

The Molecular Genetics of Crop Domestication

John F. Doebley, Brandon S. Gaut, and Bruce D. Smith

Table S1. Some Genes of Interest in Crop Domestication and Improvement

Gene(s)	Crop	Molecular and Phenotypic Function	Controls Phenotype ¹	Selection Evidence ²	Causative Change ³	Reference
Genes Identified as Controlling Domestication Traits						
<i>tb1</i>	Maize	Transcriptional regulator (TCP); plant and inflorescence structure	Yes	Yes	Reg	Wang et al., 1999
<i>tga1</i>	Maize	Transcriptional regulator (SBP); seed casing	Yes	Yes	AC	Wang et al., 2005
<i>qSH1</i>	Rice	Transcriptional regulator (homeodomain); abscission layer formation, shattering	Yes	N.T.	Reg	Konishi et al., 2006
<i>Rc</i>	Rice	Transcriptional regulator (bHLH); seed color	Yes	N.T.	Coding	Sweeney et al., 2006
<i>sh4</i>	Rice	Transcriptional regulator (Myb3); abscission layer formation, shattering	Yes	N.T.	Reg/AC	Li et al., 2006
<i>fw2.2</i>	Tomato	Cell signaling; fruit weight	Yes	N.T.	Reg	Frary et al., 2000
<i>Q</i>	Wheat	Transcriptional regulator (AP2); inflorescence structure	Yes	N.T.	Reg/AC	Simons et al., 2006
Genes Identified as Controlling Varietal Differences						
<i>c1</i>	Maize	Transcriptional regulator (MYB); kernel color	Yes	Yes	Reg	Hanson et al., 1996
<i>r1</i>	Maize	Transcriptional regulator (bHLH); kernel color	Yes	N.T.	Reg	Hanson et al., 1996
<i>sh2</i>	Maize	pyrophosphorylase; supersweet sweet corn	Yes	N.T.	TE	Bhave et al., 1990
<i>sul</i>	Maize	isoamylase; sweet corn gene	Yes	Yes	AC	Dinges et al., 2001
<i>y1</i>	Maize	Phytoene synthase; carotenoid content	Yes	Yes	Reg	Palaisa et al., 2003
<i>brix9-2-5</i>	Tomato	Invertase; fruit soluble solid content	Yes	N.T.	Reg	Fridman et al., 2000, 2004
<i>ovate</i>	Tomato	Unknown; fruit shape	Yes	N.T.	EStp	Liu et al., 2002
<i>rin</i>	Tomato	Transcriptional regulator (MADS); fruit ripening	Yes	N.T.	Reg	Vrebalov et al., 2002
<i>sp</i>	Tomato	Cell signaling; determinant plant growth	Yes	N.T.	AC	Pnueli et al., 1998
<i>R</i>	Pea	Starch branching enzyme; seed sugar content	Yes	N.T.	TE	Bhattacharyya et al., 1990
<i>ehd1</i>	Rice	B-type response regulator; flowering time	Yes	N.T.	AC	Doi et al., 2004
<i>gn1</i>	Rice	Cytokinin oxidase/dehydrogenase; grain number	Yes	N.T.	Reg/EStp	Ashikari et al., 2005
<i>hd1</i>	Rice	Transcriptional regulator (zinc finger); flowering time	Yes	N.T.	Coding	Yano et al., 2000
<i>hd6</i>	Rice	Protein kinase; flowering time	Yes	N.T.	EStp	Takahashi et al., 2001
<i>sdl</i>	Rice	GA20 oxidase; plant height	Yes	Yes	Coding	Hedden, 2003; Nagano et al., 2005;

<i>waxy</i>	Rice	Starch synthase; sticky grains	Yes	Yes	Splice	Wang et al., 1995; Olsen and Purugganan, 2002
<i>rht</i>	Wheat	Transcriptional regulator (SH2); plant height	Yes	N.T.	EStp	Peng et al., 1999
<i>vrn1</i>	Wheat	Transcriptional regulator (MADS); vernalization	Yes	N.T.	Reg	Yan et al., 2003
<i>vrn2</i>	Wheat	Transcriptional regulator (ZCCT); vernalization	Yes	N.T.	AC	Yan et al., 2004
Genes Identified by Selection Screens Targeted on Individual Candidate Genes						
<i>boCal</i>	Cauliflower	Transcriptional regulator (MADS); inflorescence structure	Candidate	Yes	EStp?	Purugganan, et al., 2000
<i>bal</i>	Maize	Transcriptional regulator (bHLH); plant and inflorescence structure	Candidate	Yes	-	Gallavotti et al., 2004
<i>ral</i>	Maize	Transcriptional regulator (MYB); inflorescence structure	Candidate	Yes	-	Vollbrecht et al. 2005
<i>su1, bt2, ael</i>	Maize	Starch biosynthetic enzymes	Candidate	Yes	-	Whitt et al., 2002
Genes Identified through Untargeted Selection Screens						
<i>zagll</i>	Maize	Transcriptional regulator (MADS)	Unknown	Yes	-	Vigouroux et al., 2002
17 genes	Maize	Varied functions, including auxin response, growth factor, kinase, methyl binding protein, transcription factors, amino acid biosynthesis and a circadian gene	Unknown	Yes	-	Yamasaki et al., 2005
~30 genes	Maize	Varied functions, including auxin response, cell elongation protein, F-box protein, growth factor, heat shock proteins, hexokinase, kinase, steroid biosynthesis, transcription factors, amino acid biosynthesis and a circadian gene	Unknown	Yes	-	Wright et al., 2005

¹For a version of the table with references for each gene see supplemental information.

²For genes listed as “candidate,” it is known that major mutations at these genes affect phenotype, but it has not been shown that natural allelic variation controls agronomically important differences between crops and progenitors or between crop varieties. For genes listed as “unknown”, there is no experimental evidence demonstrating an effect of these genes on agronomic phenotypes in the crop listed.

³N.T. signifies not tested.

⁴AC = amino acid change, coding = disrupted coding sequence, EStp = early stop codon, Reg = regulatory change, Splice = intron splicing defect, and TE= transposon insertion.

Supplemental References

- Ashikari, M., Sakakibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., Angeles, E. R., Qian, Q., Kitano, H., and Matsuoka, M. (2005). Cytokinin oxidase regulates rice grain production. *Science* 309, 741-745.
- Bhattacharyya, M. K., Smith, A. M., Ellis, T. H., Hedley, C., and Martin, C. (1990). The wrinkled-seed character of pea described by Mendel is caused by a transposon-like insertion in a gene encoding starch-branching enzyme. *Cell* 60, 115-122.
- Bhave, M. R., Lawrence, S., Barton, C., and Hannah, L. C. (1990). Identification and molecular characterization of shrunken-2 cDNA clones of maize. *Plant Cell* 2, 581-588.
- Dinges, J., Colleoni, C., Myers, A., and James, M. (2001). Molecular structure of three mutations at the maize *sugary1* locus and their allele-specific phenotypic effects. *Plant Physiology* 125, 1406-1418.
- Doi, K., Izawa, T., Fuse, T., Yamanouchi, U., Kubo, T., Shimatani, Z., Yano, M., and Yoshimura, A. (2004). Ehd1, a B-type response regulator in rice, confers short-day promotion of flowering and controls FT-like gene expression independently of Hd1. *Genes Dev* 18, 926-936.
- Frary, A., Nesbitt, T. C., Grandillo, S., Knaap, E., Cong, B., Liu, J., Meller, J., Elber, R., Alpert, K. B., and Tanksley, S. D. (2000). fw2.2: a quantitative trait locus key to the evolution of tomato fruit size. *Science* 289, 85-88.
- Fridman, E., Carrari, F., Liu, Y. S., Fernie, A. R., and Zamir, D. (2004). Zooming in on a quantitative trait for tomato yield using interspecific introgressions. *Science* 305, 1786-1789.
- Fridman, E., Pleban, T., and Zamir, D. (2000). A recombination hotspot delimits a wild-species quantitative trait locus for tomato sugar content to 484 bp within an invertase gene. *Proc Natl Acad Sci U S A* 97, 4718-4723.
- Gallavotti, A., Zhao, Q., Kyojuka, J., Meeley, R. B., Ritter, M. K., Doebley, J. F., Pe, M. E., and Schmidt, R. J. (2004). The role of barren stalk1 in the architecture of maize. *Nature* 432, 630-635.
- Hanson, M. A., Gaut, B. S., Stec, A. O., Fuerstenberg, S. I., Goodman, M. M., Coe, E. H., and Doebley, J. F. (1996). Evolution of anthocyanin biosynthesis in maize kernels: the role of regulatory and enzymatic loci. *Genetics* 143, 1395-1407.
- Hedden, P. (2003). The genes of the Green Revolution. *Trends Genet* 19, 5-9.
- Li, C., Zhou, A., and Sang, T. (2006). Genetic analysis of rice domestication syndrome with the wild annual species, *Oryza nivara*. *New Phytologist* (*in press*).
- Liu, J., Van Eck, J., Cong, B., and Tanksley, S. D. (2002). A new class of regulatory genes underlying the cause of pear-shaped tomato fruit. *Proc Natl Acad Sci U S A* 99, 13302-13306.
- Konishi, S., T. Izawa, et al. (2006). An SNP caused loss of seed shattering during rice domestication. *Science* 312, 1392-1396.
- Nagano, H., Onishi, K., Ogasawara, M., Horiuchi, Y., and Sano, Y. (2005). Genealogy of the "Green Revolution" gene in rice. *Genes Genet Syst* 80, 351-356.
- Olsen, K. M., and Purugganan, M. D. (2002). Molecular evidence on the origin and evolution of glutinous rice. *Genetics* 162, 941-950.
- Palaisa, K. A., Morgante, M., Williams, M., and Rafalski, A. (2003). Contrasting effects of selection on sequence diversity and linkage disequilibrium at two phytoene synthase loci. *Plant Cell* 15, 1795-1806.

- Peng, J., Richards, D. E., Hartley, N. M., Murphy, G. P., Devos, K. M., Flintham, J. E., Beales, J., Fish, L. J., Worland, A. J., Pelica, F., *et al.* (1999). 'Green revolution' genes encode mutant gibberellin response modulators. *Nature* *400*, 256-261.
- Pnueli, L., Carmel-Goren, L., Hareven, D., Gutfinger, T., Alvarez, J., Ganai, M., Zamir, D., and Lifschitz, E. (1998). The SELF-PRUNING gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of CEN and TFL1. *Development* *125*, 1979-1989.
- Purugganan, M. D., Boyles, A. L., and Suddith, J. I. (2000). Variation and selection at the CAULIFLOWER floral homeotic gene accompanying the evolution of domesticated Brassica oleracea. *Genetics* *155*, 855-862.
- Simons, K. J., Fellers, J. P., Trick, H. N., Zhang, Z., Tai, Y. S., Gill, B. S., and Faris, J. D. (2006). Molecular characterization of the major wheat domestication gene q. *Genetics* *172*, 547-555.
- Sweeney, M. T., Thomson, M. J., Pfeil, B. E., and McCouch, S. (2006). Caught red-handed: Rc encodes a basic helix-loop-helix protein conditioning red pericarp in rice. *Plant Cell* *18*, 283-294.
- Takahashi, Y., Shomura, A., Sasaki, T., and Yano, M. (2001). Hd6, a rice quantitative trait locus involved in photoperiod sensitivity, encodes the alpha subunit of protein kinase CK2. *Proc Natl Acad Sci U S A* *98*, 7922-7927.
- Vigouroux, Y., McMullen, M., Hittinger, C. T., Houchins, K., Schulz, L., Kresovich, S., Matsuoka, Y., and Doebley, J. (2002). Identifying genes of agronomic importance in maize by screening microsatellites for evidence of selection during domestication. *Proc Natl Acad Sci U S A* *99*, 9650-9655.
- Vrebalov, J., Ruezinsky, D., Padmanabhan, V., White, R., Medrano, D., Drake, R., Schuch, W., and Giovannoni, J. (2002). A MADS-box gene necessary for fruit ripening at the tomato *ripening-inhibitor (rin)* locus. *Science* *296*, 343-346.
- Vollbrecht, E., Springer, P. S., Goh, L., Buckler, E. S. t., and Martienssen, R. (2005). Architecture of floral branch systems in maize and related grasses. *Nature* *436*, 1119-1126.
- Wang, H., Nussbaum-Wagler, T., Li, B., Zhao, Q., Vigouroux, Y., Faller, M., Bomblies, K., Lukens, L., and Doebley, J. F. (2005). The origin of the naked grains of maize. *Nature* *436*, 714-719.
- Wang, R. L., Stec, A., Hey, J., Lukens, L., and Doebley, J. (1999). The limits of selection during maize domestication. *Nature* *398*, 236-239.
- Wang, Z. Y., Zheng, F. Q., Shen, G. Z., Gao, J. P., Snustad, D. P., Li, M. G., Zhang, J. L., and Hong, M. M. (1995). The amylose content in rice endosperm is related to the post-transcriptional regulation of the waxy gene. *Plant J* *7*, 613-622.
- Whitt, S. R., Wilson, L. M., Tenaillon, M. I., Gaut, B. S., and Buckler, E. S. t. (2002). Genetic diversity and selection in the maize starch pathway. *Proc Natl Acad Sci U S A* *99*, 12959-12962.
- Wright, S. I., and Gaut, B. S. (2005). Molecular population genetics and the search for adaptive evolution in plants. *Mol Biol Evol* *22*, 506-519.
- Yamasaki, M., Tenaillon, M. I., Bi, I. V., Schroeder, S. G., Sanchez-Villeda, H., Doebley, J. F., Gaut, B. S., and McMullen, M. D. (2005). A large-scale screen for artificial selection in maize identifies candidate agronomic loci for domestication and crop improvement. *Plant Cell* *17*, 2859-2872.

- Yan, L., Loukoianov, A., Blechl, A., Tranquilli, G., Ramakrishna, W., SanMiguel, P., Bennetzen, J. L., Echenique, V., and Dubcovsky, J. (2004). The wheat VRN2 gene is a flowering repressor down-regulated by vernalization. *Science* *303*, 1640-1644.
- Yan, L., Loukoianov, A., Tranquilli, G., Helguera, M., Fahima, T., and Dubcovsky, J. (2003). Positional cloning of the wheat vernalization gene VRN1. *Proc Natl Acad Sci U S A* *100*, 6263-6268.
- Yano, M., Katayose, Y., Ashikari, M., Yamanouchi, U., Monna, L., Fuse, T., Baba, T., Yamamoto, K., Umehara, Y., Nagamura, Y., and Sasaki, T. (2000). Hd1, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the Arabidopsis flowering time gene CONSTANS. *Plant Cell* *12*, 2473-2484.