Hybridization: Expressing yourself in a crowd

Hegarty, Matthew John

Published in:
Current Biology

DOI:
10.1016/j.cub.2011.02.035

Publication date:
2011

Citation for published version (APA):
Hegarty, M. J. (2011). Hybridization: Expressing yourself in a crowd. *Current Biology*, *21*(7), R254-R255. https://doi.org/10.1016/j.cub.2011.02.035

Hybridization: Expressing Yourself in a Crowd

What happens to the expression of homeologous gene copies during the formation of new allopolyploid hybrids and their subsequent evolution? Recent studies have shown that hybridisation may relax transcriptional regulation and enable subsequent allopolyploid generations to develop novel patterns of parental gene expression.

Matthew Hegarty

The union of two or more divergent plant genomes within a single nucleus has been the focus of increasing research as genomic techniques have become available, enabling us to deconvolute the immediate effects of hybridization from those of whole genome duplication (polyploidy). These two phenomena are often correlated in natural populations, as structural incompatibilities between the two genomes can be resolved through duplication, giving each chromosome an identical partner for meiotic pairing. One major area of study is the impact these two phenomena have on the expression of homeologous parental gene copies. Research in a variety of hybrid/allopolyploid systems has shown that the combining of divergent genomes can lead to a number of effects on gene expression, ranging from almost complete suppression of transcripts from one genome (nucleolar dominance) [1], to widespread up- or down-regulation of expression [2–4], and perhaps most intriguingly to tissue-specific silencing of one gene copy [5,6]. This latter process may occur in a reciprocal manner in different tissues, leading to partitioning of gene expression (a form of subfunctionalization). These processes are all examples of nonadditive changes to gene expression, also termed 'transcriptomic shock', in that the expression level in the hybrid is not merely additive of that observed in the parental taxa. In a new study reported in this issue of *Current Biology*, Buggs *et al.* [7] surveyed tissue-specific expression of homeologs in two populations of the allotetraploid *Tragopogon miscellus*, representing the first study of transcriptomic shock in natural populations of a recent (formed 40 generations ago) allopolyploid. Their findings help unravel the pace at which changes to gene expression occur in natural hybrid/allopolyploid populations.

Possibly one of the most interesting recent discoveries regarding gene expression in allopolyploids is the process of expression partitioning. This was first noted by Adams and co-workers [5,6] in studies of allotetraploid cotton, who noted reciprocal silencing of parental gene copies in a tissue-specific manner. This resulted in a form of subfunctionalization, allowing retention of duplicated gene copies by assigning each copy a different role within the whole organism. Later research in cotton also demonstrated that partitioning of expression could be modified in response to abiotic stimuli [8], suggesting a possible explanation for the widespread success of allopolyploid plant species. By 'selecting' which parental copy to express in a tissue, an allopolyploid can effectively 'put the best foot forward' in response to environmental change [9].

The latest study by Buggs *et al.* [7] examines the expression of 144 homeologs in the allotetraploid hybrid *Tragopogon miscellus*, which has formed reciprocally between the diploid species *T. dubius* and *T. pratensis* on multiple occasions over the last 80 years. Tissue-specific expression patterns were surveyed for two natural populations of the allotetraploid, along with *in vitro* 'hybrids' created by equal mixing of parental RNA, actual F_1 diploid hybrids and synthetic (S_1) allotetraploids. They found that, while partitioning of gene expression was frequent in the natural allotetraploids and the *in vitro* hybrids, it was markedly less common in actual F_1 hybrids and the synthetic allotetraploids. Instead, they discovered evidence of global relaxation of transcriptional regulation upon hybridization, suggesting that, unlike the rapid expression biases seen in systems such as cotton, partitioning of homeologous gene expression can instead emerge more gradually in the generations following allopolyploid formation.

Previous studies of expression bias in cotton [5,6,10], wheat [4,11] and *Arabidopsis* [2,12] had shown that hybridisation and polyploidy can immediately result in "massive and saltational disruption of ancestral expression patterns" [13], causing biases in expression of parental alleles, whether this disruption be tissue-specific or more generalized. A study of 63 gene pairs across 24 tissues in cotton [14] showed that the primary cause of this bias was hybridization, although genome duplication did reinforce and add to the effect. This was consistent with previous studies in cotton [10,12] and other systems such as rice [15], *Senecio* [3] and potato [16]. However, Chaudhary's study [14] represented the first to disentangle the effects of genome divergence, hybridization, genome duplication and allopolyploid evolution.

The findings of Buggs *et al.* [7] are therefore somewhat surprising, given that they found little evidence of partitioning in the F_1 and S_1 allopolyploids. However, their study differs from most previous assays in that they found frequent evidence of tissue-specific silencing in the diploid parents: previous studies tended to focus on genes which were expressed in both parents. In these cases, the normally silenced homeolog was reactivated in the F_1 hybrid. This phenomenon had also been observed by Chaudhary *et al.* [14] in their study of F_1 and S_1 cotton, but not on such a large scale. Chaudhary *et al.* termed this phenomenon 'expression neofunctionalization' and remarked on the consequences in terms of both duplicate gene retention and phenotypic novelty in hybrids and allopolyploids. Consistent with Buggs *et al.* [7], Chaudhary *et al.* [14] also showed that some non-partitioned homeologs could become so over the course of subsequent allopolyploid generations, revealing two distinct temporal phases of the evolution of gene expression following genome merger and duplication.

The suggestion from these findings is that tissue-specific repression of gene expression in the parent is relaxed following hybridization. This is not an

unknown phenomenon in hybrid plants: McClintock's 'genome shock' theory first proposed widespread activation of normally silenced transposons and other repetitive elements in 1984 [17] and a wealth of evidence has subsequently confirmed her hypothesis [18,19]. That a similar effect may occur in native coding elements has not been fully investigated, but Buggs *et al.* [7] suggest some examples and discuss their findings in light of research into microRNA (miRNA) and small interfering RNA (siRNA) activity in allopolyploids. Research into the allotetraploid *Arabidopsis suecica* [20] showed that siRNAs associated with transposons and other repetitive elements show global repression in S_1 allopolyploids, leading to widespread activation of normally silent elements present in the parental genomes. Expression of these siRNAs recovered in subsequent allopolyploid generations. While the *Arabidopsis* study concluded that siRNA repression had little effect on nonadditive gene expression resulting from genome merger, it also found rapid reprogramming of miRNAs and *trans*-acting siRNA (tasiRNAs) which correlated with nonadditive changes in gene expression. In *Arabidopsis,* hybridization and genome duplication occur simultaneously. Buggs *et al.* [7] propose that miRNA and siRNA repression of expression in specific tissues of the parental species is reduced in diploid F_1 hybrids and restored as the allopolyploid stabilizes. As more hybrid and allopolyploid genomes are sequenced, the role of small-RNA-mediated regulation of gene expression can be investigated in more detail.

The work of Buggs *et al.* [7] adds yet another piece to the complicated puzzle of how different hybrid systems may respond to genome mergers. Factors such as the degree of parental divergence and the mechanism of hybrid formation can result in different outcomes, explaining the differences seen in the various studies discussed here. The value of a multiple model approach to studying allopolyploidy and hybridization is therefore clear.

References

1. Pikaard, C.S. (1999). Nucleolar dominance and silencing of transcription. Trends Plant Sci. *4*, 478–483.
2. Wang, J., Tian, L., Lee, H.-S., Wei, N.E., Jiang, H., Watson, B., Madlung, A., Osborn, T.C., Doerge, R.W., Comai, L., *et al*. (2006). Genomewide nonadditive gene regulation in *Arabidopsis* allotetraploids. Genetics *172*, 507–517.
3. Hegarty, M.J., Barker, G.L., Wilson, I.D., Abbott, R.J., Edwards, K.J., and Hiscock, S.J. (2006). Transcriptome shock after interspecific hybridisation in *Senecio* is ameliorated by genome duplication. Curr. Biol. *16*, 1652–1659.
4. He, P., Friebe, B.R., Gill, B.S., and Zhou, J.M. (2003). Allopolyploidy alters gene expression in the highly stable hexaploid wheat. Plant Mol. Biol. *52*, 401–412.
5. Adams, K.L., Cronn, R., Percifield, R., and Wendel, J.F. (2003). Genes duplicated by polyploidy show unequal contributions to the transcriptome and organ-specific reciprocal silencing. Proc. Natl. Acad. Sci. USA *100*, 4649–4654.
6. Adams, K.L., Percifield, R., and Wendel, J.F. (2004). Organ-specific silencing of genes in a newly synthesized cotton allotetraploid. Genetics *168*, 2217–2226.
7. Buggs, R.J., Zhang, L., Miles, N., Tate, J.A., Gao, L., Wei, W., Schnable, P.S., Barbazuk, W.B., Soltis, P.S., and Soltis, D.E. (2011). Transcriptomic shock generates evolutionary novelty in a newly formed, natural allopolyploid plant. Curr. Biol. *21*, 551–556.
8. Liu, Z., and Adams, K.L. (2007). Expression partitioning between genes duplicated by polyploidy under abiotic stress and during organ development. Curr. Biol. *17*, 1669–1674.
9. Hegarty, M.J., and Hiscock, S.J. (2008). Genomic clues to the evolutionary success of polyploid plants. Curr. Biol. *18*, R435–R444.
10. Adams, K.L., and Wendel, J.F. (2005). Allele-specific, bidirectional silencing of an alcohol dehydrogenase gene in different organs of interspecific diploid cotton hybrids. Genetics *171*, 2139–2142.
11. Levy, A.A., and Feldman, M. (2004). Genetic and epigenetic reprogramming of the wheat genome upon allopolyploidization. Biol. J. Linn. Soc. *82*, 607–613.
12. Comai, L., Tyagi, A.P., Winter, K., Holmes-Davis, R., Reynolds, S.H., Stevens, Y., and Byers, B. (2000). Phenotypic instability and rapid gene silencing in newly formed *Arabidopsis* allotetraploids. Plant Cell *12*, 1551–1567.
13. Flagel, L.E., Udall, J., Nettleton, D., and Wendel, J. (2008). Duplicate gene expression in allopolyploid *Gossypium* reveals two temporally distinct phases of expression evolution. BMC Biol. *6*, 16.
14. Chaudhary, B., Flagel, L., Stupar, R.M., Udall, J.A., Verma, N., Springer, N.M., and Wendel, J.F. (2009). Reciprocal silencing, transcriptional bias and functional divergence of homeologs in polyploid cotton (*Gossypium*). Genetics *182*, 503–517.
15. Wang, Y.-M., Dong, Z.-Y., Zhang, Z.-J., Lin, X.-Y., Shen, Y., Zhou, D., and Liu, B. (2005). Extensive *de novo* genomic variation in rice induced by introgression from wild rice (*Zizania latifolia* Griseb.). Genetics *170*, 1945–1956.
16. Stupar, R.M., Bhaskar, P.B., Yandell, B.S., Rensink, W.A., Hart, A.L., Ouyang, S., Veilleux, R.E., Busse, J.S., Erhardt, R.J., and Buell, C.R. (2007). Phenotypic and transcriptomic changes associated with potato autopolyploidization. Genetics *176*, 2055–2067.
17. McClintock, B. (1984). The significance of responses of the genome to challenge. Science *226*, 792–801.
18. Comai, L., Madlung, A., Josefsson, C., and Tyagi, A. (2003). Do the different parental 'heteromes' cause genomic shock in newly formed allopolyploids? Phil. Trans. R. Soc. Lond. Ser. B *358*, 1149–1155.
19. Kashkush, K., Feldman, M., and Levy, A.A. (2003). Transcriptional activation of retrotransposons alters the expression of adjacent genes in wheat. Nat. Genet. *33*, 102–106.
20. Ha, M., Lu, J., Tian, L., Ramachandran, V., Kasschau, K.D., Chapman, E.J., Carrington, J.C., Chen, X., Wang, X.-J., and Chen, Z.J. (2009). Small RNAs serve as a genetic buffer against genomic shock in *Arabidopsis* interspecific hybrids and allopolyploids. Proc. Natl. Acad. Sci. USA *106*, 17835–17840.

Aberystwyth University, IBERS Penglais, Edward Llwyd Building, Aberystwyth, SY23 3DA, UK.
E-mail: ayh@aber.ac.uk

DOI: 10.1016/j.cub.2011.02.035

Cytoskeletal Regulation: Sorting Out Stress Fibers with Tropomyosin

Mechanisms governing the specification and function of non-muscle actomyosin structures, such as contractile rings and stress fibers, are poorly understood. An interesting new study now sheds some light on this topic by examining the role of tropomyosin in stress fiber organization.

Matthew Lord

Understanding how actin is harnessed for different tasks in the cell represents a major question in the cytoskeletal field. One protein that appears to play a key role in the specification of actin structures is tropomyosin, a flexible coiled-coil protein that binds along the length of actin filaments. A compelling (and somewhat historical) illustration of tropomyosin's influence here originates from studies on cancer cells. Cell transformation involves cytoskeletal rearrangements characterized by reduced numbers of stress fibers in favor of a more dynamic actin network that promotes cell protrusion, motility, and invasive growth. Numerous studies on a variety of cancer cells have shown that this rearrangement relies on downregulation of tropomyosin expression and the RhoA/ROCK/Lim