Investigating chromosome pairing in bread wheat using *ASYNAPSIS I*

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References

Able JA, Langridge P (2006) Wild sex in the grasses. *Trends Plant Sci* **11:** 261-263

Able JA, Langridge P, Milligan AS (2007) Capturing diversity in the cereals: many options but little promiscuity. *Trends Plant Sci* **12:** 71-79

Agarwal S, Roeder GS (2000) Zip3 provides a link between recombination enzymes and synaptonemal complex proteins. *Cell* **102:** 245-255

Al-Kaff N, Knight E, Bertin I, Foote T, Hart N, Griffiths S, Moore G (2007) Detailed dissection of the chromosomal region containing the *Ph1* locus in wheat *Triticum aestivum*: With deletion mutants and expression profiling. *Ann Bot - London* **101:** 863-872

Albini SM, Jones GH (1988) Synaptonemal complex spreading in *Allium cepa* and *Allium fistulosum* .2. Pachytene observations - The SC karyotype and the correspondence of late recombination nodules and chiasmata. *Genome* **30:** 399-410

Alexander M (1969) Differential staining of aborted and nonaborted pollen. *Stain Technology* **44:** 117-122

Allers T, Lichten M (2001) Differential timing and control of noncrossover and crossover recombination during meiosis. *Cell* **106:** 47-57

Anand A, Trick HN, Gill BS, Muthukrishnan S (2003) Stable transgene expression and random gene silencing in wheat. *Plant Biotechnol J* **1:** 241-251

Anderson LK, Doyle GG, Brigham B, Carter J, Hooker KD, Lai A, Rice M, Stack SM (2003) High-resolution crossover maps for each bivalent of *Zea mays* using recombination nodules. *Genetics* **165:** 849-865

Anderson LK, Hooker KD, Stack SM (2001) The distribution of early recombination nodules on zygotene bivalents from plants. *Genetics* **159:** 1259-1269

Anderson LK, Stack SM (2005) Recombination nodules in plants. *Cytogenet Genome Res* **109:** 198-204

Anderson LK, Stack SM, Todd RJ, Ellis RP (1994) A monoclonal-antibody to lateral element proteins in synaptonemal complexes of *Lilium longiflorum*. *Chromosoma* **103:** 357-367

Anuradha S, Muniyappa K (2004a) Meiosis-specific yeast Hop1 protein promotes synapsis of double-stranded DNA helices *via* the formation of guanine quartets. *Nucleic Acids Res* **32:** 2378-2385

Anuradha S, Muniyappa K (2004b) *Saccharomyces cerevisiae* Hop1 zinc finger motif is the minimal region required for its function *in vitro*. *J Biol Chem* **279:** 28961-28969

Aragon-Alcaide L, Reader S, Beven A, Shaw P, Miller T, Moore G (1997) Association of homologous chromosomes during floral development. *Curr Biol* **7:** 905-908

Aravind L, Iyer L (2002) The SWIRM domain: a conserved module found in chromosomal proteins points to novel chromatin-modifying activities. *Genome Biol* **3:** 1-7

Aravind L, Koonin E (1998) The HORMA domain: a common structural denominator in mitotic checkpoints, chromosome synapsis and DNA repair. *Trends Biochem Sci* **23:** 284-286

Armstrong S, Caryl A, Jones G, Franklin F (2002) Asy1, a protein required for meiotic chromosome synapsis, localizes to axis-associated chromatin in Arabidopsis and *Brassica*. *J Cell Sci* **115:** 3645-3655

Armstrong S, Franklin F, Jones G (2001) Nucleolus-associated telomere clustering and pairing precede meiotic chromosome synapsis in *Arabidopsis thaliana*. *J Cell Sci* **114:** 4207-4217

Bass HW (2003) Telomere dynamics unique to meiotic prophase: formation and significance of the bouquet. *Cell Mol Life Sci* **60:** 2319-2324

Bass HW, Marshall WF, Sedat JW, Agard DA, Cande WZ (1997) Telomeres cluster *de novo* before the initiation of synapsis: A three-dimensional spatial analysis of telomere positions before and during meiotic prophase. *J Cell Biol* **137:** 5-18

Baurle I, Dean C (2006) The timing of developmental transitions in plants. *Cell* **125:** 655-664

Bennett M, Smith J (1972) The effects of polyploidy on meiotic duration and pollen development in cereal anthers. *Proc R Soc Lond Ser B* **181:** 81-107

Bennett M, Smith J, Bayliss M (1973) Cell development in the anther, the ovule, and the young seed of *Triticum aestivum* L. var. Chinese Spring. *Phil Trans R Soc Lond Ser* **266:** 39-81

Bennett M, Smith J, Simpson S, Wells B (1979) Intranuclear fibrillar material in cereals pollen mother cells. *Chromosoma* **71:** 289-332

Bennett MD, Chapman V, Riley R (1971) Duration of meiosis in pollen mother cells of wheat, rye and triticale. *Proc R Soc Lond Ser B* **178:** 259

Bernstein E, Caudy AA, Hammond SM, Hannon GJ (2001) Role for a bidentate ribonuclease in the initiation step of RNA interference. *Nature* **409:** 363-366

Bishop DK (1994) RecA homologs Dmc1 and Rad51 interact to form multiple nuclear-complexes prior to meiotic chromosome synapsis. *Cell* **79:** 1081-1092

Bishop DK, Zickler D (2004) Early decision: Meiotic crossover interference prior to stable strand exchange and synapsis. *Cell* **117:** 9-15

Boden SA, Shadiac N, Tucker EJ, Langridge P, Able JA (2007) Expression and functional analysis of TaASY1 during meiosis of bread wheat (*Triticum aestivum*). *BMC Mol Biol* **8:** doi:10.1186/1471-2199-1188-1165

Bogdanov Y, Dadashev S, Grishaeva T (2003) *In silico* search for functionally similar proteins involved in meiosis and recombination in evolutionary distant organisms. *In Silico Biol* **3:** 173-185

Borner GV, Kleckner N, Hunter N (2004) Crossover/noncrossover differentiation, synaptonemal complex formation, and regulatory surveillance at the leptotene/zygotene transition of meiosis. *Cell* **117:** 29-45

Bradford M (1976) A rapid and sensitive method for quantification of microgram quantities of protein utilizing the principle of protein-dye-binding. *Anal Biochem* **72:** 248-254

Burton R, Shirley N, King B, Harvey A, Fincher G (2004) The CesA gene family of barley. Quantitative analysis of transcripts reveals two groups of co-expressed genes. *Plant Physiol* **134:** 224-236

Carballo JA, Johnson AL, Sedgwick SG, Cha RS (2008) Phosphorylation of the axial element protein Hop1 by Mec1/Tel1 ensures meiotic interhomolog recombination. *Cell* **132:** 758-770

Carpenter A (1975) Electron microscopy of meiosis in *Drosophila melanogaster* females. I. Structure, arrangement and temporal change of the synaptonemal complex in wild-type. *Chromosoma* **51:** 157-182

Carpenter T (1979) Synaptonemal complex and recombination nodules in wild type *Drosophila melanogaster* females. *Genetics* **92:** 511-541

Carpenter T (1987) Gene conversion, recombination nodules, and the initiation of meiotic synapsis. *Bioessays* **6:** 232-236

Carpenter T (1988) Thoughts on recombination nodules, meiotic recombination, and chiasmata. In *Genetic recombination*, Kucherlapati R, Smith G (eds), pp 529-548. Washington DC: American Society of Microbiology

Carpentier S, Witters E, Laukens K, Deckers P, Sweenen R, Panis B (2005) Preparation of protein extracts from recalcitrant plant tissues: an evaluation of different methods for two-dimensional gel electrophoresis analysis. *Proteomics* **5:** 2497-2507

Caryl AP, Armstrong SJ, Jones GH, Franklin FCH (2000) A homologue of the yeast HOP1 gene is inactivated in the Arabidopsis meiotic mutant *asy1*. *Chromosoma* **109:** 62-71

Chand J (2004) *TaASY1*: A putative matchmaker. Department of Plant and Pest Science, University of Adelaide, Adelaide

Chelysheva L, Diallo S, Vezon D, Gendrot G, Vrielynck N, Belcram K, Rocques N, Marquez-Lema A, Bhatt AM, Horlow C, Mercier R, Mezard C, Grelon M (2005) AtREC8 and AtSCC3 are essential to the monopolar orientation of the kinetochores during meiosis. *J Cell Sci* **118:** 4621-4632

Chen CB, Zhang W, Timofejeva L, Gerardin Y, Ma H (2005) The Arabidopsis ROCK-N-ROLLERS gene encodes a homolog of the yeast ATP-dependent DNA helicase MER3 and is required for normal meiotic crossover formation. *Plant J* **43:** 321-334

Cogoni C, Macino G (1999) Gene silencing in *Neurospora crassa* requires a protein homologous to RNA-dependent RNA polymerase. *Nature* **399:** 166-169

Colas I, Shaw P, Prieto P, Wanous M, Spielmeyer W, Mago R, Moore G (2008) Effective chromosome pairing requires chromatin remodeling at the onset of meiosis. *Proc Natl Acad Sci U S A* **105:** 6075-6080

Comai L, Tyagi AP, Lysak MA (2003) FISH analysis of meiosis in Arabidopsis allopolyploids. *Chromosome Res* **11:** 217-226

Couteau F, Nabeshima K, Villeneuve A, Zetka M (2004) A component of *C. elegans* meiotic chromosome axes at the interface of homolog alignment, synapsis, nuclear reorganization, and recombination. *Curr Biol* **14:** 585-592

Crismani W, Baumann U, Sutton T, Shirley N, Webster T, Spangenberg G, Langridge P, Able JA (2006) Microarray expression analysis of meiosis and microsporogenesis in hexaploid bread wheat. *BMC Genomics* **7:** doi: 10.1186/1471-2164-1187-1267

Cunado N, Blazquez S, Melchor L, Pradillo M, Santos JL (2005) Understanding the cytological diploidization mechanism of polyploid wild wheats. *Cytogenet Genome Res* **109:** 205-209

Czechowski T, Stitt M, Altmann T, Udvardi MK, Scheible WR (2005) Genome-wide identification and testing of superior reference genes for transcript normalization in Arabidopsis. *Plant Physiol* **139:** 5-17

Dalmay T, Hamilton A, Rudd S, Angell S, Baulcombe DC (2000) An RNA-Dependent RNA polymerase gene in Arabidopsis is required for post-transcriptional gene silencing mediated by a transgene but not by a virus. *Cell* **101:** 543-553

de los Santos T, Hollingsworth NM (1999) Red1p, a MEK1-dependent phosphoprotein that physically interacts with Hop1p during meiosis in yeast. *J Biol Chem* **274:** 1783-1790

De Muyt A, Vezon D, Gendrot G, Gallois JL, Stevens R, Grelon M (2007) AtPRD1 is required for meiotic double strand break formation in *Arabidopsis thaliana*. *EMBO J* **26:** 4126-4137

Dernburg A, Sedat J, Cande W, Bass HW (1995) Cytology of telomeres. In *Telomeres*, Blackburn E, Greider C (eds), pp 295–338. Cold Spring Harbor, NY: Cold Spring Harbor Lab

Doutriaux MP, Couteau F, Bergounioux C, White C (1998) Isolation and characterisation of the RAD51 and DMC1 homologs from *Arabidopsis thaliana*. *Mol Gen Genet* **257:** 283-291

Driscoll C (1972) Genetic suppression of homologous chromosome pairing in hexaploid wheat. *Can J Genet Cytol* **14:** 39-42

Dvorak J, Lukaszewski AJ (2000) Centromere association is an unlikely mechanism by which the wheat *Ph1* locus regulates metaphase I chromosome pairing between homoeologous chromosomes. *Chromosoma* **109:** 410-414

Endo T, Gill B (1996) The deletion stocks of common wheat. *J Hered* **87:** 295-307

Fedotova YS, Kolomiets OL, Bogdanov YF (1989) Synaptonemal complex transformations in rye microsporocytes at the diplotene stage of meiosis. *Genome* **32:** 816-823

Feldman M (1966) The effect of chromosome 5A, 5B and 5D on chromosome pairing in *Triticum aestivum*. *Proc Natl Acad Sci U S A* **55:** 1447 - 1453

Feldman M (1993) Cytogenetic activity and mode of action of the pairing homoeologous (*Ph1*) gene of wheat. *Crop Sci* **33:** 894-897

Feldman M, Levy AA (2005) Allopolyploidy - a shaping force in the evolution of wheat genomes. *Cytogenet Genome Res* **109:** 250-258

Feldman M, Lupton F, Miller T (1995) *Evolution in crop plants*, 2 edn. London: Longman Scientific.

Feldman M, Mello-Sampayo T (1967) Suppression of homoeologous pairing in hybrids of polyploid wheats x *Triticum speltoides*. *Can J Genet Cytol* **9:** 307-313

Franklin AE, McElver J, Sunjevaric I, Rothstein R, Bowen B, Cande WZ (1999) Three-dimensional microscopy of the Rad51 recombination protein during meiotic prophase. *Plant Cell* **11:** 809-824

Fung J, Marshall W, Dernburg A, Agard D, Sedat J (1998) Homologous chromosome pairing in *Drosophila melanogaster* proceeds through multiple independent initiations *J Cell Biol* **141:** 5-20

Furuse M, Nagase Y, Tsubouchi H, Murakami-Murofushi K, Shibata T, Ohta K (1998) Distinct roles of two separable *in vitro* activities of yeast Mre11 in mitotic and meiotic recombination. *EMBO J* **17:** 6412-6425

Gaut BS (2001) Patterns of chromosomal duplication in maize and their implications for comparative maps of the grasses. *Genome Res* **11:** 55-66

Gaut BS, Doebley JF (1997) DNA sequence evidence for the segmental allotetraploid origin of maize. *Proc Natl Acad Sci U S A* **94:** 6809-6814

Gill KS, Gill BS, Endo TR, Mukai Y (1993) Fine physical mapping of *Ph1*, a chromosome-pairing regulator gene in polyploid wheat. *Genetics* **134:** 1231-1236

Giroux CN, Dresser ME, Tiano HF (1989) Genetic-control of chromosome synapsis in yeast meiosis. *Genome* **31:** 88-94

Goldstein P, Slaton D (1982) Synaptonemal complexes of *Caenorhabditis elegans*: Comparison of wild-type and mutant strains and pachytene karyotype analysis of wild-type. *Chromosoma* **84:** 585-597

Golubovskaya I, Hamant O, Timofejeva L, Wang C, Braun D, Meeley R, Cande W (2006) Alleles of *afd1* dissect REC8 functions during meiotic prophase I. *J Cell Sci* **119:** 3306-3315

Golubovskaya IN, Harper LC, Pawlowski WP, Schichnes D, Cande WZ (2002) The *pam1* gene is required for meiotic bouquet formation and efficient homologous synapsis in maize (*Zea mays* L.). *Genetics* **162:** 1979-1993

Gomez MI, Islam-Faridi MN, Zwick MS, Czeschin DG, Hart GE, Wing RA, Stelly DM, Price HJ (1998) Tetraploid nature of sorghum bicolor (L.) Moench. *J Hered* **89:** 188-190

Grant D, Cregan P, Shoemaker RC (2000) Genome organisation in dicots: Genome duplication in Arabidopsis and synteny between soybean and Arabidopsis. *Proc Natl Acad Sci USA* **97:** 4168-4173

Grant V (1971) *Plant speciation*, New York: Columbia University Press.

Gregory RI, Chendrimada TP, Cooch N, Shiekhattar R (2005) Human RISC couples microRNA biogenesis and posttranscriptional gene silencing. *Cell* **123:** 631-640

Grelon M, Vezon D, Gendrot G, Pelletier G (2001) AtSPO11-1 is necessary for efficient meiotic recombination in plants. *EMBO J* **20:** 589-600

Griffiths S, Sharp R, Foote TN, Bertin I, Wanous M, Reader S, Colas I, Moore G (2006) Molecular characterization of *Ph1* as a major chromosome pairing locus in polyploid wheat. *Nature* **439:** 749-752

Hamant O, Ma H, Cande W (2006) Genetics of meiotic prophase I in plants. *Annu Rev Plant Biol* **57:** 267-302

Hammond SM, Bernstein E, Beach D, Hannon GJ (2000) An RNA-directed nuclease mediates post-transcriptional gene silencing in *Drosophila* cells. *Nature* **404:** 293-296

Hannon GJ (2002) RNA interference. *Nature* **418:** 244-251

Harper L, Golubovskaya I, Cande WZ (2004) A bouquet of chromosomes. *J Cell Sci* **117:** 4025-4032

Henderson KA, Keeney S (2004) Tying synaptonemal complex initiation to the formation and programmed repair of DNA double-strand breaks. *Proc Natl Acad Sci U S A* **101:** 4519-4524

Heyer WD (1994) The search for the right partner: homologous pairing and DNA strand exchange proteins in eukaryotes. *Experientia* **50:** 223-233

Heyting C (1996) Synaptonemal complexes: structure and function. *Curr Opin Cell Biol* **8:** 389-396

Higgins JD, Armstrong SJ, Franklin FCH, Jones GH (2004) The Arabidopsis MutS homolog AtMSH4 functions at an early step in recombination: evidence for two classes of recombination in Arabidopsis. *Gene Dev* **18:** 2557-2570

Higgins JD, Sanchez-Moran E, Armstrong SJ, Jones GH, Franklin FCH (2005) The Arabidopsis synaptonemal complex protein ZYP1 is required for chromosome synapsis and normal fidelity of crossing over. *Gene Dev* **19:** 2488-2500

Hiraoka T (1952) Observational and experimental studies of meiosis with special reference to the bouquet stage. VIII. An experimental study on the cell and nuclear conditions in the bouquet stage. *Cytologia* **16:** 335-340

Hollingsworth NM, Byers B (1989) Hop1 - A yeast meiotic pairing gene. *Genetics* **121:** 445-462

Hollingsworth NM, Goetsch L, Byers B (1990) The Hop1 gene encodes a meiosis-specific component of yeast chromosomes. *Cell* **61:** 73-84

Hollingsworth NM, Ponte L (1997) Genetic interactions between HOP1, RED1 and MEK1 suggest that MEK1 regulates assembly of axial element components during meiosis in the yeast *Saccharomyces cerevisiae*. *Genetics* **147:** 33-42

Holm P (1988) Chromosome pairing and synaptonemal complex formation in hexaploid wheat, nullisomic for chromosome 5B. *Carlsberg Res Commun* **53:** 91-100

Holm P, Wang X (1988) The effect of chromosome 5B on synapsis and chiasma formation in wheat *Triticum aestivum* cv. Chinese Spring. *Carlsberg Res Commun* **53:** 191-208

Hunter N (2003) Synaptonemal complexities and commonalities. *Mol Cell* **12:** 533-535

Hunter N, Kleckner N (2001) The single-end invasion: An asymmetric intermediate at the double-strand break to double-holliday junction transition of meiotic recombination. *Cell* **106:** 59-70

Jackson N, Sanchez-Moran E, Buckling E, Armstrong SJ, Jones GH, Franklin FCH (2006) Reduced meiotic crossovers and delayed prophase I progression in AtMLH3-deficient Arabidopsis. *EMBO J* **25:** 1315-1323

Jones G (1987) Chiasmata. In *Meiosis*, Moens P (ed). New York: Academic Press Inc.

Jordan P (2006) Initiation of homologous chromosome pairing during meiosis. *Biochem Soc T* **34:** 545-549

Keeney S, Giroux CN, Kleckner N (1997) Meiosis-specific DNA double-strand breaks are catalyzed by Spo11, a member of a widely conserved protein family. *Cell* **88:** 375-384

Kerzendorfer C, Vignard J, Pedrosa-Harand A, Siwiec T, Akimcheva S, Jolivet S, Sablowski R, Armstrong S, Schweizer D, Mercier R, Schlogelhofer P (2006) The *Arabidopsis thaliana* MND1 homologue plays a key role in meiotic homologous pairing, synapsis and recombination. *J Cell Sci* **119:** 2486-2496

Khodjakov A, Gabashvili IS, Rieder CL (1999) "Dumb" versus "smart" kinetochore models for chromosome congression during mitosis in vertebrate somatic cells. *Cell Motil Cytoskel* **43:** 179-185

Kihara H (1919) Uber cytologische Studien bei einigen Getreidearten. I. Species-Bastarde des Weizens und Weizenroggen-Bastarde. *Bot Mag (Tokyo)* **33:** 17-38

Kironmai K, Muniyappa K, Friedman D, Hollingsworth N, Byers B (1998) DNA-binding activities of Hop1 protein, a synaptonemal complex component from *Saccharomyces cerevisiae*. *Mol Cell Biol* **18:** 1424–1435

Kleckner N (1996) Meiosis: How could it work? *Proc Natl Acad Sci U S A* **93:** 8167-8174

Kleckner N (2006) Chiasma formation: chromatin/axis interplay and the role(s) of the synaptonemal complex. *Chromosoma* **115:** 175-194

Klein F, Mahr P, Galova M, Buonomo SBC, Michaelis C, Nairz K, Nasmyth K (1999) A central role for cohesions in sister chromatid cohesion, formation of axial elements, and recombination during yeast meiosis. *Cell* **98:** 91-103

Klimyuk VI, Jones JDG (1997) AtDMC1, the Arabidopsis homologue of the yeast DMC1 gene: Characterization, transposon-induced allelic variation and meiosis-associated expression. *Plant J* **11:** 1-14

La Cour LF, Wells B (1970) Meiotic prophase in anthers of asynaptic wheat - a light and electron microscopical study. *Chromosoma* **29:** 419-427

Lhuissier FGP, Offenberg HH, Wittich PE, Vischer NOE, Heyting C (2007) The mismatch repair protein MLH1 marks a subset of strongly interfering crossovers in tomato. *Plant Cell* **19:** 862-876

Li WX, Chen CB, Markmann-Mulisch U, Timofejeva L, Schmelzer E, Ma H, Reiss B (2004) The Arabidopsis *AtRAD51* gene is dispensable for vegetative development but required for meiosis. *Proc Natl Acad Sci U S A* **101:** 10596-10601

Luo MC, Dubcovsky J, Dvorak J (1996) Recognition of homeology by the wheat *Ph1* locus. *Genetics* **144:** 1195-1203

Ma TL, Van Tine BA, Wei Y, Garrett MD, Nelson D, Adams PD, Wang J, Qin J, Chow LT, Harper JW (2000) Cell cycle-regulated phosphorylation of p220(NPAT) by cyclin E/Cdk2 in Cajal bodies promotes histone gene transcription. *Gene Dev* **14:** 2298-2313

Ma XF, Gustafson JP (2005) Genome evolution of allopolyploids: a process of cytological and genetic diploidization. *Cytogenet Genome Res* **109:** 236-249

MacQueen AJ, Colaiacovo MP, McDonald K, Villeneuve AM (2002) Synapsis-dependent and -independent mechanisms stabilize homolog pairing during meiotic prophase in *C. elegans*. *Gene Dev* **16:** 2428-2442

MacQueen AJ, Phillips CM, Bhalla N, Weiser P, Villeneuve AM, Dernburg AF (2005) Chromosome sites play dual roles to establish homologous synapsis during meiosis in *C. elegans*. *Cell* **123:** 1037-1050

Manton I (1950) *Problems of cytology and evolution in the Pteridophyta*, Cambridge: Cambridge University Press.

Martinez-Perez E, Moore G (2008) To check or not to check? The application of meiotic studies to plant breeding. *Curr Opin Plant Biol* **11:** 222-227

Martinez-Perez E, Shaw P, Moore G (2001) The *Ph1* locus is needed to ensure specific somatic and meiotic centromere association. *Nature* **411:** 204-207

Martinez-Perez E, Shaw P, Reader S, Aragon-Alcaide L, Miller T, Moore G (1999) Homologous chromosome pairing in wheat. *J Cell Sci* **112:** 1761 - 1769

Martinez-Perez E, Shaw P, Aragon - Alcaide L, Moore G (2003) Chromosomes form into 7 groups in hexaploid and tetraploid wheat as a prelude to meiosis. *Plant J* **36:** 21-29

Martinez J, Patkaniowska A, Urlaub H, Luhrmann R, Tuschl T (2002) Single-stranded antisense siRNAs guide target RNA cleavage in RNAi. *Cell* **110:** 563-574

Martini G, Bozzini A (1966) Radiation induced asynaptic mutations in durum wheat (*Triticum durum desf*). *Chromosoma* **20:** 251-266

McFadden E, Sears E (1946) The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *J Hered* **37:** 81-89; 107-116

McKim KS, Hayashi-Hagihara A (1998) mei-W68 in *Drosophila melanogaster* encodes a Spo11 homolog: evidence that the mechanism for initiating meiotic recombination is conserved. *Gene Dev* **12:** 2932-2942

Mello-Sampayo T (1972) Compensated monosomic 5B-trisomic 5A plants in tetraploid wheat. *Can J Genet Cytol* **14:** 463-475

Mello-Sampayo T, Canas P (1973) Suppressors of meiotic chromosome pairing in common wheat. In *Proc. 4th Int. Wheat Genet. Sym.*, pp 709-713. University of Missouri, Columbia, Mo

Mercier R, Armstrong SJ, Horlow C, Jackson NP, Makaroff CA, Vezon D, Pelletier G, Jones GH, Franklin FCH (2003) The meiotic protein SWI1 is required for axial element formation and recombination initiation in Arabidopsis. *Development* **130:** 3309-3318

Mercier R, Grelon M (2008) Meiosis in plants: ten years of gene discovery. *Cytogenet Genome Res* **120:** 281-290

Mercier R, Jolivet S, Vezon D, Huppe E, Chelysheva L, Giovanni M, Nogue F, Doutriaux MP, Horlow C, Grelon M, Mezard C (2005) Two meiotic crossover classes cohabit in Arabidopsis: One is dependent on MER3, whereas the other one is not. *Curr Biol* **15:** 692-701

Mette MF, Aufsatz W, van der Winden J, Matzke MA, Matzke AJM (2000) Transcriptional silencing and promoter methylation triggered by double-stranded RNA. *EMBO J* **19:** 5194-5201

Meuwissen R, Meerts I, Hoovers J, Leschot N, Heyting C (1992) Human synaptonemal complex protein 1 (SCP1): Isolation and characterization of the cDNA and chromosomal localization of the gene. *Genomics* **39:** 377–384

Mikhailova E, Phillips D, Sosnikhina S, Lovtsyus A, Jones R, Jenkins G (2006) Molecular assembly of meiotic proteins Asy1 and Zyp1 and pairing promiscuity in rye (*Secale cereale* L.) and its synaptic mutant sy10. *Genetics* **174:** 1247-1258

Miller TE, Reader SM, Gale MD (1983) The effect of homoeologous group-3 chromosomes on chromosome-pairing and crossability in *Triticum aestivum*. *Can J Genet Cytol* **25:** 634-641

Moens PB, Kolas NK, Tarsounas M, Marcon E, Cohen PE, Spyropoulos B (2002) The time course and chromosomal localization of recombination-related proteins at meiosis in the mouse are compatible with models that can resolve the early DNA-DNA interactions without reciprocal recombination. *J Cell Sci* **115:** 1611-1622

Moore G (2002) Meiosis in allopolyploids - the importance of 'Teflon' chromosomes. *Trends Genet* **18:** 456-463

Moreau S, Ferguson JR, Symington LS (1999) The nuclease activity of Mre11 is required for meiosis but not for mating type switching, end joining, or telomere maintenance. *Mol Cell Biol* **19:** 556-566

Morris L, Allen KE, La Thangue NB (2000) Regulation of E2F transcription by cyclinE-Cdk2 kinase mediated through p300/CBP co-activators. *Nature Cell Biol* **2:** 232-239

Moses M (1968) Synaptonemal complex. *Annu Rev Genet* **2:** 363-412

Muniyappa K, Anuradha S, Byers B (2000) Yeast meiosis-specific protein Hop1 binds to G4 DNA and promotes its formation. *Mol Cell Biol* **20:** 1361-1369

Nabeshima K, Villeneuve AM, Hillers KJ (2004) Chromosome-wide regulation of meiotic crossover formation in *Caenorhabditis elegans* requires properly assembled chromosome axes. *Genetics* **168:** 1275-1292

Nonomura K, Nakano M, Eiguchi M, Suzuki T, Kurata N (2006) PAIR2 is essential for homologous chromosome synapsis in rice meiosis I. *J Cell Sci* **119:** 217-225

Nonomura K, Nakano M, Murata K, Miyoshi K, Eiguchi M, Miyao A, Hirochika H, Kurata N (2004) An insertional mutation in the rice *PAIR2* gene, the orthologue of Arabidopsis *ASY1*, results in a defect in homologous chromosome pairing during meiosis. *Mol Genet Genomics* **271:** 121-129

Novina CD, Sharp PA (2004) The RNAi revolution. *Nature* **430:** 161-164

Okamoto M (1957) Asynaptic effect of chromosome V. *Wheat Inf Serv* **5:** 6

Orr-Weaver T (1995) Meiosis in *Drosphila*: seeing is believing. *Proc Natl Acad Sci USA* **92:** 10443-10449

Ortega S, Prieto I, Odajima J, Martin A, Dubus P, Sotillo R, Barbero JL, Malumbres M, Barbacid M (2003) Cyclin-dependent kinase 2 is essential for meiosis but not for mitotic cell division in mice. *Nature Genet* **35:** 25-31

Osman K, Sanchez-Moran E, Higgins J, Jones G, Franklin F (2006) Chromosome synapsis in Arabidopsis: analysis of the transverse filament protein ZYP1 reveals novel functions for the synaptonemal complex. *Chromosoma* **115:** 212-219

Page S, Hawley R (2001) c(3)G encodes a *Drosophila* synaptonemal complex protein. *Gene Dev* **15:** 3130–3143

Page S, Hawley R (2004) The genetics and molecular biology of the synaptonemal complex. *Annu Rev Cell Dev Biol* **20:** 525-558

Paques F, Haber JE (1999) Multiple pathways of recombination induced by double-strand breaks in *Saccharomyces cerevisiae*. *Microbiol Mol Biol R* **63:** 349-404

Pawlowski WP, Golubovskaya IN, Cande WZ (2003) Altered nuclear distribution of recombination protein RAD51 in maize mutants suggests the involvement of RAD51 in meiotic homology recognition. *Plant Cell* **15:** 1807-1816

Pawlowski WP, Golubovskaya IN, Timofejeva L, Meeley RB, Sheridan WF, Cande WZ (2004) Coordination of meiotic recombination, pairing, and synapsis by PHS1. *Science* **303:** 89-92

Pellegrineschi A, Noguera LM, Skovmand B, Brito RM, Velazquez L, Salgado MM, Hernandez R, Warburton M, Hoisington D (2002) Identification of highly transformable wheat genotypes for mass production of fertile transgenic plants. *Genome* **45:** 421-430

Peoples-Holst TL, Burgess SM (2005) Multiple branches of the meiotic recombination pathway contribute independently to homolog pairing and stable juxtaposition during meiosis in budding yeast. *Gene Dev* **19:** 863-874

Prieto P, Shaw P, Moore G (2004) Homologue recognition during meiosis is associated with a change in chromatin conformation. *Nature Cell Biol* **9:** 906-908

Raymond WE, Kleckner N (1993) Rad50 protein of *Saccharomyces cerevisiae* exhibits ATP-dependent DNA-binding. *Nucleic Acids Res* **21:** 3851-3856

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. *Nature* **182:** 713-715

Riley R, Chapman V (1975) Genetic control of the cytological diploid behaviour of hexaploid wheat. *Nat Rev Mol Cell Bio* **182:** 712-715

Riley R, Chapman V, Young R, Belfield A (1966) Control of meiotic chromosome pairing by the chromosomes of homoeologous group 5 of *Triticum aestivum*. *Nature* **212:** 1475-1477

Roberts M, Reader S, Dalgliesh C, Miller T, Foote T, Fish L, Snape J, Moore G (1999) Induction and characterisation of *Ph1* wheat mutants. *Genetics* **153:** 1909 - 1918

Rockmill B, Sym M, Scherthan H, Roeder GS (1995) Roles for 2 RecA homologs in promoting meiotic chromosome synapsis. *Gene Dev* **9:** 2684-2695

Romanienko PJ, Camerini-Otero RD (2000) The mouse Spo11 gene is required for meiotic chromosome synapsis. *Mol Cell* **6:** 975-987

Ross K, Fransz P, Armstrong S, Vizir I, Mulligan B, Franklin F, Jones G (1997) Cytological characterisation of four meiotic mutants of Arabidopsis isolated from T-DNA transformed lines. *Chromosome Res* **5:** 551-559

Sambrook F, Fritsch E, Maniatis F (1989) *Molecular Cloning: A Laboratory Manual*, 2nd edn. Cold Spring Harbour: Cold Spring Habour Laboratory Press.

Sanchez-Moran E, Santos JL, Jones GH, Franklin FCH (2007) ASY1 mediates AtDMC1-dependent interhomolog recombination during meiosis in Arabidopsis. *Gene Dev* **21:** 2220-2233

Sanchez Moran E, Armstrong SJ, Santos JL, Franklin FCH, Jones GH (2001) Chiasma formation in *Arabidopsis thaliana* accession Wassileskija and in two meiotic mutants. *Chromosome Res* **9:** 121-128

Sax K (1927) Chromosome behaviour in *Triticum* hybrids. In *Verhandlungen des V. Int. Kongresses fur Vererbungswissenschaft*, Vol. 2, pp 1267-1284. Berlin

Schalk JAC, Dietrich AJJ, Vink ACG, Offenberg HH, van Aalderen M, Heyting C (1998) Localization of SCP2 and SCP3 protein molecules within synaptonemal complexes of the rat. *Chromosoma* **107:** 540-548

Scherthan H (2001) A bouquet makes ends meet. *Nat Rev Mol Cell Bio* **2:** 621-627

Schommer C, Beven A, Lawrenson T, Shaw P, Sablowski R (2003) AHP2 is required for bivalent formation and for segregation of homologous chromosomes in Arabidopsis meiosis. *Plant J* **36:** 1-11

Schultz A (1913) *Die Geschichte der kultivierten Getreide*, Halle: Nebert.

Sears E (1976) Genetic control of chromosome pairing in wheat. *Annu Rev Genet* **10:** 31-51

Sears E (1977) An induced mutant with homoeologous pairing in common wheat. *Can J Genet Cytol* **19:** 585–593

Sears E (1982) A wheat mutation conditioning an intermediate level of homoeologous chromosome pairing. *Can J Genet Cytol* **24:** 715-719

Sears E, Okamoto M (1958) Intergenomic chromosome relationships in hexaploid wheat. In *Proc. 10th Int. Cong. Genet.*, Vol. 2, pp 258-259. Montreal

Sharma A, Sharma A (1980) Chromosome techniques – Theory and Practice. pp 155-188 London: Butterworths

Shoemaker RC, Polzin K, Labate J, Specht J, Brummer EC, Olson T, Young N, Concibido V, Wilcox J, Tamulonis JP, Kochert G, Boerma HR (1996) Genome duplication in soybean (Glycine subgenus soja). *Genetics* **144:** 329-338

Sijen T, Fleenor J, Simmer F, Thijssen KL, Parrish S, Timmons L, Plasterk RHA, Fire A (2001) On the role of RNA amplification in dsRNA-triggered gene silencing. *Cell* **107:** 465-476

Smith A, Roeder G (1997) The yeast Red1 protein localizes to the cores of meiotic chromosomes. *J Cell Biol* **136:** 957-967

Stack SM, Anderson LK (1986a) The relation between synapsis, the synaptonemal complex, and crossing over in *Zea mays*. *Am J Bot* **73:** 687-688

Stack SM, Anderson LK (1986b) Two-dimensional sreads of synaptonemal complexes from solanaceous plants .2. synapsis in *Lycopersicon esculentum* (Tomato). *American Journal Of Botany* **73:** 264-281

Stack SM, Anderson LK, Sherman JD (1989) Chiasmata and recombination nodules in *Lilium longiflorum*. *Genome* **32:** 486-498

Stebbins G (1950) *Variation and evolution in plants*, New York: Columbia University Press.

Stebbins G (1971) *Chromosomal evolution in higher plants*, London: Edward Arnold Publishers.

Sutton T, Whitford R, Baumann U, Dong C, Able J, Langridge P (2003) The *Ph2* pairing homoeologous locus of wheat (*Triticum aestivum*): identification of candidate meiotic genes using a comparative genomics approach. *Plant J* **36:** 443-456

Sym M, Engebrecht J, Roeder G (1993) ZIP1 is a synaptonemal complex protein required for meiotic chromosome synapsis. *Cell* **72:** 365–378

Thomas CL, Jones L, Baulcombe DC, Maule AJ (2001) Size constraints for targeting post-transcriptional gene silencing and for RNA-directed methylation in *Nicotiana benthamiana* using a potato virus X vector. *Plant J* **25:** 417-425

Tsubouchi T, Roeder GS (2005) A synaptonemal complex protein promotes homology-independent centromere coupling. *Science* **308:** 870-873

Uanschou C, Siwiec T, Pedrosa-Harand A, Kerzendorfer C, Sanchez-Moran E, Novatchkova M, Akimcheva S, Woglar A, Klein F, Schlogelhofer P (2007) A novel plant gene essential for meiosis is related to the human CtIP and the yeast COM1/SAE2 gene. *EMBO J* **26:** 5061-5070

Vandesompele J, De Preter K, Pattyn F, Poppe B, Van Roy N, De Paepe A, Speleman F (2002) Accurate normalization of real-time quantitative RT-PCR data by geometric averaging of multiple internal control genes. *Genome Biol* **3:** 1-11

Vignard J, Siwiec T, Chelysheva L, Vrielynck N, Gonord F, Armstrong SJ, Schlogelhofer P, Mercier R (2007) The interplay of RecA-related proteins and the MND1-HOP2 complex during meiosis in *Arabidopsis thaliana*. *PLoS Genet* **3:** doi:10.1371/journal.pgen.0030176

Vision TJ, Brown DG, Tanksley SD (2000) The origins of genomic duplications in Arabidopsis. *Science* **290:** 2114-2117

von Wettstein D, Rasmussen S, Holm P (1984) The synaptonemal complex in genetic segregation. *Annu Rev Genet* **18:** 331-413

Wall A, Riley R, Chapman V (1971a) Wheat mutants permitting homoeologous meiotic chromosome pairing. *Genet Res* **18:** 311-328

Wall A, Riley R, Gale M (1971b) The position of a locus on chromosome 5B of *Triticum aestivum* affecting homoeologous meiotic pairing. *Genet Res* **18:** 329-339

Wan Y, Poole RL, Huttly AK, Toscano-Underwood C, Feeney K, Welham S, Gooding MJ, Mills C, Edwards KJ, Shewry PR, Mitchell RAC (2008) Transcriptome analysis of grain development in hexaploid wheat. *BMC Genomics* **9:** doi:10.1186/1471-2164-1189-1121

Wassenegger M, Heimes S, Riedel L, Sanger HL (1994) RNA-directed de-novo methylation of genomic sequences in plants. *Cell* **76:** 567-576

Wilson PJ, Riggs CD, Hasenkampf CA (2005) Plant chromosome homology: hypotheses relating rendezvous, recognition and reciprocal exchange. *Cytogenet Genome Res* **109:** 190-197

Woltering D, Baumgartner B, Bagchi S, Larkin B, Loidl J, de los Santos T, Hollingsworth N (2000) Meiotic segregation, synapsis and recombination checkpoint functions require physical interaction between chromosomal proteins Red1p and Hop1p. *Mol Cell Biol* **20:** 6646-6658

Wright M, Dawson J, Dunder E, Suttie J, Reed J, Kramer C, Chang Y, Novitzky R, Wang H, Artim-Moore L (2000) Efficient biolistic transformation of maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) using the phosphomannose isomerase gene, *pmi*, as the selectable marker. *Plant Cell Rep* **20:** 429-436

Xing SP, Zachgo S (2007) Pollen lethality: A phenomenon in Arabidopsis RNA interference plants. *Plant Physiol* **145:** 330-333

Yu HG, Koshland DE (2003) Meiotic condensin is required for proper chromosome compaction, SC assembly, and resolution of recombination-dependent chromosome linkages. *J Cell Biol* **163:** 937-947

Zamore PD, Tuschl T, Sharp PA, Bartel DP (2000) RNAi: Double-stranded RNA directs the ATP-dependent cleavage of mRNA at 21 to 23 nucleotide intervals. *Cell* **101:** 25-33

Zetka M, Kaawasaki I, Strome S, Muller F (1999) Synapsis and chiasma formation in *Caenorhabditis elegans* require HIM-3, a meiotic chromosome core component that functions in chromosome segregation. *Gene Dev* **13:** 2258-2270

Zhao JY, Kennedy BK, Lawrence BD, Barbie DA, Matera AG, Fletcher JA, Harlow E (2000) NPAT links cyclin E-Cdk2 to the regulation of replication-dependent histone gene transcription. *Gene Dev* **14:** 2283-2297

Zickler D, Kleckner N (1998) The leptotene-zygotene transition of meiosis. *Annu Rev Genet* **32:** 619-697

Zickler D, Kleckner N (1999) Meiotic chromosomes: intergrating structure and function. *Annu Rev Genet* **33:** 603-754

Zilberman D, Cao XF, Jacobsen SE (2003) ARGONAUTE4 control of locus-specific siRNA accumulation and DNA and histone methylation. *Science* **299:** 716-719

Appendix A

Figure 1 - *TaASY1* cDNA sequence.

ATGGTGATGGCTCAGAAGACGAAGGAGGCGGAGATCACGGAGCAGGACTCGCTGCTTCTAACAAGGAATT
TGCTCCGGATTGCTATATACAACATCAGCTACATCAGAGGCCTATTCCCTGAGAAGTACTTCAATGATAA
GTCTGTTCCGGCACTAGAGATGAAGATTAAGAAGCTGATGCCCATGGATGCTGAATCCAGGAGGTTGATT
GATTGGATGGAGAAAGGTGTCTATGATGCCTTACAAAAGAAATATCTCAAGACCCTTCTCTTCTGTATAT
GTGAGAAGGAGGAAGGCCCAATGATTGAAGAGTATGCCTTCTCATTTAGCTACCCCAACGCAAACGGGGA
GGAAGTTGCAATGAACATGAGTCGCACAGGGAGCAAAAAGAATAGTGCCACATTCAAGTCAAATGCAGCA
GAAGTCACTCCTGATCAGATGAGGAGCTCTGCTTGTAAGATGATCAGAACGCTAGTTTCACTTATGAGGA
CCTTGGACCAAATGCCAGAGGAGCGAACCATTCTAATGAAGCTGCTATACTATGATGATGCTACACCTGA
GGATTACGAGCCTCCCTTCTTTAAGGGTTGTGCTGAGAATGAGGCCGTAAATATATGGAACAAGAACCCC
TTGAAGATGGAAGTGGGGAATGTCAATAGCAAGCATCTTGTGTTAGCTTTGAAGGTTAAGAGTGTCCTTG
ATCCATGTGATGCTAATGATGCTAACAGTGATGATGACAAGATGAGCGTGGGTCATGAGTCAGACCAAGA
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CTCAAGTAAGAGCATGGGTATGCTCAAGAAACATGGGTACTGTTAATGCTTCAGATGTCCTTTCCAACTA
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CAGAGCACAGTCCGAAAGTTGATGGACAAAATGGTGCAAGATGGATACATTAAGAATTCAGGCAACAGAA
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CAAACGGCTGACCAGGAAATGAAAGATGGCTCGACAAACGGCCGCTTCCAGTCAGTTGGATCTGATCTTA
CCCGCACACGGGAGCTGCCGGAGCAGCAGCAGACTAACAAGGACCCAAGCAGGACTCCCACAAGCAATCG
CGAGTCGGCCACGTCCCTGGAGAGTGGGGTGCTCGGGCAGAGGATCAGGAAGTCTCTGGCTGGCGAAGAG
TCGATGTGCATGCCGGACAAGCGGACCAGGAAGGCCAGCATGGTGAAGGAGCCGATCCTCCAGCAGGTCA
AGCGCCAGAAGTCCTAG

Figure 2 - *TaASY1* genomic DNA sequence. The gene sequence of *TaASY1*, with exon sequence highlighted in yellow, and intron sequence with no background.

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GTCGATGTGCATGCCGGACAAGCGGACCAGGAAGGCCAGCATGGTAAGGAAAAAGTTCCACCTTCCTCCA
GTTAACCAAAATGATCAAATCCACAAATCTCACGCATGTGACATGCTCATCACCCTTTCAGTTGCATCAG
TTTAACAGAAACCATAAGCTTGACCACCCCTGAATTCTGCCAGCATGGTGAAGGAGCCGATCCTCCAGCA
GGTCAAGCGCCAGAAGTCCTAGTTCAGTGAGGCGGCACGGAATCGCAAGGAGCCTCGGCGCAAC

Figure 3 - *TaASY1* promoter sequence. The isolated promoter sequence of *TaASY1*, with the start codon (ATG) of the cDNA sequence shown in red.

CGACGGCCCGGGCTGGTTACTTGGCGCACATTCATGGCTAAACCAACATCAAGAGTAGCCTACCCATAATCGAGA
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TCATTGGTATTGATTACTTCACGGGGTTGGTTTTGAAAATGTGGGAAGACGTCCTAAGGCACCCTGTCCGACTAG
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AGACACCACCTACGTGTCAGGCCCACTATAGGNCACNCGTGGNCNACNGCCNGNGCNGNTATCCAAGTGAGATCT
ATGAATGGCGGACTCCATGATCATCACGTGGTTGTGCCTAGAGGCAAGACCAACAAGCCAAGTGTTCCTACTCGA
ACACATGATTGTAACGAGCAGACCCTTTCGCAACCACCTACTCGCGCATCGCCCCGTATAAAATCAAGGAGTACA
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AACAGAAACAGTTGAGGGGGGTGCCGGTCAGCCTGGCCATTTGAGGGCCGCTTGAGAGGCCCATCTAGGTCAAAA
AATCGTGACCGACCAGTGACATGGCGGATCCGCCCAGACGTATAAGGCGGGTTTGAGAGATCCGCTTGTAGATGC
TCTAAGCGCAACAAGGTAGTTGTTGCAAAGGTCCTCAACTAGCTATGATGGTAGATCAGACTGCTATTGTTATAA
ATGTTTCTGCAACCCCGTTCTTGTTGCAAGGAAGGTTACACACGTGGATGAGTAGATCGAATGGCCATTCTTGTG
CCCATCCAACGACCAGTTACGTGGCGGATGTTTTCTACTTATTCGCCGGCTGACGCGTAGCATGTCATACTCATC
TCTTTTTATTGTAATCGAACGACGGTGTAATCCGGCGATGCTGTGAGATTCGACGCACGCTTTCTGATCGACGGA
TTTAAATTTTAAATTTATTTACTAGCAGATACTAGTATTGATAGTTTTGAATGACTGGCTCGCGCATCCATGTCT
ACGATCCGCCACGGATGAAATGCCCTTAAATTCAATGCATAAAAAAACATCGAAATTTAAAGCGCTCCACAATTC
AAACAGAGCGAGACTTTCCAGCTGTCACAAGTGAAAAGGTGAACCCCTCCCGTGTCTTCTTGTCCACGCCTCGGG
GCTGGAGCCACTGCCCCGTCCTCTACAAGTACCCCTCCCATACCAAACCCCTCACGTCACCAGTCACCACCCTCT
CTCCTCTCTCTCTCCCCTCCCACCTTCCCACGCGCGCACACAACACACGCCCACCACCAGGGCGGCAAAATGGTG
AGTTCTCCCGCGCCCCCGCCCCCGCCCCCGCCCTCATCCCGTGGTTGCGCCGCCGCGCGCCCTTCCCGTCATGCT
AACCGGCGCCCCGTCGCTCTTCTCCGGTGG

Appendix B

Figure 1 – Schematic diagram of protein expression vector with *TaASY1* open reading frame.

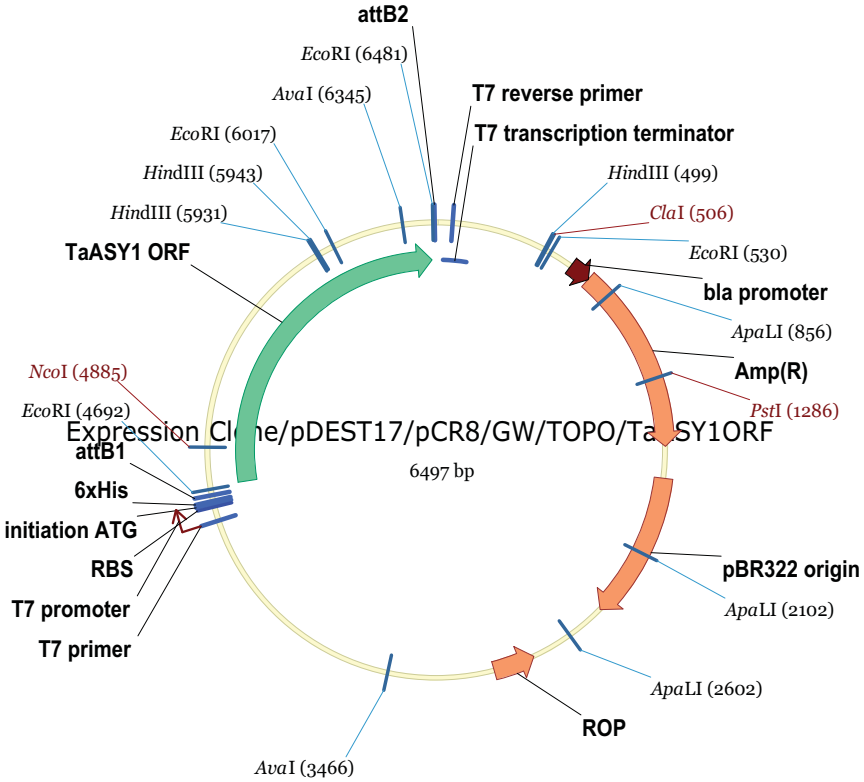
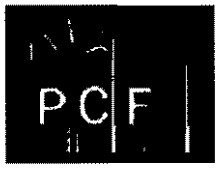


Figure 2 – Mass spectrometry report. The expressed recombinant protein displayed similarity to *Os*PAIR2, and therefore, it was identified as *Ta*ASY1.



Hanson Institute
Protein Core Facility

Mass Spectrometry Report

Jan 20, 2006

Sample: C:\MS Files\20-1-06\06-006-1.raw

Samples for identification by mass spectrometry were digested with trypsin under standardised conditions. The resulting peptides were reduced with TCEP and desalted through a C18 reverse phase silica column into the Q-Tof2 Mass Spectrometer, via a NanoSource.

The spectrometer was calibrated against the fragmentation pattern of [Glu]-Fibrino peptide B and found to be accurate to within 30 ppm.

Data was collected as intensity versus mass over charge (Th, Thompsons) and multiply charged ions (+2, +3, +4) were automatically detected and subjected to fragmentation.

The collected fragmentation data was the analysed using ProteinLynx software and searched against a FASTA protein database.

Protein identification matches were assigned if 2 or more sequenced peptides were identified from a protein in the database.

Regards,

Hanson Institute Protein Core Facility
Division of Human Immunology Level 3
IMVS Building Frome Road, Adelaide,
SA, 5000

Protein Match Details

Sample: *C:\MS Files\20-1-06\06-006-1.raw*
Accession: *37999050*
Name: *37999050*
Description: *essential protein for meiotic synapsis Oryza sativa japonica cultiv*
Confidence: *100.0*
Coverage: *7.377*
Matches: *5*
Score: *14.7098*

37999050 Coverage Map

```
1       MVMAQKTEA     EITEQDSLLL    TRNLLRIAIY    NISYIRGLFP    EKYFNDKSVP
51      ALEMKIKKLM    PMDTESRRLI    DWMERGVYDA    LQKKYLKTLL    FCICEKEEGP
101     MIEEYAFSFS    YPNTSGDEVA    MNLSRTGSKK    NSATFSNAA     EVTPDQMRS
151     ACKMIRTLVS    LMFTLDQMPE    ERTILMKLLY    YDDVTPEDYE    PPFFKCCADN
201     EAINIWNKNP    LKMEVGNVNS    KHLVLALKVK    SVLDPCDDNN    VNSEDDNMSL
251     DNESDQDNDF    SDTEVRPSEA    ERYIVAPNDG    TCKGQNGTIS    EDDTQDPVHE
301     EELTAQVREW    ICSRDTESLE    VSDVLVNFPD    ISMEMVEDIM    ERLLKDGLLS
351     RAKKDSYSVN    KIADPTTPHI    KKEVIMQNVS    PTEGTKNSNG    DLMYMKALYH
401     ALPMDYVSVG    KLHGKLDGEA    SQNMVRKLIE    KMVQDGYVKN    SANRRLGKAV
451     IHSEVTNRKL    LEIKKILEVD    IAEQMAIDTN    AEPGEPERKD    HLSGHEMRDG
501     STMGCLQSVG    SDLTRTRELP    EPQQNVSMQS    GQEASTVDKD    PSRTPTSVRE
551     QASVCSLESG    VLGQKVRKSL    AGAGGTQCSQ    DKRFRKASTV    KEPILQYVKR
601     QKSQVQVQVQ
```

Figure 3 – Negative control for immuno-gold localisation of *Ta*ASY1 by transmission electron microscopy. The negative control used in this assay was a goat anti-rabbit secondary antibody, which could not bind to the mouse anti-*Ta*ASY1 antibody. The structure shown in the image is a synaptonemal complex at pachytene. Scale bar, 200 μm.

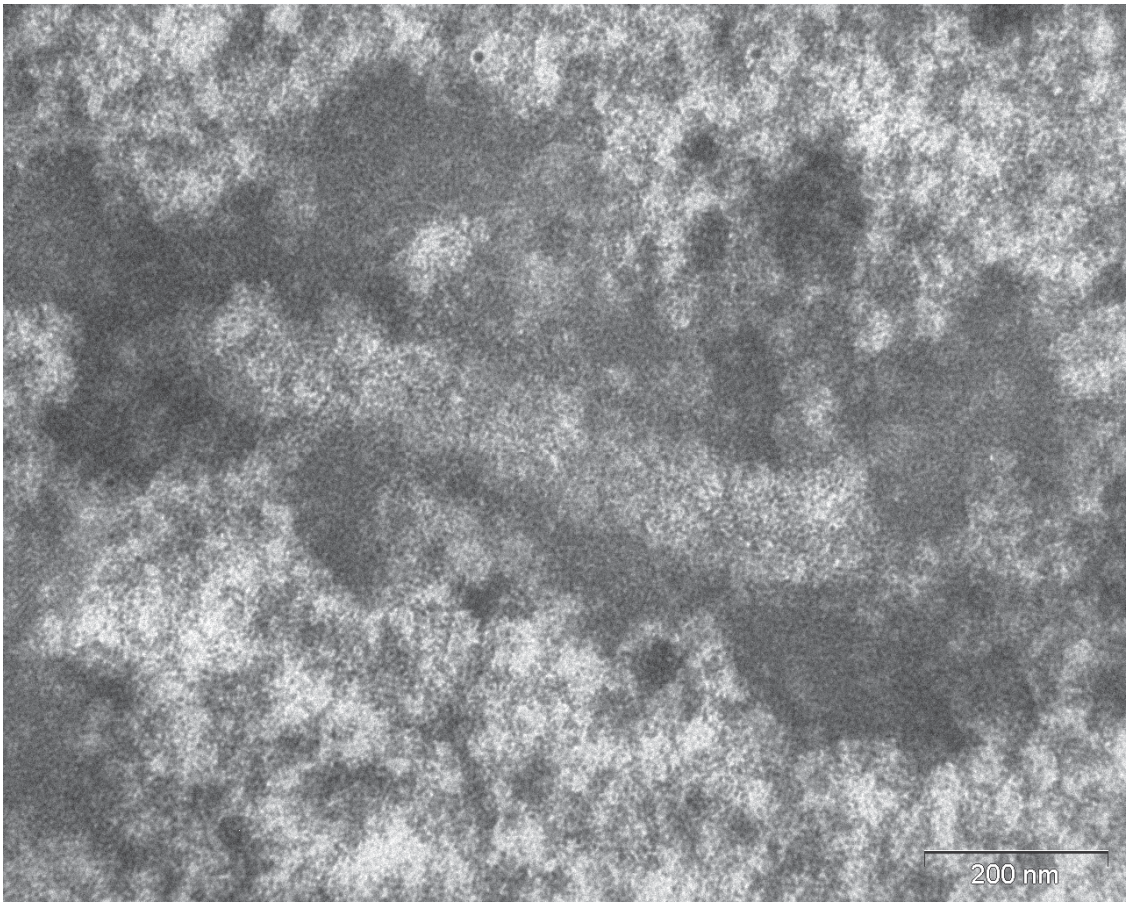
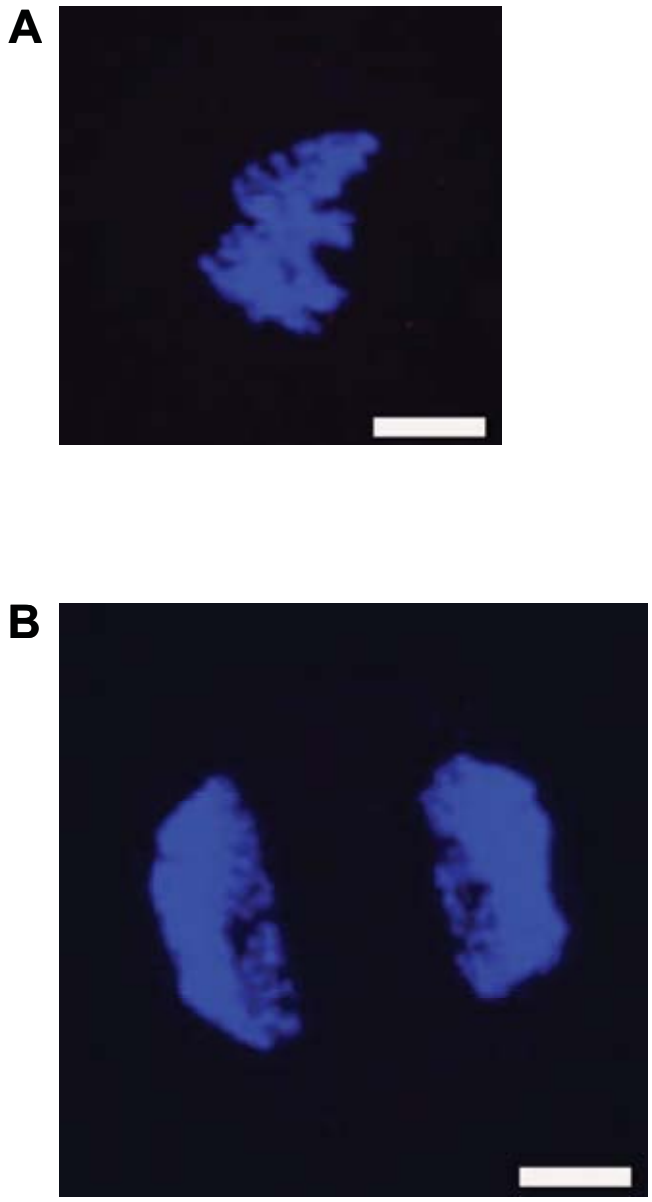


Figure 4 – Immuno-fluorescence analysis of (A) metaphase I and (B) late anaphase I cells using rabbit anti-*Ta*ASY1 antibody. These results show that during the later stages of meiosis I, there is no longer any *Ta*ASY1 protein. Scale bars, 10 μm.



Appendix C

Figure 1 – Schematic diagram of vector that was used to generate the *Taasy1* RNAi mutants. JAUA03 regions represent sense and anti-sense *TaASY1* sequence.

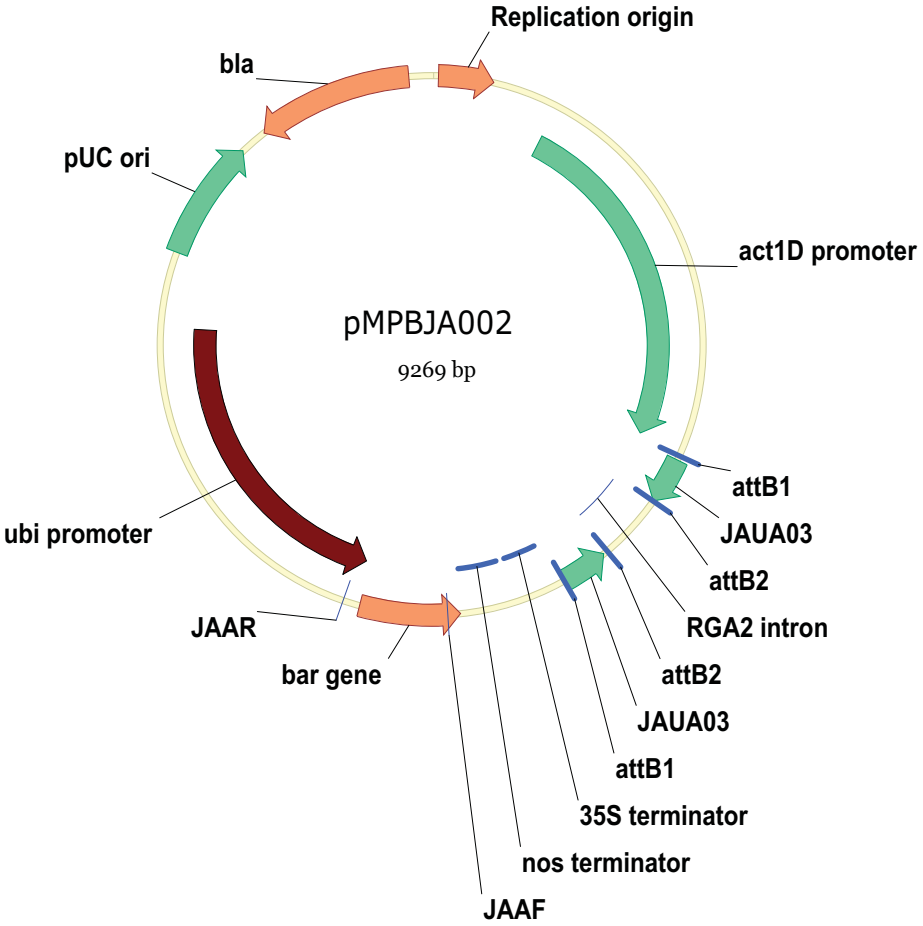


Figure 2 – Genotype analysis of T_1 generation *Taasy1* RNAi mutants. (A) Gel images of PCR analysis used to identify positive plants of lines (A) NW2804, (B) SB1984 and (C) SB1534. The fragment at 1749 bp represents the transgene fragment amplified in positive transgenic plants, while the band at 762 bp represents the endogenous *TaASY1* gene fragment conferring genomic DNA integrity. Lanes that contain both bands represent positive plants. In each sample, P = plasmid DNA control from Figure 1, W = Bob White MPB26 DNA control. The marker (M) used in (A), (B) and (C), was the Bioline Hyperladder I (Bioline, New South Wales, Australia).

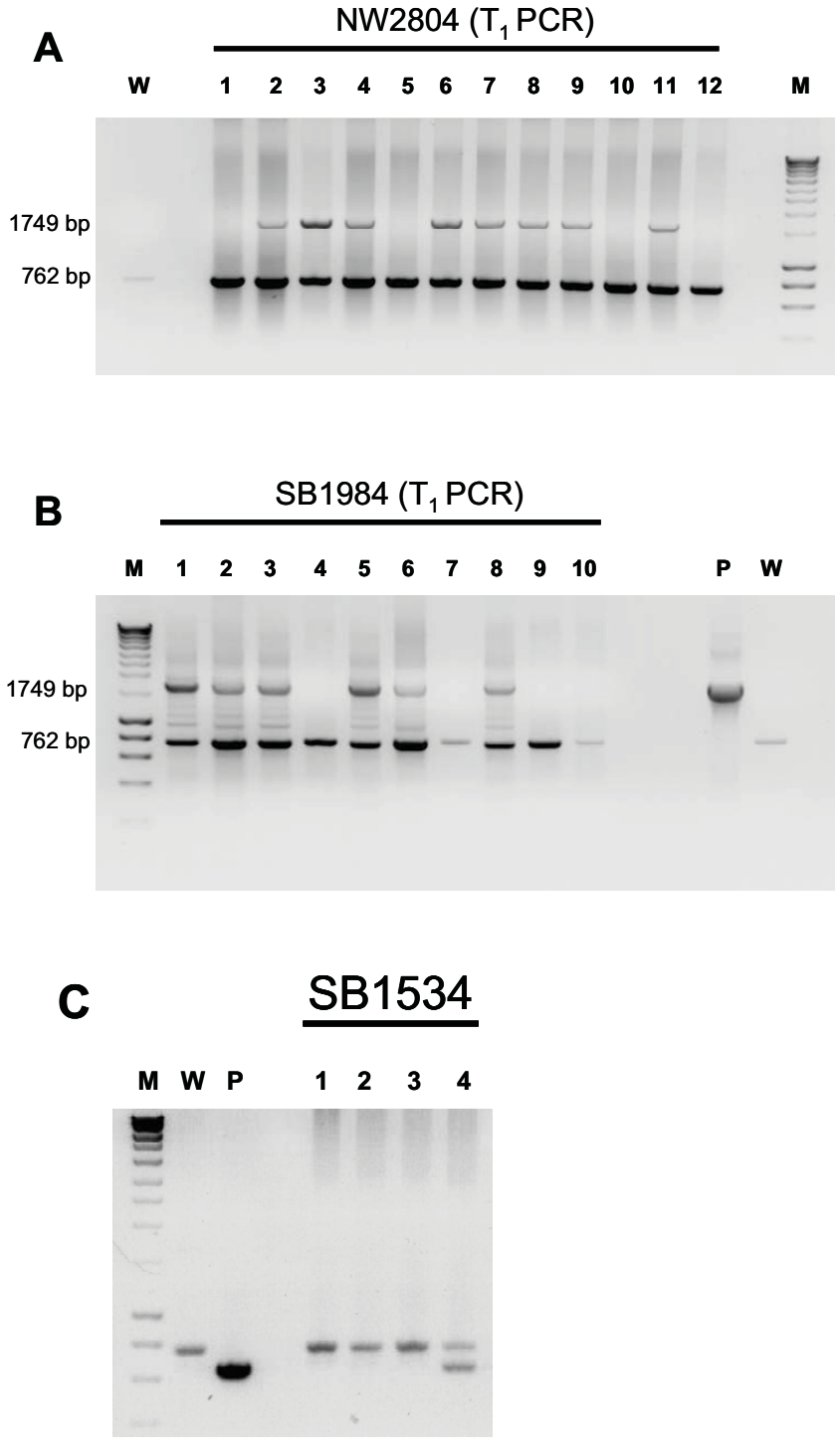

A
NW2804 (T1 PCR)
W 1 2 3 4 5 6 7 8 9 10 11 12 M
1749 bp
762 bp
B
SB1984 (T1 PCR)
M 1 2 3 4 5 6 7 8 9 10 P W
1749 bp
762 bp
C
SB1534
M W P 1 2 3 4

Figure 3 – Southern blot analysis of *Taasy1* RNAi mutants. DNA of positive plants from Figure 2 were used to identify the number of transgene insertions per line. (A) NW2804 contains 1 transgene copy, (B) SB1984 contains 6 or 7 copies, and the number of insertions for lines SB1753 and SB1534 (C) was not determined. In each blot, P = plasmid DNA control and W = Bob White MPB26 DNA control.

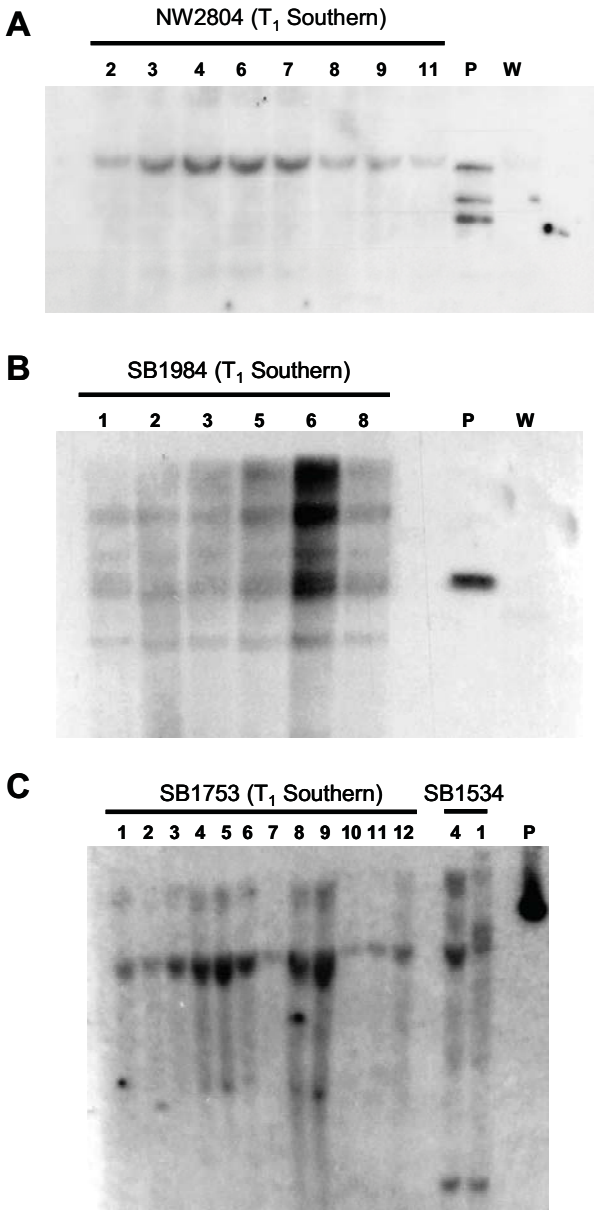
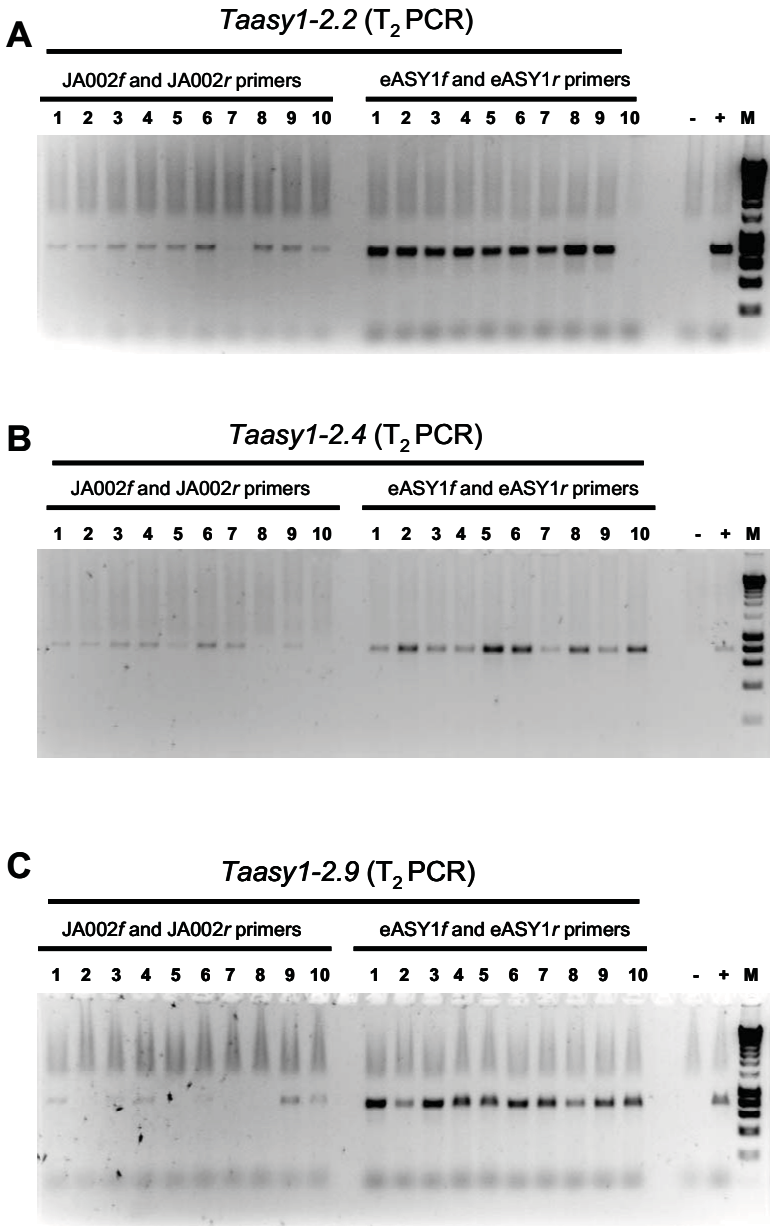
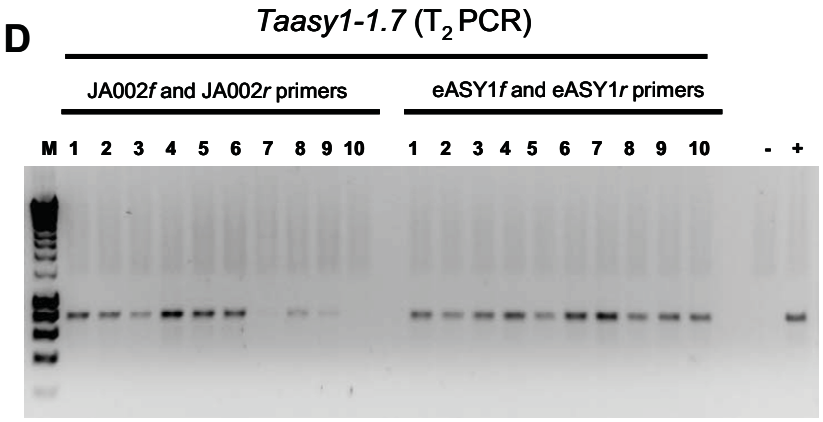
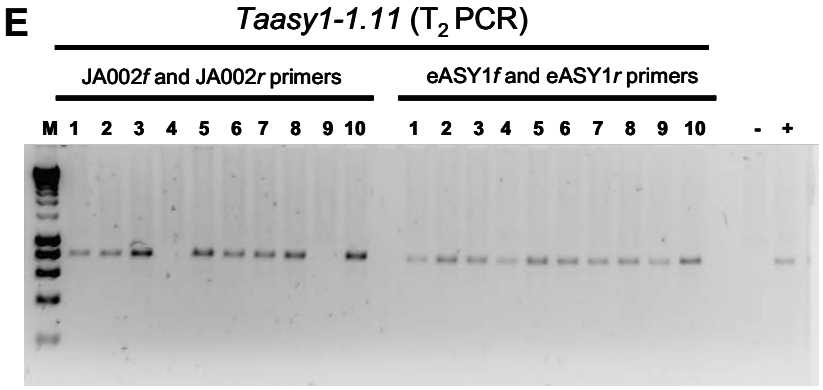
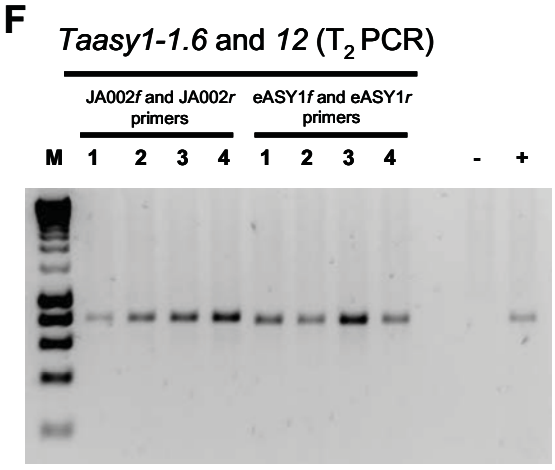


Figure 4 – PCR based genotype analysis of T_2 generation *Taasy1* mutants. T_2 PCR analysis was performed using primers JA002*f* and JA002*r* (788 bp product) to confirm presence of the transgene. Primers eASY1*f* and eASY1*r* (762 bp product) were used to confirm the genomic DNA integrity in these samples. (A) *Taasy1-2.2*; (B) *Taasy1-2.4*; (C) *Taasy1-2.9*; (D) *Taasy1-1.7*; (E) *Taasy1-1.11*; (F) *Taasy1-1.6* (lane 1) and *1.12* (lanes 2-4). (G) Lane 4 = *Taasy1-2.2.7* (from (A)), as a repeat reaction of lane 7 from (A). Other lanes in (G) equal repeat reactions of negative plants from (A)-(E). Negative control (-) = Bob White MPB26, positive control (+) = plasmid DNA from Figure 1. The marker (M) used was the Bioline Hyperladder I (Bioline).




D
Taasy1-1.7 (T2 PCR)
JA002f and JA002r primers
eASY1f and eASY1r primers
M 1 2 3 4 5 6 7 8 9 10 1 2 3 4 5 6 7 8 9 10 - +


E
Taasy1-1.11 (T2 PCR)
JA002f and JA002r primers
eASY1f and eASY1r primers
M 1 2 3 4 5 6 7 8 9 10 1 2 3 4 5 6 7 8 9 10 - +


F
Taasy1-1.6 and 12 (T2 PCR)
JA002f and JA002r primers
eASY1f and eASY1r primers
M 1 2 3 4 1 2 3 4 - +

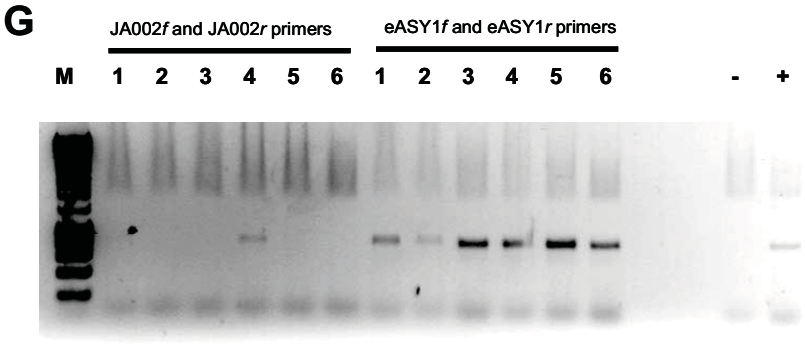

G
JA002f and JA002r primers
eASY1f and eASY1r primers
M 1 2 3 4 5 6 1 2 3 4 5 6 - +

Table 1 – Summary of fertility analysis from T_1 generation *Taasy1* mutants. For each line, an average of the fertility for the positive plants is provided, which is also expressed as a percentage of average fertility of wild-type. There is also a total provided for the number of heads (n) that were analysed.

Line	Plant	Heads	Seeds	Seed/head	Individual	Average of positives	% of Wt	n (positive heads)
SB1525	1	1	42	42	99.34%			
SB1525	2	2	0	0	0.00%			
SB1525	3	2	0	0	0.00%			
SB1525	4	3	99	33	78.06%			
SB1525	5	3	95	31.6666667	74.90%			
SB1525	6	3	1	0.33333333	0.79%			
SB1525	7	3	75	25	59.13%			
SB1525	8	3	113	37.6666667	89.09%			
SB1525	9	2	31	15.5	36.66%			
SB1525	10	3	90	30	70.96%			
SB1525	11	3	104	34.6666667	82.00%			
SB1525	12	2	6	3	7.10%	18.35	43.40%	24
NW2804	1	4	134	33.5	79.24%			
NW2804	2	2	33	16.5	39.03%			
NW2804	3	3	74	24.6666667	58.34%			
NW2804	4	2	48	24	56.77%			
NW2804	5	3	66	22	52.04%			
NW2804	6	0	0	0	0.00%			
NW2804	7	1.5	25	16.6666667	39.42%			
NW2804	8	2	58	29	68.59%			
NW2804	9	2	69	34.5	81.60%			
NW2804	10	1.5	49	32.6666667	77.27%			
NW2804	11	3	98	32.6666667	77.27%			
NW2804	12	2	76	38	89.88%	22.25	52.63%	15.5

SB1687	1	3	120	40	94.61%			
SB1687	2	1	41	41	96.98%			
SB1687	3	2	76	38	89.88%			
SB1687	4	2	68	34	80.42%			
SB1687	5	2	56	28	66.23%			
SB1687	6	4	87	21.75	51.45%			
SB1687	7	3	116	38.6666667	91.46%			
SB1687	8	4	94	23.5	55.58%			
SB1687	9	2.5	91	36.4	86.10%			
SB1687	10	2	39	19.5	46.12%			
SB1687	11	2	64	32	75.69%			
SB1687	12	4	161	40.25	95.20%	26.28333333	62.17%	15
SB1984	1	5	239	47.8	113.06%			
SB1984	2	2	68	34	80.42%			
SB1984	3	3	90	30	70.96%			
SB1984	4	4	155	38.75	91.66%			
SB1984	5	2	50	25	59.13%			
SB1984	6	4	167	41.75	98.75%			
SB1984	7	4	179	44.75	105.85%			
SB1984	8	3	144	48	113.53%			
SB1984	9	3	132	44	104.07%			
SB1984	10	2	90	45	106.44%	37.75833333	89.31%	19
SB1534	4	5	59	11.8	27.91%	11.8	27.91%	5
WT	1	4	154	38.5		42.27777778		8
WT	2	3	120	40				
WT	3	3	145	48.33				

Appendix D

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