.05, 8.05	−16	*Oryza sativa*
Proteolipid, vacuolar ATPase	csu30		*atp1*	3.05	−17	*Gossypium hirsutum*
Pyrophosphate-energized proton pump, vacuolar	csu220	T18800	*ppp1*	5.07	−17	*bovine*
Pyruvate deydrogenase phosphatase	csu675	AA072449	*csu675a(prh), csu675b(prh)*	1.05–1.06, 8.01	−8	*Giardia lamblia*
Pyruvate kinase	cdo127		*cdo127a(pyk), cdo127b(pyk)*	4.08, 10.01	−10	*Saccharomyces cerevisiae*
Pyruvate, orthophosphate dikinase	csu314	T26948	*pdk1*	6.05	−25	*Zea mays*
Pyruvate, orthophosphate dikinase	C4PPDK(4)		*pdk1, pdk2*	6.05, 8.04		
Pyruvate, orthophosphate dikinase	csu155		*pdk1, pdk2*	6.05, 8.04	−40	*Zea mays*
Pyruvate, orthophosphate dikinase	csu540	AA030719	*pdk1*	6.05	−24	*Zea mays*
Pyruvate, orthophosphate dikinase	csu764	AA143928	*pdk1, pdk2*	6.05, 8.04	−50	*Zea mays*
Pyruvate, orthophosphate dikinase	umc173		*pdk1*	6.05		
rga1 protein	cdo344		*cdo344a(rga), cdo344c(rga)*	3.05, 1.05	−11	*Arabidopsis thaliana*
Ribonucleoprotein A3	rz323U:		*rnp2*	8.01	−18	*Homo sapiens*
Ribosomal inactivating protein	cb70-1		*ncr200b(rip)*	5.03		
Ribosomal protein Po, acidic	csu565	AA051879	*csu565(rpPo)*	4.04–4.05	−12	*Oryza sativa*
Ribosomal protein, 60S acidic	csu745	AA143921	*csu745a(rpPo), csu745b(rpPo), csu745c(rpPo), csu745d(rpPo), csu745e(rpPo)*	10.05, 4.09, 10.03, 1.03, 1.09	−29	*Zea mays*
Ribosomal protein CL9, plastid	csu799L	AA661454	*csu799(rpL9)*	5.07–5.08	−29	*Arabidopsis thaliana*
Ribosomal protein L10	5C01D03		*uaz198a(rpL10), uaz198c(rpL10), uaz198d(rpL10)*	3.09–3.10, 1.05, 1.04	−11	*Caenorhabditis elegans*
Ribosomal protein L11	csu862L	W11778	*csu862a(rpL11), csu862b(rpL11)*	5.04, 4.09	−38	*Medicago sativa*
Ribosomal protein L14	csu36		*csu36a(rpL19), csu36b(rpL19)*	4.09–4.10, 5.03–5.04	−16	*Medicago truncatula*
Ribosomal protein L15	rgp c1122		*rgpc1122a(rpL15), rgpc1122b(rpL15), rgpc1122c(rpL15), rgpc1122d(rpL15), rgpc1122e(rpL15)*	2.07, 7.01, 1.02, 10.03, 5.03	−62	*Arabidopsis thaliana*
Ribosomal protein L17	csu590	AA051898	*csu590(rpL17)*	1.06	−42	*Hordeum vulgare*
Ribosomal protein L19	csu566	AA051880	*rpl19*	5.05	−15	*Cyanophora paradoxa*
Ribosomal protein L21	csu883L	W21610	*csu883(rpL21)*	9.07	−33	*Arabidopsis thaliana*
Ribosomal protein L27a	csu652	AA072430	*csu652(rpL27)*	5.03	−38	*Arabidopsis thaliana*
Ribosomal protein L30	csu891	W21692	*csu891(rpL30)*	8.01	−26	*Homo sapiens*
Ribosomal protein L39	csu651	AA072429	*csu651(rpL39)*	9.02	−6	*Oryza sativa*
Ribosomal protein L39	csu733	AA143911	*csu733(rpL39)*	9.02	−32	*Oryza sativa*
Ribosomal protein L5	5C05D07		*uaz260a(rpL5), uaz260b(rpL5)*	3.06, 1.01	−7	*Oryza sativa*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Ribosomal protein L5	rgp c385		*rgpc385a(rpL5), rgpc385b(rpL5)*	1.01, 3.05	−54	*Oryza sativa*
Ribosomal protein L7	csu202	T18786	*csu202(rpL7)*	4.08	−13	*Solanum tuberosum*
Ribosomal protein L7	csu505	AA030697	*csu505(rpL7)*	1.06	−57	*Oryza sativa*
Ribosomal protein L9 precursor	csu695	AA072464	*csu695(rpL9)*	5.07–5.08	−9	*Arabidopsis thaliana*
Ribosomal protein S12	5C08C03		*uaz351a(rpS12)*	7.02	−31	*Sus scrofa*
Ribosomal protein S12	pCrp1-3		*uor1a(rpS12), uor1b(rpS12), uor1c(rpS12)*	6.08, 8.03, 7.02		
Ribosomal protein S14	csu474	AA011877	*csu474(rpS14)*	4.04–4.05	−16	Datura
Ribosomal protein S22	csu28		*csu28a(rpS22)*	9.06	−18	*Oryza sativa*
Ribosomal protein S25	csu974	W21680	*rps25*	3.04	−35	*Lycopersicum esculentum*
Ribosomal protein S7	csu742	AA143919	*csu742b(rpS7), csu742a(rpS7)*	4.05, 8.05	−21	*Xenopus laevis*
Ribosomal protein S8	csu34		*csu34b(rpS8)*	4.09		
Ribosomal protein S9	rgp c6		*rgpc6(rpS9)*	3.04–3.05	−37	*Dictyostelium discoideum*
Ribosome-inactivating protein	umc197		*umc197a(rip)*	1.09		
Ribosome-inactivating protein	ZmRIP3		*rip1*	8.04		
Ribulose 1,5-bisphosphate carboxylase activase	csu901	W21622	*rca1*	4.00–4.01	−25	*Hordeum vulgare*
Rieske iron-sulfur protein, chloroplast	csu271	W49887	*ris2*	4.09	−21	*Spinacia oleracea*
RNA binding protein	csu17		*csu17b(rnp)*	2.07–2.08	−13	*Nicotiana plumbaginifolia*
RNA binding protein	rgp c746		*rgpc746(rnp)*	1.09	−19	*Arabidopsis thaliana*
RNA binding protein	ZmRNP1		*uwm2(rnp)*	5.02		
RNA helicase	csu554	AA051871	*csu554a(rnh), csu554b(rnh)*	1.09, 5.02	−46	*Arabidopsis thaliana*
S-adenosyl-l-homocysteine hydrolase	rz900		*rz900(ahh)*	4.04	−76	*Catharanthus roseus*
S-adenosylmethionine decarboxylase	csu6		*sam1*	10.04–10.05	−15	*Arabidopsis thaliana*
S-adenosylmethionine decarboxylase	rz740		*rz740(sam)*	10.05	−41	*Oryza sativa*
S-receptor kinase	csu811	W21732	*srk1*	2.09	−13	*Brassica oleracea*
Salt-inducible protein	rz166		*rz166(nac)*	5.04–5.05	−14	*Nicotiana tabacum*
sec3 protein, root hair defective mutant	ias7		*rth1*	1.09		
sec61 protein γ-subunit	csu923	W21637	*csu923(sec61)*	6.02–6.03	−7	*Oryza sativa*
Serine carboxypeptidase I	csu649	AA054821	*csu649(scp)*	1.04	−15	*Oryza sativa*
Serine/threonine protein phosphatase	umc202		*prh1*	4.07		
Serine/threonine protein kinase	asg45		*asg45(ptk)*	1.04	−22	*Brassica napus*
Serine/threonine protein kinase	cdo87		*cdo87a(ptk), cdo87b(ptk)*	5.01, 1.10–1.11	−6	*Caenorhabditis elegans*
Seryl tRNA synthase	cdo520		*cdo520(ser)*	4.01–4.02	−7	*Haloarcula marismortui*
Shikimate-5-dehydrogenase	rz261		*rz261a(sad), rz261b(sad)*	10.03, 3.04–3.05	−15	*Nicotiana tabacum*
Shrunken-initiator binding protein	pFLK4		*ibp1*	9.06		
SIK1P-suppressor of 1κ B	rgp c198		*rgpc198a(sik), rgpc198b(sik)*	1.04, 8.06	−51	*Arabidopsis thaliana*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Soluble inorganic pyrophosphatase	csu571	AA051884	*csu571a(ipp), csu571b(ipp)*	2.03, 10.07	−26	*Hordeum vulgare*
Steroid membrane binding protein	rz583		*rz583a(msb)*	1.08	−15	*Sus scrofa*
Sucrose phosphate synthase	csu328	T26951	*sps2*	3.05	−40	*Zea mays*
Sucrose synthase	umc190		*sus1*	9.04		
Sucrose synthase	umc207		*sh1*	9.01		
Sugar transporter	rz500		*rz500(stp)*	1.05	−11	*Arabidopsis thaliana*
Sulfate adenyltransferase	rz630		*rz630a(sat), rz630b(sat)*	1.10, 4.03	−62	*Solanum tuberosum*
Superoxide dismutase	csu182	T18842	*sod4*	1.04	−55	*Zea mays*
TATA-binding protein	pTBI		*tbp1, tbp2*	1.09, 5.02–5.03		
Teosinte branched-like protein	php20581		*php20581a(tb), ph20581b(tb)*	7.01, 2.10	−11	*Arabidopsis thaliana*
Thiol protease	ccp2		*tjp1(thp)*	2.07		
Thiol protease	Mir1		*mir1*	6.02		
Thiol protease	mir2		*mir2(thp)*	6.02		
Thiol protease	mir3		*mir3a(thp), mir3b(thp), mir3c(thp)*	9.01, 2.02, 10.07		
Thiol protease	mir4		*mir4(thp)*	6.02		
Thiol protease inhibitor	csu96		*csu96a(psei), csu96b(psei)*	3.06, 8.08	−24	*Zea mays*
Thioredoxin	csu727	AA143909	*csu727(trh)*	6.06	−22	*Arabidopsis thaliana*
Thioredoxin	csu604	AA054787	*csu604a(trh), csu604b(trh)*	1.11, 5.00–5.01	−16	*Arabidopsis thaliana*
Thioredoxin M	csu439	W59835	*csu439(trm)*	3.05	−32	*Zea mays*
Threonine synthase	csu189	T18847	*csu189(thr)*	3.07–3.08	−14	*Arabidopsis thaliana*
Thylakoid assembly protein	pThal1-2		*tha1*	3.04		
Transcription factor	csu38		*csu38a(taf), csu38b(taf)*	3.06, 8.07	−26	*Homo sapiens*
Translation initiation factor 2B δ subunit	csu574	AA051886	*csu547a(eif2B), csu574b(eif2B)*	5.02–5.03, 1.06	−24	*Schizosaccharomyces pombe*
Transmembrane protein	pZSS4		*inra1(tmp)*	2.03		
Triose-phosphate isomerase	csu301	W49890	*tpi4*	3.04	−28	*Zea mays*
Tryptophan A	csu868	W21714	*csu868(trp)*	1.11	−35	*Zea mays*
Tryptophan synthase B-subunit	umc193		*orp1, orp2, umc193c(orp), umc193d(orp)*	4.04–4.05, 10.04, 7.02, 4.05		
ts2 mutant, short-chain alcohol dehydrogenase	csu149		*sca1*	5.00–5.01	−11	*Zea mays*
Ubiquinol-cytochrome C-reductase	csu536	AA030716	*csu536(ccr)*	1.11	−33	*Solanum tuberosum*
Ubiquitin	csu562	AA051877	*csu377a(ubi), csu562b(ubi)*	4.10, 5.03–5.04	−59	*Antirrhinum majus*
Ubiquitin	csu533	AA030713	*csu377a(ubi)*	4.10	−63	*Phaseolus vulgaris*
Ubiquitin-carrier protein	csu591	AA051899	*csu591(uce)*	8.08	−33	*Lycopersicum esculentum*
Ubiquitin-carrier protein	csu797	W21709	*csu797(uce)*	10.03–10.04	−38	*Triticum aestivum*
Ubiquitin-conjugating enzyme	csu204	T18788	*csu204(uce)*	8.04	−10	*Caenorhabditis elegans*
Ubiquitin-conjugating enzyme	5C05D12		*uce1*	1.08	−83	*Arabidopsis thaliana*
Ubiquitin-conjugating enzyme	csu456	AA011862	*csu456(uce)*	3.08	−25	*Arabidopsis thaliana*

(*continued*)

TABLE 2

(Continued)

Gene match[a]	Probe	Accession no.[b]	Locus names	Bin[c]	*P* value[d]	Organism[e]
Ubiquitin-conjugating enzyme	csu694	AA072463	*csu694a(uce), csu694b(uce)*	9.04, 1.04–1.05	−8	*Arabidopsis thaliana*
Ubiquitin-conjugating enzyme	pAS20a		*std20a(uce), std20b(uce)*	9.07, 1.01		
Ubiquitin-conjugating enzyme	UBC7		*uwm1a(uce), uwm1b(uce), uwm1c(uce)*	8.04, 9.03, 8.07		
Ubiquitin-conjugating enzyme	csu786	W21700	*csu786(uce)*	8.08	−50	*Arabidopsis thaliana*
Ubiquitin ribosomal protein 28	csu377	T27566	*csu377a(ubi), csu377b(ubi)*	4.10, 5.04	−35	*Solanum tuberosum*
UDP-glucose pyrophosphorylase	5C02H07L:		*ugp1*	2.07	−77	*Hordeum vulgare*
UMP/CMP kinase	csu612	AA054793	*uck1*	6.01	−41	*Arabidopsis thaliana*
Vacuolar ATPase	csu848	W21765	*csu848a(vpp), csu848b(vpp)*	4.09, 7.02	−26	*Zea mays*
Vesicle fusion ATPase	E92		*umc272(vfa)*	9.07		
Water-stress-induced protein	csu222	T18802	*csu222a(wsi), csu222b(wsi)*	1.09, 5.02–5.03	−10	*Oryza sativa*
Water-stress-induced protein	csu924	W21638	*csu924(wsi)*	1.04	−49	*Oryza sativa*
Zein-1, α zein	phi096		*zp1***	4.04		
Zinc-finger protein	rgp c975		*rgpc975(zfp)*	5.01	−78	*Hordeum vulgare*

*Locus detected by isozymes. **Locus detected by SSRs.

[a]Functions were determined by contributing individuals for individual cDNAs and by homology search as detailed in the materials and methods section for core markers and *csu* clones.

[b]Multiple accession numbers supplied where more than one sequence of the probe was submitted.

[c]Bin assignments are presented in locus order.

[d]*P* value is given as the exponent of 10 (*i.e.*, 13 = 10^{-13}).

[e]Only the organism with the lowest *P* value is listed for each probe.

DISCUSSION

The map presented here provides a more than five-fold increase in number of loci compared to the map previously published in this population (Chao *et al.* 1994). It is slightly smaller than the total map lengths of 1883.6 cM for the 1995 Brookhaven maize map (Matz *et al.* 1995) and 1765 cM for the INRA maize map (Causse *et al.* 1996). The smaller population used to construct this map, in comparison with that used for the BNL and INRA maps, may be partially responsible for the difference in map length, as fewer recombinants would be expected in the smaller sample. This difference may also be the result of fewer telomere loci, which often show high rates of recombination, being located on the present map (four compared to eight on the Brookhaven map), and indicates that mapping additional telomeres would be desirable. The map presented here is substantially smaller than the 1996 BNL maize map, which has a total length of 2048.6 cM (B. Burr, personal communication; ftp://ftp.bio.bnl.gov/pub/maize/chrom.map). The remaining gaps are likely to represent regions of small physical *vs.* large genetic distance rather than marker-poor regions because increased rates of recombination are observed in telomeric regions where many of the gaps of >10 cM occur. Syntenic analysis of maize and rice indicates that the remaining internal gaps are also likely to be regions of small physical *vs.* large genetic distance, suggesting that all chromosomes are adequately marked (G. Davis, unpublished results).

Given the rate at which sequence information is being generated and the resolution ability of this and other current mapping populations, a threshold has been reached where future local ordering will be unfeasible and/or impractical. Precise local order and distance information is a necessary component of many gene discovery experiments. Therefore, alternative types of mapping populations are a requirement for advances in plant genetics in the near future. The current automated sequencing technologies have accelerated the pace at which unique clones can be identified to the point where the increases of population size in F_2, recombinant inbred, or backcross populations required to order tightly linked markers will no longer be feasible or economical. Development of radiation hybrid mapping panels (Cox *et al.* 1990), physical approaches such as YAC or BAC contigs (Schmidt *et al.* 1995; Zachgo

TABLE 3
Core markers, sequence accession numbers, homologies, and corresponding maize bin

Probe	GenBank Number	Homology[b]	*P(N)*	Bin
p-tub1[a]	X52878	Maize β-1 tubulin	isolated gene	1.01
p-umc157	G10822, G10823	None		1.02
		None		
p-umc76	G10865, G10866	None		1.03
		None		
p-asg45[a]	G10756, G10757	Serine-threonine protein kinase	4.3e-10	1.04
		Rice cDNA	3e-8	
p-csu3[a]	T12525, T12526	None		1.05
		None		
p-umc67	G10864, G13173	None		1.06
		None		
p-asg62[a]	G13181, G13182	None		1.07
		None		
p-umc128	G10812, G10813	None		1.08
		None		
p-csu164[a]	T12748	None		1.09
		None		
p-umc107[a]	G10803, G10804	Picea CROC-1-like protein	2.8e-36	1.10
		Arabidopsis cDNA	1.2e-39	
p-umc161[a]	G10824, G10825	None		1.11
		Arabidopsis cDNA	7.7e-17	
p-bnl6.32	G10770, G10771	None		1.12
		None		
p-bnl8.45[a]	G10776, G10777	None		2.01
		None		
p-umc53	G10851, G10852	None		2.02
		None		
p-umc6	G10855, G10856	None		2.03
		None		
p-umc34	G10839, G10840	None		2.04
		None		
p-umc131	G10816, G10817	None		2.05
		None		
p-umc255[a]	G10834	None		2.06
		Rice cDNA	4.7e-21	
p-umc5	G10847, G10848	None		2.07
		Arabidopsis cDNA	5.8e-24	
p-asg20[a]	G10750, G10751	None		2.08
		None		
p-umc49	G10845, G10846	None		2.09
		None		
p-php20581[a]	G10795, G10796	Arabidopsis teosinte branched-like protein	5.6e-11	2.10
		Arabidopsis cDNA	1.1e-10	
p-umc32	G10837, G10838	None		3.01
		None		
p-csu32[a]	T12669	None		3.02
		None		
p-asg24[a]	G10752, G10753	Glutaminyl-tRNA synthetase	4.8e-15	3.03
		Arabidopsis cDNA	5.2e-13	
p-asg48[a]	G13183, G13184	None		3.04
		None		
p-umc102	G10801, G10802	None		3.05
		None		
p-bnl5.37	G10766, G10767	None		3.06
		None		
p-bnl6.16[a]	G10768, G10769	Arabidopsis unknown protein	2.1e-20	3.07
		Arabidopsis cDNA	2.2e-23	
p-umc17[a]	G10828, G10829	None		3.08
		None		

(*continued*)

TABLE 3

(Continued)

Probe	GenBank Number	Homology[b]	*P(N)*	Bin
p-umc63	G10857	None		3.09
		None		
p-csu25[a]	T12664	Obtusifoliol 14-alpha demethylase	4.8e-35	3.10
		None		
p-agrr115[a]	—			4.01
p-php20725[a]	—			4.02
p-umc31	G10835, G10836	None		4.03
		None		
p-npi386[a]	G10786, G10787	Arabidopsis GA1	4.4e-12	4.04
		Arabidopsis cDNA	7.1e-9	
p-agrr37[a]	G10748, G10749	None		4.05
		None		
p-umc156[a]	G10820, G10821	None		4.06
		None		
p-umc66	G10862, G10863	Lectin receptor	1.1e-09	4.07
		Rice cDNA	1.3e-18	
p-umc127[a]	G13175, G13176	None		4.08
		None		
p-umc52	G10849, G10850	None		4.09
		Arabidopsis cDNA	3.8e-08	
p-php20608	G10797, G10798	None		4.10
		None		
p-umc169[a]	G15653, G15654	None		4.11
		None		
p-npi409[a]	G10788, G13178	None		5.01
		None		
p-umc90[a]	G10870, G10871	None		5.02
		None		
p-tub4[a]	L10635	Maize beta-4 tubulin	isolated gene	5.03
p-bnl4.36[a]	—			5.04
p-csu93[a]	T12714	None		5.05
		None		
p-umc126	G10810, G10811	None		5.06
		None		
p-umc108	G10805, G10806	None		5.07
		Arabidopsis cDNA	2.2e-9	
p-bnl5.24[a]	G10764, G10765	None		5.08
		None		
p-php10017	G10791, G10792	None		5.09
		None		
p-umc85	G10869	None		6.01
		None		
p-umc59	G10853, G10854	None		6.02
		Rice cDNA	6.7e-6	
p-npi393[a]	G13180	None		6.03
		None		
p-umc65	G10860, G10861	None		6.04
		None		
p-umc21	G10830, G10831	None		6.05
		None		
p-umc38	G10841, G10842	None		6.06
		None		
p-umc132	G10818, G10819	Choline kinase	8.8e-12	6.07
		rice cDNA	7.7e-12	
p-asg7[a]	G10760, G10761	None		6.08
		None		
p-asg8[a]	G10762, G10763	myb-related protein	9.3e-10	7.01
		Dictyostelium cDNA	9.1e-10	

(*continued*)

TABLE 3

(Continued)

Probe	GenBank Number	Homology[b]	*P(N)*	Bin
pasg34[a]	G10754, G10755	Methylmalonate semi-aldehyde dehydrogenase	1.2e-24	7.02
		Drosophila cDNA	3.4e-16	
p-asg49[a]	G10758, G10759	None		7.03
		None		
p-umc254[a]	G10832, G10833	None		7.04
		None		
p-umc245[a]	G13169, G13170	None		7.05
		None		
p-umc168[a]	G13171, G13172	None		7.06
		None		
p-npi220	G10780, G10781	None		8.01
		rice cDNA	2.8e-09	
p-bnl9.11	G10778, G10779	Leucyl-tRNA synthetase	2.4e-9	8.02
		Rice cDNA	4.6e-16	
p-umc124	G10808, G10809	Choline kinase	2.4e-23	8.03
		Mesembryanthemum cDNA	7.5e-16	
p-bnl7.08[a]	G10772, G10773	None		8.04
		None		
p-bnl2.369[a]	—			8.05
p-csu31[a]	T12667, T12668	None		8.06
		None		
p-npi268	G10782, G10783	None		8.07
		None		
p-npi414	G10789, G10790	None		8.08
		None		
p-agrr21[a]	—			8.09
p-umc109	G10807, G13177	None		9.01
		None		
p-umc192[a]	X13502	Maize bronze-1	Isolated gene	9.02
p-umc25[a]	X03935	NDP-glucose-starch glucosyltransferase, starch granule bound (*waxy1*)	Isolated gene	9.03
p-csu147[a]	T12740	None		9.04
		None		
p-umc95	G10872	None		9.05
		None		
p-csu61[a]	T12691	None		9.06
		None		
p-asg12[a]	G13185, G13186	None		9.07
		None		
p-csu54[a]	T12684	Arabidopsis unknown protein	1.9e-25	9.08
		None		
p-php20075	G10793, G10794	GASA5-like protein	2.4e-34	10.01
		Capsicum cDNA	1.2e-32	
p-npi285	G10784, G10785	None		10.02
		None		
p-umc130	G10814, G10815	None		10.03
		None		
p-umc64	G10858, G10859	None		10.04
		None		
p-umc259[a]	—			10.05
p-umc44	G10843, G10844	None		10.06
		None		
p-bnl7.49[a]	G10774, G10775	Homeobox protein	1.4e-36	10.07
		Arabidopsis cDNA	2.6e-18	

[a]These probes are new core markers not in the original set published by Gardiner *et al.* (1993).

[b]Except for the cases where the clone was an isolated maize gene (*i.e.*, derived by targeted cloning), each entry in the table lists two homologies. The first line is that found using BLASTX *vs.* the NCBI nr database while the second line is for TBLASTX *vs.* dbEST. In all cases only the match with the highest significance is shown.

et al. 1996; Zhang and Wing 1997), or DNA microchip arrays for genome scanning (Nelson *et al.* 1993; Shalon *et al.* 1996) currently provide the best prospects to meet the needs of maize researchers.

Four features combined to heighten the utility of this map as a foundation for basic and applied investigations in such areas as gene organization, gene and genome evolution, cloning of single genes, and dissection of complex traits. They are the use of a variety of probe types, availability of sequence information for a majority of the loci, designation of a group of core markers, and mapping of grass genome reference points.

Varied probe types: In this study we have utilized both cDNA and genomic clones as probes. Initial maize maps were based primarily on random genomic DNA probes, which have the advantage of being relatively straightforward and rapid to make. Most genomic probes have been derived by cutting hypomethylated regions with *Pst*I. The copy number is usually lower for genomic than cDNA probes, possibly because of exon or 5′/3′-UTR divergence of the genomic fragments. Given the chromosomal duplication present in the maize genome, genomic probes are often advantageous as reference markers in comparisons between different maize mapping populations. Because many of the genomic clones are single copy, it is easy to infer position information from one genetic background to another because there is no confusion regarding which fragment corresponds to which locus. Use of ESTs as probes for mapping, on the other hand, facilitates the association of functionality with phenotype—for example, coincidental location of an EST having a known product with a phenotypic mutant with the appropriate developmental or biochemical defect (see examples later in this discussion). In addition to traditional hybridization-based markers, several SSR loci have been mapped. SSRs offer a more rapid, radiation-free alternative to hybridization-based marker technologies. Although these markers are more easily adapted to high-throughput mapping, further development in maize is needed to generate enough markers to provide thorough coverage of the entire genome in diverse genetic backgrounds.

Data from 1383 markers that have been mapped in rice indicate that 33% of the rice markers were single copy and another 31% were "near single copy" (Kurata *et al.* 1994). These percentages are much greater than the 19% for single-copy markers observed in this study. The higher hybridization temperatures used in the maize study would favor lower copy number of clones in maize relative to rice if hybridization conditions were responsible for the observed difference in magnitude of single-copy clones. The difference between maize and rice in percentage of low-copy-number markers likely reflects the chromosomal duplication present in the maize genome (Wendel *et al.* 1986; Helentjaris *et al.* 1988).

Sequence availability: Only 34% of the loci with sequence information remain functionally uncharacterized by the criteria used in this experiment. This is encouraging, both because a high percentage of loci with sequence information could be tentatively assigned functions and because the number of loci without putative function should decrease with time as additional information regarding sequence and function is made available through the public sequence databases. As of July 20, 1998, Arabidopsis, rice, and maize represent only 3.9% of the 1.7 million sequences in dbEST. To continue to fully utilize the molecular map as a discovery and development tool, additional plant cDNAs must be sequenced and mapped. Sequence information is fundamental in unraveling the relationship of biochemical processes to developmental and agronomic characteristics. The sequence from a given maize cDNA can be searched against a continuously expanding library of sequence information within maize, among other plant species, and more broadly among the animal and human sequences that are publicly available. Matches can be used in an attempt to assign functionality to a given phenotype.

Although the number of maize genes sequenced is much lower than that of Arabidopsis genes, the number of loci mapped is comparable and the percentage with putative function is greater. The Arabidopsis EST project has sequenced ~10,000 distinct genes, representing about half of the estimated total gene number (Delseny *et al.* 1997). Of those, 40% have putative function and 1500 ESTs have been placed on the physical map. The comparison with rice is somewhat different. More than 10,500 unique sequences have been identified representing approximately one-third of all the rice genes; however, only 25% of the clones have significant protein similarity (Yamamoto and Sasaki 1997). The lower similarity compared to maize and Arabidopsis may reflect the differences in number and types of tissues used to construct the cDNA libraries in each organism. Approximately 2300 DNA markers, including 2000 RFLP markers, have been mapped on the RGP rice map (Nagamura *et al.* 1997). The number of loci mapped in any of the plant species pales by comparison to the more than 10,400 loci mapped in a single STS map of the human genome (Stewart *et al.* 1997). Recent estimates indicate that approximately one-half of the total genes in the human genome have been sequenced and that only ~21% of these have significant similarity to a known protein (Schuler *et al.* 1996). It is speculated that the lower percentage of putative functions identified for the human genome sequences is the result of bias introduced by ESTs that contain 3′-untranslated regions that are not protein encoding and thus are not capable of matching known proteins.

Constructing a molecular map containing expressed sequence-tagged sites is the first step toward generating an expression map for an organism. This information

can be used to examine tissue, organ, and/or developmental specificity of gene expression for individual members of a multigene family. Alternatively, it can be used to examine the pattern of gene expression along a particular region of a chromosome to answer such questions as, "are the genes for a particular developmental event clustered on the chromosome?" Additional information to be gained includes common motifs or higher order structures obtained through comparison of promoter regions from different genes expressed in the same tissue or organ or at the same developmental time.

Core markers: The entire set of core markers and their sequences are publicly available. This enables the chromosomal regions identified as significant contributors to qualitative and quantitative traits to be assigned to bins on the same framework, referred to as the bin map. Alignment of RFLP, genetic, and cytological maps can also be made on the basis of the framework established by the core markers. The five *csu* clones that encode isozymes previously placed by phenotype on the genetic map provide new reference points for integrating the molecular and classical genetic maps. Additional ESTs from the Brookhaven and INRA maize maps (Burr *et al.* 1996; Causse *et al.* 1996) can be assigned relative map positions, thereby enhancing the number of loci with information about function. The 376 common loci that exist between this map and the BNL map will provide for alignment among maize molecular maps. Currently, a resource of 5179 loci that have been catalogued to bin is available in MaizeDB.

The combination of sequence and function information for an increasing proportion of the loci on the map, coupled with cataloguing of loci into bins delineated by the core markers, opens the door for identification of potential associations of functions with phenotypes by coincidence, serendipity, and concurrence. One such example involves clone p-csu186, a single-copy cDNA that maps to bin 2.02. Sequence similarity information indicates this clone has homology to ent-kaurene synthase B from *Cucurbita maxima*. Examination of phenotypic mutants present in bin 2.02 identified a dwarf mutant, *d5*, that has been biochemically characterized as a defect in cyclization to ent-kaurene synthase B (Phinney 1984). The coincidental location of a putative ent-kaurene synthase B cDNA with a phenotypic mutant altered in the same biochemical reaction illustrates the potential of utilizing the maize bins to group molecular and phenotypic information to facilitate molecular dissection of traits.

Grass genome reference points: Several investigators have identified a colinear relationship among loci in members of the grass family (Hulbert *et al.* 1990; Whitkus *et al.* 1992; Bennetzen and Freeling 1993; Moore *et al.* 1993). Alignment of sequence data and map locations across organisms will become an increasingly important aspect of future discovery and development strategies. To facilitate this alignment, 237 loci identified with nonmaize probes have been included in the map to provide grass genome reference points. Alignment of common markers on maps of other members of the grass family with those on the maize map allows tentative assignment of additional functionality to the maize map by relative placement of loci not mapped in maize onto the maize bin map. This type of electronic mapping will speed the progress of gene discovery while reducing costs. Such electronic mapping is not without caveats. Although colinearity among grasses exists for large genomic regions, chromosomal rearrangements and genome divergence necessitate a moderately high number of reference points between species before a meaningful integration of information can be achieved between organisms. Once integrated, the markers represent a tentative assignment of additional functions to a particular bin because of potential differences in gene copy number and tissue specificity that have occurred during the course of speciation and evolution. Currently, 221 loci are shared with the RGP rice map, 237 loci with the Cornell University map, and a similar number with the sorghum map. The loci catalogued to bin will be expanded in the near future by the addition of EST and phenotypic loci from analogous regions in rice (G. Davis, unpublished results).

Just as in the case cited earlier of coincidental function and phenotype within maize, sequence homology information and mapping information from different species can be combined to provide a powerful discovery tool for comparisons of function *vs.* phenotype. An example of this involves a candidate cDNA, p-csu838, and a phenotype represented by a QTL for days to pollen shed. This cDNA has homology to a LUMINIDEPENDENS protein from Arabidopsis that corresponds to an Arabidopsis mutant that displays a late-flowering phenotype. The maize cDNA maps to bin 3.05. QTL data from a tropical maize population collected at two locations indicate that a QTL for days to pollen shed also occurs in bin 3.05 (Cimmyt 1994). This example shows a potential link between phenotypes from a dicot and a monocot on the basis of sequence homology and relative map position.

Colinearity combined with homology information leads to the next phase of discovery: comparing function, expression, and phenotype across species. This increases the power to determine what makes each species unique and how evolutionary forces work to shape a new species.

The information presented here coupled with map and sequence information from other maize studies and other grass species provides a strong foundation upon which to build an integrated understanding of sequence, biochemical and metabolic functions, and phenotypic effect. Future large-scale sequencing and mapping efforts will expand on these discovery tools.

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LITERATURE CITED

Agrama, H. A. S., and M. E. Moussa, 1996 Mapping QTLs in breeding for drought tolerance in maize (*Zea mays* L.) Euphytica **91:** 89–97.

Ajmone-Marsan, P., G. Monfredini, W. F. Ludwig, A. E. Melchinger, P. Franceschini *et al.*, 1994 Identification of genomic regions affecting plant height and their relationship with grain yield in an elite maize cross. Maydica **39:** 133–139.

Altschul, S. F., W. Gish, W. Miller, E. W. Myers and D. J. Lipman, 1990 Basic local alignment search tool. J. Mol. Biol. **215:** 403–410.

Austin, D. F., and M. Lee, 1996a Genetic resolution and verification of quantitative trait loci for flowering and plant height with recombinant inbred lines of maize. Genome **39:** 957–968.

Austin, D. F., and M. Lee, 1996b Comparative mapping in F-2:3 and F-6:7 generations of quantitative trait loci for grain yield and yield components in maize. Theor. Appl. Genet. **92:** 817–826.

Beavis, W. D., and D. Grant, 1991 A linkage map based on information from four F_2 populations of maize (*Zea mays* L.). Theor. Appl. Genet. **82:** 636–644.

Beavis, W. D., M. Lee, D. Grant, A. R. Hallauer, T. Owens *et al.*, 1992 The influence of random mating on recombination among RFLP loci. Maize Gen. Coop. Newsl. **66:** 52–53.

Beckett, J. B., 1991 Cytogenetic, genetic, and plant breeding applications of B-A translocations in maize, pp. 493–529 in *Chromosome Engineering in Plants: Genetics, Breeding, and Evolution*, Part A, edited by P. K. Gupta and T. Tsuchiya. Elsevier Science Publishers, Amsterdam.

Bennetzen, J. L., and M. Freeling, 1993 Grasses as a single genetic system: genome composition, colinearity, and compatibility. Trends Genet. **9:** 259–261.

Birnboim, H. C., 1983 A rapid alkaline extraction method for the isolation of plasmid DNA. Methods Enzymol. **100:** 243–255.

Boguski, M. S., T. M. Lowe and C. M. Tolstoshev, 1993 dbEST—database for "expressed sequence tags." Nat. Genet. **4**(4): 332–333.

Bohn, M., M. Khairallah, D. Gonzalez de Leon, D. A. Hoisington, H. Utz *et al.*, 1996 QTL mapping in tropical maize. 1. Genomic regions affecting leaf feeding resistance to sugarcane borer and other traits. Crop Sci. **36:** 1352–1361.

Burr, B., F. A. Burr, K. H. Thompson, M. C. Albertsen and C. W. Stuber, 1988 Gene mapping with recombinant inbreds in maize. Genetics **118:** 519–526.

Burr, B., F. A. Burr and E. Matz, 1996 Molecular map of T232 × CM37 and CO159 × Tx303 recombinant inbred populations. Maize Genome Database (http://www.agron.missouri.edu).

Byrne, P. F., M. D. McMullen, M. E. Snook, T. Musket, J. M. Theuri *et al.*, 1996 Quantitative trait loci and metabolic pathways: genetic control of the concentration of maysin, a corn earworm resistance factor, in maize silks. Proc. Natl. Acad. Sci. USA **93:** 8820–8825.

Causse, M., J. P. Rocher, A. M. Henry, A. Charcosset, J. L. Prioul *et al.*, 1995 Genetic dissection of the relationship between carbon metabolism and early growth in maize, with emphasis on key-enzyme loci. Mol. Breed. **1:** 259–272.

Causse, M., S. Santoni, C. Damerval, A. Maurice, A. Charcosset *et al.*, 1996 A composite map of expressed sequences in maize. Genome **39:** 418–432.

Chao, S., C. Baysdorfer, O. Heredia-Diaz, T. Musket, G. Xu *et al.*, 1994 RFLP mapping of partially sequenced leaf cDNA clones in maize. Theor. Appl. Genet. **88:** 717–721.

Cimmyt, 1994 QTL data for populations Ki3 × CML139 and CML131 × CML67. Maize Genome Database (http://www.agron.missouri.edu).

Coe, E. H., D. A. Hoisington and M. G. Neuffer, 1987 Linkage map of corn(maize) (*Zea mays* L.). Maize Genet. Coop. Newslett. **61:** 116–147.

Coe, E. H., G. L. Davis, M. D. McMullen, T. Musket and M. Polacco, 1995 Gene list and working maps. Maize Genet. Coop. Newslett. **69:** 191–192.

Cox, D. R., M. Burmeister, E. R. Price, S. Kim and R. M. Myers, 1990 Radiation hybrid mapping: a somatic cell genetic method for constructing high-resolution maps of mammalian chromosomes. Science **250:** 245–250.

Damerval, C., A. Maurice, J. M. Josse and D. de Vienne, 1994 Quantitative trait loci underlying gene product variation: a novel perspective for analyzing regulation of genome expression. Genetics **137:** 289–301.

Delseny, M., R. Cooke, M. Raynal and F. Grellet, 1997 The *Arabidopsis thaliana* cDNA sequencing projects. FEBS Letters **405:** 129–132.

Edwards, M. D., T. Helentjaris, S. Wright and C. W. Stuber, 1992 Molecular-marker-facilitated investigations of quantitative trait loci in maize. 4. Analysis based on genome saturation with isozyme and restriction fragment length polymorphism markers. Theor. Appl. Genet. **83:** 765–774.

Emerson, R. A., G. W. Beadle and A. C. Fraser, 1935 A summary of linkage studies in maize. Cornell Univ. Agric. Exp. Stn. Memoir **180:** 1–83.

Frova, C., and M. Sari-Gorla, 1994 Quantitative trait loci (QTLs) for pollen thermotolerance detected in maize. Mol. Gen. Genet. **245:** 424–430.

Gardiner, J., E. H. Coe, Jr., S. Melia-Hancock, D. A. Hoisington and S. Chao, 1993 Development of a core RFLP map in maize using an Immortalized-F_2 population. Genetics **134:** 917–930.

Harushima, Y., M. Yano, A. Shomura, M. Sato, T. Shimano *et al.* 1998 A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics **148:** 479–494.

Helentjaris, T., M. Slocum, S. Wright, A. Schaefer and J. Nienhuis, 1986 Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. Theor. Appl. Genet. **72:** 761–769.

Helentjaris, T., D. Weber and S. Wright, 1988 Identification of the genomic locations of duplicate nucleotide sequences in maize by analysis of restriction fragment length polymorphisms. Genetics **118:** 353–363.

Hulbert, S. H., T. E. Richter, J. D. Axtell and J. L. Bennetzen, 1990 Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. Proc. Natl. Acad. Sci. USA **87:** 4251–4255.

Keith, C. S., D. O. Hoang, B. M. Barrett, B. Feigleman, M. C. Nelson *et al.*, 1993 Partial sequence analysis of 130 randomly selected maize cDNA clones. Plant Physiol. **101:** 329–332.

Kurata, N., Y. Nagamura, K. Yamamoto, Y. Harushima, N. Sue *et al.*, 1994 A 300 kilobase interval genetic map of rice including 883 expressed sequences. Nature Genet. **8:** 365–372.

Lebreton, C., V. Lazic-Jancic, A. Steed, S. Pekic and S. A. Quarrie, 1995 Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. J. Exp. Bot. **46:** 853–865.

Lubberstedt, T., A. E. Melchinger, C. C. Schon, H. Utz and D. Klein, 1997 QTL mapping in testcrosses of European flint lines of maize. 1. Comparison of different testers for forage yield traits. Crop Sci. **37:** 921–931.

Matz, E. C., F. A. Burr and B. Burr, 1995 Molecular map based

on TxCM and COxTx recombinant inbred families. Maize Gen. Coop. Newsl. **69:** 257–267.

Moore, G., M. D. Gale, N. Kurata and R. B. Flavell, 1993 Molecular analysis of small grain cereal genomes: current status and prospects. Bio/Technology **11:** 594–599.

Nagamura, Y., B. A. Antonio and T. Sasaki, 1997 Rice molecular genetic map using RFLPs and its application. Plant Mol. Biol. **35:** 79–87.

Nelson, S. F., J. H. McCusker, M. A. Sander, Y. Kee, P. Modrich *et al.*, 1993 Genomic mismatch scanning: a new approach to genetic linkage mapping. Nat. Genet. **4**(1): 11–18.

Pe, M. E., L. Gianfranceschi, G. Taramino, R. Tarchini, P. Angelini *et al.*, 1993 Mapping quantitative trait loci (QTLs) for resistance to *Gibberella zeae* infection in maize. Mol. Gen. Genet. **241:** 11–16.

Phinney, B. O., 1984 Gibberellin A1, dwarfism, and the control of shoot elongation in higher plants, pp. 17–41 in *The Biosynthesis and Metabolism of Plant Hormones*, edited by A. Crozier and F. R. Hillman. Cambridge University Press, Cambridge, United Kingdom.

Quarrie, S. A., A. Steed, C. Lebreton, M. Gulli, C. Calestani *et al.*, 1994 QTL analysis of ABA production in wheat and maize and associated physiological traits. Russ. J. Plant Physiol. **41:** 565–571.

Roman, H., and A. J. Ullstrup, 1951 The use of A-B translocations to locate genes in maize. Agron. J. **43:** 450–454.

Saghai-Maroof, M. A., K. M. Soliman, R. Jogensen and R. W. Allard, 1984 Ribosomal DNA Spacer length in barley: Mendelian inheritance, chromosomal location, and population dynamics. Proc. Natl. Acad. Sci. USA **81:** 8014–8018.

Sari-Gorla, M., M. E. Pe and L. Rossini, 1994 Detection of QTLs controlling pollen germination and growth in maize. Heredity **72:** 332–335.

Schmidt, R., J. West, K. Love, Z. Lenchan, D. Lister *et al.*, 1995 Physical map and organization of *Arabidopsis thaliana* chromosome 4. Science **270:** 480–483.

Schuler, G. D., M. S. Boguski, E. A. Stewart, L. D. Stein, G. Gyapay *et al.*, 1996 A gene map of the human genome. Science **274:** 540–546.

Senior, M. L., and M. Heun, 1993 Mapping maize microsatellites and polymerase chain reaction confirmation of the targeted repeats using a CT primer. Genome **36**(5): 884–889.

Shalon, D., S. J. Smith and P. O. Brown, 1996 A DNA microarray system for analyzing complex DNA samples using two-color fluorescent probe hybridization. Genome Res. **6:** 639–645.

Stewart, E. A., K. B. McKusick, A. Aggarwal, E. Bajorek, S. Brady *et al.*, 1997 An STS-based radiation hybrid map of the human genome. Genome Res. **7**(5): 422–433.

Taramino, G., and S. Tingey, 1996 Simple sequence repeats for germplasm analysis and mapping in maize. Genome **39**(2): 277–287.

Veldboom, L. R., and M. Lee, 1994 Molecular-marker-facilitated studies of morphological traits in maize. 2. Determination of QTLs for grain yield and yield components. Theor. Appl. Genet. **89:** 451–458.

Veldboom, L. R., M. Lee and W. L. Woodman, 1994 Molecular-marker-facilitated studies in an elite maize population. 1. Linkage analysis and determination of QTL for morphological traits. Theor. Appl. Genet. **88:** 7–16.

Weber, D., and T. Helentjaris, 1989 Mapping RFLP loci in maize using B-A translocations. Genetics **121:** 583–590.

Wendel, J. F., C. W. Stuber, M. D. Edwards and M. M. Goodman, 1986 Duplicated chromosome segments in maize (*Zea mays* L.): further evidence from hexokinase isozymes. Theor. Appl. Genet. **72:** 178–185.

Whitkus, R., J. Doebley and M. Lee, 1992 Comparative genome mapping of sorghum and maize. Genetics **132:** 1119–1130.

Yamamoto, K., and T. Sasaki, 1997 Large-scale EST sequencing in rice. Plant Mol. Biol. **35:** 135–144.

Zachgo, E. A., M. L. Wang, J. Dewdney, D. Bouchez, C. Camilleri *et al.*, 1996 A physical map of chromosome 2 of *Arabidopsis thaliana*. Genome Res. **6:** 19–25.

Zhang, H. B., and R. A. Wing, 1997 Physical mapping of the rice genome with BACs. Plant Mol. Biol. **35:** 115–127.

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