

Dual fertilization, intragenomic conflict, genome downsizing, and angiosperm dominance

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New work suggests ‘subgenome dominance’ in polyploids may only occur in angiosperms. Subgenome dominance could explain angiosperm-specific genome reduction, with potential implications for angiosperms’ global dominance. I suggest that evolution of the endosperm could have selected for the evolution of subgenome dominance, due to increased hybrid/polyploid incompatibilities and/or through direct reciprocal suppression of maternally- and paternally-inherited genomes.

Genome dynamics and angiosperm exceptionalism

Flowering plants dominate nearly every terrestrial system, having risen to global dominance rapidly during the Cretaceous¹. A wide variety of explanations have been offered, largely focused on organismal features including insect pollination, reduced seed size, self incompatibility, more efficient water transport, and many others, although others have suggested that a variety of factors likely contributed¹. Study of genomic features have suggested two additional potential contributors. First, angiosperms have generally smaller genomes than other land plants². Because large genomes require a large minimum cell size, smaller genomes could have allowed for previously inaccessible morphologies, allowing for increased metabolic efficiency and morphological innovation². Second, studies have revealed high rates of polyploidy in angiosperms over various timescales³⁻⁵, of potential importance given evidence that polyploidization may be important for robustness to extinction and for morphological innovation³⁻⁶.

However, these two features – smaller genome sizes and a tendency to multiply genome size through polyploidization – are clearly in tension. Comparative work suggests a partial resolution: following polyploidization, many angiosperms (though not all) appear to undergo genome size shrinkage and genome rearrangement (this point and many below are covered by excellent recent reviews³⁻⁵). (Although given that downsizing is not immediate, how early polyploids persist despite selection against increased cell size remains to be addressed.) This rapid downsizing is in contrast to both non-angiosperm plants and most studied non-plants, in which polyploids appear to generally retain roughly doubled genome sizes and chromosome numbers for long periods^{3-5,7}.

Subgenome dominance

The phenomenon of subgenome dominance appears to be central to genome downsizing and rearrangement³⁻⁵. Whereas classical models of polyploidization predict largely balanced expression of parental genomes (as in various non-plant polyploids³⁻⁵), under subgenome dominance, one parental genome remains robustly expressed while the other undergoes chromatin changes and gene silencing³⁻⁵. In addition to gene expression, transposable elements from the non-dominant genome are also extensively silenced by methylation, which may also play a role in silencing of neighboring genes³⁻⁵. Subgenome

1 dominance seems to be associated with hybridization rather than polyploidization *per se*, as
2 it is observed in diploid interspecific hybrids^{6,8}, and generally in allopolyploids (combining
3 genomes from different parental species) rather than autopolyploids (same species)³⁻⁵.
4 Subgenome dominance also appears in more complex polyploids, with one of several
5 contributing parental genomes being dominant³⁻⁵.

6
7 Subgenome dominance appears to facilitate genomic downsizing in multiple ways. First,
8 subgenome dominance likely reduces selection against loss of lowly-expressed genes, and
9 preferential gene loss from the non-dominant genome is observed, through both single gene
10 and longer deletions³⁻⁵. Second, subgenome dominance may accelerate genomic
11 rearrangements and loss of repetitive sequences, including biased replacement of longer
12 regions from the submissive genome by shorter regions from the dominant genome
13 through homeologous chromosome exchange^{3-5,9}.

14
15 While timescales vary across lineages, polyploid genome downsizing and rearrangement
16 under subgenome dominance can be quite rapid, with changes observed over timescales
17 ranging from a single F1 family to the history of a population to hundreds of thousands of
18 years. Remarkably, changes can occur within the first generation³⁻⁵. Thus subgenome
19 dominance may facilitate rapid 'rediploidization' following polyploidization both by
20 increasing the rates at which mutations that remove genome sequence occur, and by
21 reducing the selective costs of such deletions.

22
23 *Is subgenome dominance specific to angiosperms?*

24
25 To date reports of subgenome dominance in plants are limited to a subset of (but not all)
26 angiosperms, however the true taxonomic distribution remains uncertain. A recent paper
27 suggests a lack of genome dominance in the gymnosperm *Ephedra*¹⁰. The authors analyze
28 the transcriptomes of two allotetraploid species created 1-3 million years ago as well as
29 their diploid progenitors. The authors find evidence for largely symmetrical evolution: both
30 subgenomes retain similar numbers of genes, show similar expression levels and
31 complexities of alternative splicing, and show similar incidences of parentally-biased
32 expression. Consistent with a role for subgenome dominance in genome size reduction, the
33 genome sizes of the tetraploid *Ephedra* species approximate the sums of those of their
34 diploid progenitors. Thus, while more data is needed, these results, coupled with
35 cytogenetic studies of the larger *Ephedra* genus and of *Juniperus*⁷, are consistent with
36 subgenome dominance being absent from gymnosperms and thus perhaps being
37 angiosperm-specific.

38
39 *Biparental endosperm and the origins of subgenome dominance*

40
41 Why did angiosperms evolve subgenome dominance? One possibility is that subgenome
42 dominance evolved in response to intragenomic conflict within the endosperm. In non-
43 angiosperm plants, transfer of maternal resources to the embryo is controlled by
44 gametophytic tissue that carries only maternal genes¹¹; by contrast, in angiosperms this
45 role is played by the endosperm, which contains both maternally- and paternally-derived
46 genes. This likely leads to intragenomic conflict: paternally-inherited alleles are generally
47 not found in the mother's other offspring, and are thus selected to extract more resources
48 from the mother, whereas maternally-inherited genes are likely to be present in the
49 mother's other offspring, and thus are selected to favor less aggressive resource
50 extraction¹²⁻¹³. Indeed, angiosperms show extensive "genomic imprinting," in which some

1 genes are expressed only from the maternally-inherited allele and others from the
2 paternally-inherited allele, a phenomenon thought to be driven by conflict¹²⁻¹³. Consistent
3 with conflict over resource extraction, manipulation of maternal and paternal ploidy levels
4 shows predictable effects, with greater paternal and lesser maternal contribution increasing
5 embryo growth¹².

6
7 Such conflicts could create the conditions for the evolution of subgenome dominance in
8 at least two ways. First, insofar as gene expression of maternally/paternally-inherited
9 genomes act to decrease/increase resource extraction, an efficient mechanism to
10 manipulate resource extraction may be wholesale genome suppression (suppression of the
11 paternal genome by maternally-expressed genes or vice versa). Within species, paternal
12 genomes will be selected to escape the suppression mechanisms of the maternal genome
13 (and vice versa), thus intraspecific crosses may not exhibit clear suppression; by contrast, in
14 interspecific crosses, the genome inherited from one parent would be newly exposed to
15 suppression mechanisms which it has not evolved resistance to. (Similarly, sex
16 chromosome drive is often only revealed in hybrids that lack the evolved drive resistance
17 mechanisms¹².)

18
19 A second possibility is that intragenomic conflict drives the rapid evolution of hybrid
20 incompatibilities, and that subgenome dominance arose to ameliorate these
21 incompatibilities. Hybrid incompatibilities are known to be important in general, and
22 interspecific incompatibilities between the nuclear genome and uniparentally inherited
23 endosymbiont genomes shapes allopolyploid angiosperm genomes¹⁴. Consistent with the
24 notion that hybrid incompatibilities arise more quickly when there is genomic conflict over
25 maternal provisioning, the placenta in mammals may be associated with radically decreased
26 rates of hybrid viability relative to other tetrapods¹⁵. In both mammals and angiosperms,
27 resource demands by the paternally-inherited genome and countermeasures by the
28 maternal-inherited genome could drive rapid turnovers in gene regulatory networks, as
29 paternally-inherited genes evolve to escape manipulation by maternally-inherited genes
30 and vice versa, leading to interspecific incompatibilities. Such incompatibilities presumably
31 arise largely from co-expression of both parental genomes (either through incompatibilities
32 between gene products or due to aberrant effects of one gene product on expression of
33 genes from the other genome). Thus such incompatibilities could be ameliorated by
34 silencing of one genome, leading to a selective advantage for genome dominance.

35
36 Notably, these dynamics are expected to apply directly only to the endosperm, raising the
37 question of their effects on embryonic tissue. The endosperm appears to be primarily
38 charged with extracting resources from the mother, suggesting that these dynamics could
39 have mostly played in genes expressed in endosperm. However, changes in gene regulatory
40 networks in one tissue are expected to also affect regulation in other tissues due to sharing
41 of regulatory elements across tissues. If this coordination is sufficiently strong, then
42 incompatibilities that arise due to conflict over the endosperm phenotype could cause
43 incompatibilities in other tissues, providing a benefit to subgenome dominance.

44 45 *Future directions*

46
47 I have proposed that an angiosperm-specific capacity for genomic downsizing by
48 subgenome dominance arose as a consequence of intragenomic conflict in the endosperm.
49 This notion remains speculative, awaiting more information about the taxonomic
50 distribution and genomic consequences of subgenome dominance. First,

genomics/transcriptomics studies of subgenome dominance in diverse angiosperms and non-angiosperms will be important both for timing the initial origins of subgenome dominance and for identifying the determinants of subgenome dominance in descendent lineages. Second, comparative genomics/transcriptomics and cytogenetic study of allopolyploids from lineages with and without subgenome dominance could test the importance of subgenome dominance for gene loss and genome downsizing. Third, characterizing the determinants of dominance in allopolyploids, and the repeatability of dominance in repeated crosses, will be necessary to test the prediction that the genomes of species experiencing more conflict tend to become dominant. The rapid increase in long-read transcriptomic and genomic sequencing data should allow rapid progress on these questions and on the angiosperm genomic distinctiveness more generally.

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