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Letters

Homoeolog expression bias and expression level dominance in allopolyploids

Polyploidy is now recognized as a characteristic feature of all angiosperm genomes (Jiao *et al.*, 2011), and remains an important speciation process today (Wendel, 2000; Comai, 2005; Doyle *et al.*, 2008; Leitch & Leitch, 2008; Soltis & Soltis, 2009; Soltis *et al.*, 2010). In allopolyploids, genomic merger and doubling are associated with myriad non-Mendelian interactions and processes, including sequence elimination (Shaked *et al.*, 2001; Ozkan *et al.*, 2003; Han *et al.*, 2005; Skalicka *et al.*, 2005; Anssour *et al.*, 2009; Tate *et al.*, 2009; Jackson & Chen, 2010), alterations of epigenetic marks (Shaked *et al.*, 2001; Madlung *et al.*, 2002; Rapp & Wendel, 2005; Chen, 2007; Doyle *et al.*, 2008; Kovarik *et al.*, 2008b; Soltis & Soltis, 2009; Soltis *et al.*, 2010), activation of genes and retroelements (O'Neill *et al.*, 1998; Kashkush *et al.*, 2003; Kraitshtein *et al.*, 2010) and several kinds of homoeologous interactions and exchanges (Gaeta *et al.*, 2007; Kovarik *et al.*, 2008a; Salmon *et al.*, 2010; Szadkowski *et al.*, 2010). Changes in duplicate gene expression are no less diverse, spanning the spectrum from expression conservation, relative to that of the diploid progenitors, to silencing of one homoeolog, to novel patterns of up- and down-regulation (transgressive expression). Each of these transcriptomic responses varies in magnitude among allopolyploid species and individuals, among tissues and organ types within any one system, and with respect to the time since polyploid formation (Flagel *et al.*, 2008; Flagel & Wendel, 2010). The phenotypic consequences of alterations in gene expression associated with hybridization and polyploidy are many and varied (Ni *et al.*, 2009; Swanson-Wagner *et al.*, 2009), underscoring the importance of understanding the expression level consequences of genome merger and doubling.

The advent and subsequent widespread utilization of microarray and next-generation sequencing technologies has led to a rapid increase in explorations of gene expression in a variety of polyploid plants. These many efforts have generated a sufficient body of empirical data that generalizations are beginning to emerge concerning transcriptome changes in allopolyploids. For example, in every allopolyploid examined to date, some fraction of the duplicate gene pairs will be expressed unequally, and this suite of unequally expressed genes may itself favor one of the co-resident genomes, leading to a transcriptome that is unequally expressed with respect to the component genomes. While these generalizations are broadly applicable, much remains to be learned regarding the mechanistic underpinnings of duplicate gene expression change, the proximate and ultimate causes of inter-taxon and inter-organ variation in the response dynamics to polyploidy, and the functional, ecological, and evolutionary significance of duplicate gene expression modification.

In addition to unequal expression of two homoeologs, other phenomena have been described which are even more poorly understood and for which fewer examples have yet been published. One of these is the concept of genome dominance (or genome expression dominance), which describes the expression condition in an allopolyploid where, for a given gene, the total expression of homoeologs is statistically the same as only one of the polyploid parents. This phenomenon was originally described for cotton allopolyploids by Rapp *et al.* (2009), confirmed and extended by Flagel & Wendel (2010), and subsequently described for both *Spartina* (Chelaifa *et al.*, 2010) and *Coffea* (Bardil *et al.*, 2011). This phenomenon is distinct from *homoeolog expression bias* (sometimes referred to as transcriptome dominance on a genome-wide basis), which describes the relative expression of homoeologs. Moreover, similar words are being used for rather different phenomena. Schnable *et al.* (2011), for example, invoked the term genomic dominance in maize, in a paper in which they demonstrated that the two subgenomes derived from the most recent polyploidy event in maize have experienced differential gene loss, with an accompanying gene expression bias favoring the more conserved subgenome (Schnable *et al.*, 2011). By other accounts (Chen, 2007; Flagel & Wendel, 2010), this would be considered homoeolog expression bias (or transcriptome dominance) of ancient homoeologs. This inconsistency of conceptual application of the term genomic dominance also applies to the preferential expression of one subgenome of wheat (Akhunova *et al.*, 2010), and to the patterns of biased expression in the fractionated subgenomes of paleohexaploid *Brassica rapa* (Cheng *et al.*, 2012; Tang *et al.*, 2012). This semantic and conceptual confusion appears to be gaining foothold in the literature; the phenomenon of preferential expression of one parental genome relative to the other in a polyploid species is termed genomic dominance in two recent reviews (Freeling *et al.*, 2012; Schnable *et al.*, 2012), citing both Schnable *et al.* (2011) and Flagel & Wendel (2010), and the term has also been applied to genomic modifications (Nicolas *et al.*, 2012). Further complicating matters is the classical genetic concept associated with the term 'dominance', which conveys the relative expression hierarchy among a set of alleles.

Against this backdrop of terminological and conceptual inconsistency, we thought it might be useful to briefly review the primary phenotypes of gene expression modification associated with allopolyploidy. Toward that end we describe and distinguish expression pattern changes observed in hybrid and polyploid species, and suggest a terminology (homoeolog expression bias and expression level dominance; Table 1; Fig. 1) that we hope will increase clarity of communication.

Table 1 Terminology for gene expression in allopolyploids

		Definition	Requirements for comparison	Scale	Synonyms and exemplar references
1	Homoeolog expression bias	Homoeolog expression ratio that is unexpected, given either: (1) the assumption of 50/50 expression levels, or (2) the ratio of expression levels derived from actual, or model, parental diploids.		Single gene	Bias Transcriptome dominance (Chen, 2007) Biased bias (Flagel & Wendel, 2010)
2A	Balanced homoeolog expression bias	Direction of bias *among genes* is equivalent overall, with respect to parental genomes; that is, an approximately equal number of genes display homoeolog expression bias in the direction of each parent	1. Measured, estimated, or assumed parental expression levels 2. Estimate of homoeolog usage for each gene	Multiple genes	Nucleolar dominance (refers to rRNA expression only; Chen & Pikaard, 1997)
2B	Unbalanced homoeolog expression bias	Direction of bias *among genes* is not equivalent overall, with respect to parental genomes; that is, more genes display homoeolog expression bias toward one parent than toward the other parent(s)			
3	Expression level dominance	The total expression level for all homoeologs of a gene in a polyploid is statistically equivalent to the expression level of one of the polyploid parents (model or actual)	1. Measured parental (actual or model) expression levels 2. Total expression level of all homoeologs	Single gene	Genomic expression dominance (Rapp *et al.*, 2009) Genomic dominance (Flagel & Wendel, 2010)
4A	Balanced expression level dominance	Direction *among genes* is equivalent overall, with respect to parental genomes; that is, an approximately equal number of genes display expression level dominance in the direction of each parent		Multiple genes	Parental dominance (Chelaifa *et al.*, 2010)
4B	Unbalanced expression level dominance	Direction *among genes* is not equivalent overall, with respect to parental genomes; that is, more genes display expression level dominance toward one parent than toward the other parent(s)			

Homoeolog expression bias

The term bias is straightforward: with respect to duplicate gene expression in an allotetraploid, bias refers to the preferential expression of one homoeolog relative to the other, although the term has also been used to describe differences in allelic expression at a locus. In an allotetraploid, when two progenitor diploids (A and B) exhibit equivalent levels of expression for a gene, but the two homoeologs (A_T and B_T, where the subscript denotes the homoeolog in a tetraploid) are expressed unequally (e.g. 80% and 20% of the total expression pool for the A_T and B_T homoeologs, respectively), then that gene is said to display biased expression, or homoeolog expression bias (Table 1; Fig. 1, upper panel). This definition of biased expression has an explicit evolutionary dimension, in that it entails a comparison of expression levels among progenitor, or model progenitor, and derivative genomes. In some cases, however, parental expression levels cannot be ascertained, and so the definition of biased expression is relaxed relative to the ancestral states; for these comparisons, the assumption of a 1:1 parental expression ratio usually is applied, for example, in maize (Schnable *et al.*, 2011). When parental expression levels are measured and are unequal, bias is more frequently assessed by comparing the expression of each homoeolog to the relative expression level of the parents or to a mid-parent expression value (Rapp *et al.*, 2009; Chague *et al.*, 2010; Flagel & Wendel, 2010). Homoeolog expression bias has been documented for many different allopolyploids, including *Gossypium* (Adams *et al.*, 2003; Yang *et al.*, 2006; Flagel *et al.*, 2008; Hovav *et al.*, 2008), *Triticum* (Mochida *et al.*, 2003; Bottley *et al.*, 2006), *Tragopogon* (Buggs *et al.*, 2010a,b; Koh *et al.*, 2010), *Arabidopsis* (Wang *et al.*, 2004; Chang *et al.*, 2010), *Brassica* (Gaeta *et al.*, 2007; Auger *et al.*, 2009), *Spartina* (Chelaifa *et al.*, 2010), and others.

Expression bias is a quantitative as well as qualitative concept. For any gene pair, biased expression of one homoeolog ranges from subtle but statistically demonstrable, to complete, whereby one

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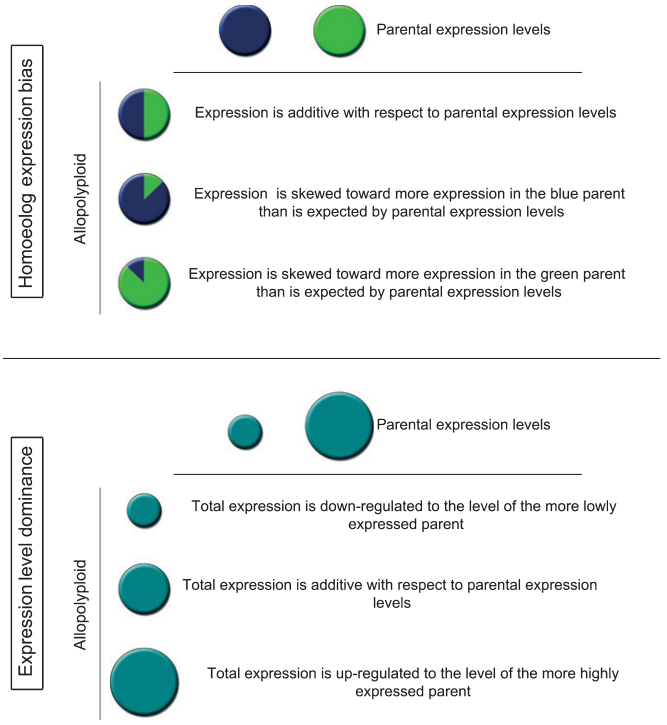

Fig. 1 Visual representation of *homoeolog expression bias* (top) and *expression level dominance* (bottom) in allopolyploids. Top panel: relative expression levels for homoeologs in an allopolyploid may be additive or biased with respect to the parents. Bottom panel: the combined expression of all homoeologs may be intermediate, or additive, relative to that of the parents, or the same as one of the two parents; the latter case is referred to as *expression level dominance*. This illustration models allotetraploidy, but the concepts may be extended to higher ploidy levels

homoeolog is fully silenced. It also is quantitative on a genome-wide scale; that is, for the transcriptome as a whole, in some cases a relatively small proportion of the total number of gene pairs examined displays homoeolog expression bias, whereas in other systems or samples, this fraction may be much higher. When referring to biased expression for the transcriptome as a whole, there may be a great deal or relatively little homoeolog expression bias. Importantly, homoeolog expression bias itself can be either balanced among the genomes comprising the polyploid (i.e. homoeolog expression bias does not favor one component genome), or unbalanced (i.e. homoeolog expression bias favors one genome). This is modeled in Fig. 2(a), which shows that when homoeolog expression bias is balanced, the number of duplicate gene pairs exhibiting biased expression toward one parental genome is equivalent to the number demonstrating biased expression toward the other parental genome. In contrast, unbalanced homoeolog expression bias refers to cases where preferential homoeolog expression is skewed with respect to the progenitor genomes (Fig. 2a); that is, two co-resident transcriptomes are not expressed equally overall. Unbalanced homoeolog expression bias in allopolyploids is commonly observed, varies in magnitude, and remains mechanistically mysterious (Chen & Pikaard, 1997; Wang *et al.*, 2006; Flagel *et al.*, 2008; Chaudhary *et al.*, 2009; Akhunova *et al.*, 2010; Buggs *et al.*, 2010a; Schnable & Freeling, 2011; Schnable *et al.*, 2011). The phenomenon of unbalanced homoeolog expression bias was described by Chen (2007) as transcriptomic dominance, and sometimes is confused with *expression level dominance*, as mentioned above and discussed further below. The concepts of homoeolog bias and balance with respect to progenitor genomes also apply to higher ploidy levels than tetraploid, but with an obvious added complexity of inference.

Expression level dominance

As mentioned above, the term genome expression dominance, or simply genomic dominance, was used by Rapp *et al.* (2009) to describe the phenomenon where the total expression of homoeologs for a given gene in an allopolyploid is statistically equivalent to the expression level of that gene in only one of the parents, irrespective of homoeolog usage and even in the absence of homoeolog usage bias (Yoo *et al.*, in press). This concept is distinct from homoeolog expression bias in that it does not consider relative expression levels of individual homoeologs, but rather refers to the total expression level of a duplicate gene pair, when measured in the allopolyploid and when compared to its parents.

Genomic dominance was first described in synthetic allopolyploid cotton for the leaf transcriptome by Rapp *et al.* (Rapp *et al.*, 2009), who also provide a useful elaboration of methods for its detection for different categories of gene expression (see Rapp *et al.*, 2009, figs 3, 4). Since that initial report, genomic dominance has been discovered in additional cotton tissues and in natural allopolyploids (Flagel & Wendel, 2010), as well as in *Spartina* (Chelaifa *et al.*, 2010), *Triticum* (Chague *et al.*, 2010; Qi *et al.*, 2012), and *Coffea* (Bardil *et al.*, 2011). Flagel & Wendel (2010) expanded the work of Rapp *et al.* (2009) to include five natural allopolyploid species, in the process demonstrating that whereas nascent allopolyploids may exhibit a high level of bias in genomic dominance, over evolutionary time the bias in genomic dominance dissipates even while its overall magnitude remains relatively high, thereby demonstrating a temporal dimension to the phenomenon. Chelaifa *et al.* (2010) described 'parental dominance' in the hybrid *Spartina* × *townsendii*, which exhibited overall expression levels that mirrored the maternal progenitor *S. alterniflora*, and noted that the allopolyploid, *Spartina anglica*, exhibited only slight overall expression levels favoring the same parent (Chelaifa *et al.*, 2010). Genomic dominance also was recently reported for *Coffea* (Bardil *et al.*, 2011), using analytical procedures similar to those employed by Rapp *et al.* (2009) and Flagel & Wendel (2010). Importantly, the magnitude of genomic dominance and biased dominance was temperature-dependent: in the allopolyploid *C. arabica* cv Java, a higher number of genes mimicked the *C. canephora* parental expression levels when the polyploid was grown under hot conditions, but no preference was exhibited in the cool conditions; this temperature-dependent genomic dominance was also demonstrated for *C. arabica* cv T18141 (Bardil *et al.*, 2011). Finally, in allohexaploid wheat, the concept of genomic dominance was also used as originally defined; however, because the analyses conducted restricted the datasets used to only those genes that were statistically different from the mid-parent value, the inference of genomic dominance was applied

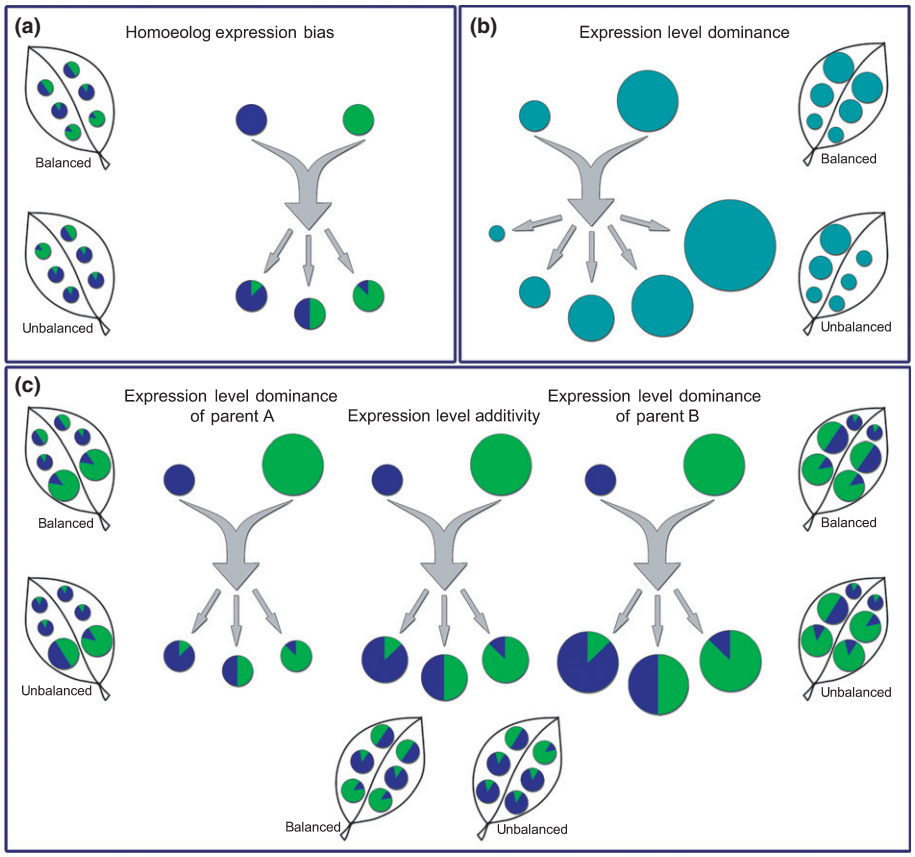

Fig. 2 Homoeolog expression bias and expression level dominance in allopolyploids. Individual gene expression levels are represented by circles, and the possible outcomes following polyploidy are illustrated below the merging arrows. Organ- or organism-wide trends for each phenomenon are displayed by multiple circles (genes) contained within leaves (representing sets of multiple genes, derived from organs, organisms, etc.), and display *balanced* and *unbalanced* cases for each. This illustration models allotetraploidy, but the general concepts may be extended to higher ploidy levels. (a) Homoeolog expression bias. Fractional homoeolog usage in the polyploid may be biased toward the blue or green homoeolog (left and right circles below the arrows, respectively), or may be equivalent (homoeolog expression additivity, middle circle). Among genes, *balanced homoeolog expression bias* is inferred when the number of genes favoring each parental genome is equivalent; homoeolog expression bias may also be *unbalanced,* when a larger proportion of the genes that display homoeolog expression bias favor one parent (e.g. blue parent, lower leaf). (b) Expression level dominance. Whereas *homoeolog expression bias* is based on homoeolog usage relative to *a priori* expectations, expression level dominance is evaluated by comparing the total expression of homoeologs in the allopolyploid relative to the expression levels found in the parental species; here, the relative levels of expression are modeled by the size of circles. Four possible outcomes of allopolyploidy are illustrated, that is, (1) transgressive expression (smallest and largest circles, left and right, respectively), when total expression is outside the range of both parents; (2) statistical equivalence to the parent with the lower expression (expression level dominance toward the left parent, smaller circle); (3) expression level additivity (expression level is intermediate among parents, intermediate circle); or (4) statistical equivalence to the parent with the higher expression (expression level dominance toward the right parent, larger circle). As with homoeolog expression bias, expression level dominance may be either *balanced* (the suite of genes that display expression level dominance in allopolyploid does not favor one parent over the other) or *unbalanced* (the suite of genes that display expression level dominance is skewed toward one parent). (c) Homoeolog expression bias and expression level dominance. When parental expression levels are measured *and* homoeolog usage in the polyploid is ascertained, both homoeolog expression bias and expression level dominance may simultaneously be evaluated. Illustrated are several possible outcomes, including (1) expression level dominance of one parent (e.g. the blue parent, left ideogram; notice that circles are small, irrespective of homoeolog use); (2) expression level additivity (middle ideogram); and (3) expression level dominance of the other parent (e.g. green; right ideogram; note that all circles are large, irrespective of homoeolog use). Within each of these categories, several possibilities for homoeolog usage are shown, representing the two types of parental homoeolog expression bias and additivity. Examples of balanced and unbalanced bias and expression level dominance are also indicated.

to a limited set of genes, leading to inferences of both genomic dominance (Qi *et al.*, 2012) and no global genomic dominance (Chague *et al.*, 2010).

Because of the confusion surrounding the phenomenon of genomic dominance and the divergent applications of the term (as introduced above), we suggest here a clarification in terminology, modifying the previously used (and confounded) term *genomic dominance* to *expression level dominance* (Table 1; Fig. 1, lower panel). In replacing 'genomic' with 'expression level', the actual phenomenon being described is invoked, as opposed to the more ambiguous word 'genomic'. For clarity, if a given gene is more highly (or lowly) expressed in parent A than in parent B but the total expression in the allopolyploid is equivalent to parent A, expression level dominance is inferred in the direction of the A parent (Fig. 2b). Importantly, this inference holds irrespective of the direction of mirroring in the allopolyploid; that is, when total

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expression ($A_T + B_T$) is statistically equivalent to that of one parent (A or B) but not the other, expression level dominance is inferred, irrespective of whether parent A is up- or down-regulated relative to B. This is illustrated in Fig. 2(b), where both 'up' and 'down' states in an allopolyploid are depicted. Importantly, expression level dominance may be inferred irrespective of whether or not a homoeolog pair exhibits bias; the two concepts are independent in this sense, although there may be mechanistic connections (Shi *et al.*, 2012; Yoo *et al.*, in press). Also, as with homoeolog expression bias, expression level dominance is quantitative (i.e. involving few to many genes), and it may be balanced (equivalent number of gene pairs exhibiting the expression level of both parents) overall or unbalanced (more gene pairs in an allopolyploid exhibiting the expression level of one parent than the other).

The evaluation and inference of expression level dominance in allotetraploids requires expression information from three entities, the two progenitor diploids and their derived polyploid. Because of this, expression level dominance is challenging to measure in paleopolyploids or those that have undergone substantial fractionation (homoeolog loss), because either the diploid parents are extinct or because of extensive homoeolog loss.

Conclusions

As discussed above, the evolution of polyploids entails complex alterations in gene expression, some of which bear on relationships among homoeolog usage only within an allopolyploid (homoeolog expression bias) and others involving comparisons of gene expression between allopolyploids and progenitor diploids (expression level dominance). It bears mention that both phenomena frequently occur in the same polyploid (Yoo *et al.*, in press), potentially even occurring in the opposite direction (e.g. homoeolog expression bias toward one parent and expression level dominance toward the other parent; Fig. 2c). An additional layer of inferential complexity arises when considering ploidy levels higher than tetraploid. In these cases measuring homoeolog expression bias and expression level dominance may be challenging, but should be feasible for plants such as hexaploid wheat, where diploid models of all three progenitor genomes remain extant.

As reviewed briefly in the introduction to this note, polyploid genomes are extraordinarily dynamic, possessing a combinatorial complexity far in excess of their diploid progenitors and a transcriptome that has undergone a massive rewiring. Homoeolog expression bias and expression level dominance appear to be two widespread consequences of genome merger and doubling. Our intention here is to draw attention to these phenomena and their distinctions, thereby facilitating the adoption of a more consistent lexicon for clear and efficient communication.

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