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THE POLYPLOIDY REVOLUTION THEN…AND NOW: STEBBINS REVISITED[1]

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Polyploidy has long been considered a major force in plant evolution. G. Ledyard Stebbins, Jr., an architect of the Modern Synthesis, elegantly addressed a broad range of topics, from genes to chromosomes to deep phylogeny, but some of his most lasting insights came in the study of polyploidy. Here, we review the immense impact of his work on polyploidy over more than 60 years, from his entrance into this fledgling field in the 1920s until the end of his career. Stebbins and his contemporaries developed a model of polyploid evolution that persisted for nearly half a century. As new perspectives emerged in the 1980s and new genetic tools for addressing key aspects of polyploidy have become available, a new paradigm of polyploidy has replaced much of the Stebbinsian framework. We review that paradigm shift and emphasize those areas in which the ideas of Stebbins continue to propel the field forward, as well as those areas in which the field was held back; we also note new directions that plant geneticists and evolutionists are now exploring in polyploidy research. Perhaps the most important conclusion from recent and ongoing studies of polyploidy is that, following Levin and others, polyploidy may propel a population into a new adaptive sphere given the myriad changes that accompany genome doubling.

Key words: autopolyploidy; diversification; epigenetics; evolution; genome doubling; genomics; G. Ledyard Stebbins, Jr.

Polyploidy, or whole genome duplication (WGD), is now recognized as a major evolutionary force not only in plants, but also in all eukaryotes (e.g., Mable, 2003; Gregory and Mable, 2005). WGD generally results in instant speciation, increasing biodiversity and providing new genetic material for evolution (e.g., Levin, 1983, 2002). Illustrating the broad impact of polyploidy, ancient WGD events have been documented in vertebrates (e.g., Cañestro, 2012; Braasch and Postlethwait, 2012), fungi (Kellis et al., 2004), and ciliates (Aury et al., 2006); both recent and ancient events occur extensively in plants, particularly in lineages such as the angiosperms. In fact, researchers have long recognized that polyploidy is an inseparable part of angiosperm biology.

Perhaps no other single person has contributed more to our understanding of polyploidy than George Ledyard Stebbins, Jr., one of the leading botanical researchers of the 1900s, with publications spanning 70 yr. His first paper (Stebbins, 1929) was on the Mt. Desert flora; his last publication (Stebbins, 1999) was "A brief summary of my ideas on evolution," which appeared in the *American Journal of Botany*. He was one of the architects of the Modern Synthesis, and his impact on plant evolutionary biology was immense (e.g., see Smocovitis, 1997, 2001; Raven, 2000). He had broad systematic and evolutionary interests, and his research spanned a diverse range of topics, including developmental genetics (Stebbins and Yagil, 1966), plant evolution, angiosperm phylogeny, and evolutionary mechanisms, especially hybridization and polyploidy. This breadth of expertise and broad influence can be seen simply by considering the topics he covered in the 20-plus papers published in the *AJB*; these address the origin of the B-genome in wheat (Sarkar and Stebbins, 1956), basic questions of plant biology (Stebbins, 1964), evolution of the grass family (Stebbins, 1956), plant morphogenesis (Stebbins, 1992), cytology and growth habits of "dicots" (Stebbins, 1938), ancestry of an amphiploid *Viola* (Stebbins et al., 1963), artificial and natural hybrids in grasses (Stebbins et al., 1946), developmental genetics in barley (Zeiger and Stebbins, 1972), studies of meiosis in *Paeonia* (Hicks and Stebbins, 1934), and chromosome numbers (and polyploidy) in *Antennaria* (Bayer and Stebbins, 1981).

STEBBINS AND POLYPLOIDY

This overview of the current understanding of genome doubling requires appropriate historical context. Plant polyploidy has been studied for over a century, dating to research by de Vries on *Oenothera lamarckiana* mut. *Gigas* (Onagraceae), which was discovered to be a tetraploid (Lutz, 1907; Gates, 1909), as well as to the suggestion by Kuwada (1911) that an ancient chromosome duplication occurred in maize (*Zea mays*). The spontaneous formation of the allopolyploid *Primula kewensis* was noted at Kew in 1905 and later confirmed to be a tetraploid (Digby, 1912). Winkler (1916) generated the first artificial polyploid and is often credited with the first use of the term "polyploidy". Winge (1917) proposed hybridization followed by doubling of the chromosomes (i.e., polyploidy) as a viable means for the origin of new species. Artificial hybridizations in *Nicotiana* (Solanaceae) and *Galeopsis* (Lamiaceae) and the production of *Raphanobrassica* (Brassicaceae) confirmed Winge's hypotheses on the origins of polyploidy (Clausen and Goodspeed, 1925; Müntzing, 1930). Kihara and Ono (1926)

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developed the terms allopolyploidy and autopolyploidy to differentiate between polyploidy accompanied by hybridization or not, respectively. Shortly thereafter, other researchers showed that many major crops—including wheat, oats, cotton, tobacco, potato, and coffee—are polyploid, with evidence provided for the parentage of wheat (McFadden and Sears, 1946), cotton (Beasley, 1940), and tobacco (Goodspeed and Clausen, 1928).

Several influential reviews of polyploidy were published from the 1930s to the 1950s, including those of Müntzing (1936), Darlington (1937), Clausen et al. (1945), and Löve and Löve (1949), but as reviewed briefly below, none were more influential than those of Stebbins (1940, 1947, 1950; later publications will be discussed further below). Stebbins (1940) called attention to the importance of polyploidy in plant evolution, and he later (Stebbins, 1947) built on the framework of earlier students of polyploidy and classified polyploids into types (e.g., auto- and allopolyploidy). However, the most influential work in the area of polyploidy was a section of his book *Variation and Evolution in Plants* (Stebbins, 1950). This synthesis of what was known about polyploidy at the time included information on the types of polyploids, as well as the evolutionary significance of polyploidy. Two of 14 chapters in *Variation and Evolution in Plants* were devoted to polyploidy. Stebbins' (1971) later book, *Chromosomal Evolution in Higher Plants*, was also influential and provided a contemporary summary of polyploidy reflecting the knowledge that had accumulated to that time—including discussions of ancient polyploidy in angiosperms, as well as recent polyploidy. He returned to the topic of polyploidy again in Stebbins (1985), where he discussed the role (or lack thereof) that polyploidy can play in colonization.

Stebbins (1950) strongly influenced thinking about polyploidy for over 50 yr. Following Stebbins (1950), much attention was subsequently focused on polyploid research, including investigation of polyploid complexes, as well as the complex relationships among groups of hybridizing species and polyploid derivatives. As a result, polyploidy played a major role in biosystematic research that continued until the era of DNA-based phylogenetics (e.g., 1990–present), when systematists shifted much of their attention to tree building (Soltis et al., 2004). However, polyploidy has experienced a tremendous resurgence of study during the genomics era (e.g., 2000– present), and that continues to this day.

Polyploidy not only represented a large component of Stebbins's research, it was also one of his favorite topics of discussion, as experienced by D. and P. Soltis during a sabbatical at the University of California, Davis, in the fall of 1988. Some of his views on polyploidy have withstood the test of time; for example, his view of a continuum between auto- and allopolyploidy, and his recognition of the difficulties in making clear distinctions between types of polyploids were on the mark. Stebbins (1971, p. 132) noted, "…any attempt to maintain a division of natural polyploids into two discrete categories, autopolyploids and allopolyploids, is more likely to confuse than to clarify a very complex system of interrelationships." Stebbins (1950, 1971) was also perceptive regarding the possible important role of ancient polyploidy in diverse lineages, particularly angiosperms, and we discuss this topic more herein. Stebbins (1971, p. 140) was also astute in summarizing the problems involved in comparing a polyploid to its diploid progenitors: "One cannot assume that the diploid ancestor or ancestors of a modern polyploid species still exist in their original form unless good evidence for their existence has been obtained, extinction or cytogenetic modification of diploid ancestors since they participated in the origin of a polyploid are likely possibilities that must always be taken into account." This remains insightful as current methods permit genomic and proteomic comparisons of allopolyploids and diploid progenitors. Stebbins realized that in only a few young polyploids are the "exact" parental genotypes that gave rise to the new allopolyploid available.

However, in other cases, Stebbins's views, which formed the accepted paradigm for decades, have been replaced over the past 15 yr by a new paradigm. As we summarize these changing views, we stress that our goal is to honor his legacy and his long and major impact on an area of study that he not only helped to popularize, but for which he also had deep affection. Ledyard was always excited by new discoveries. He would certainly have been thrilled to see the renewed interest in polyploidy over the past 15 yr, stimulated in large part by the availability of powerful genetic and now genomic tools as well as advances in computational biology. These tools have facilitated in-depth examination of many of the hypotheses championed by Stebbins in a manner not previously possible. In this regard, in our discussions with Ledyard, we were often impressed with his interest in new methodological advances (e.g., allozymes in the 1980s and DNA-based research in the late 1980s and 1990s) and their applications to questions in evolutionary biology.

Generations of polyploid researchers (including those now employing genomics and computational methods) are grounded in a research foundation that was in large part established by Stebbins, whether they recognize this fact or not. His impact was enormous and continues to this day—we are all in a sense "Stebbinsians". Modern polyploid researchers should be reminded of a quotation often attributed to Isaac Newton, "If I have seen further it is by standing on the shoulders of giants." Ledyard was that giant. Our hope is that Ledyard would have appreciated the monumental advances in our understanding of polyploidy that have been achieved so recently and rapidly.

STEBBINS AND THE CENTRAL TENETS OF POLYPLOIDY IN THE 1900s

***Background*—**Through several classic books and papers (e.g., Stebbins, 1947, 1950, 1971), Stebbins was largely responsible for developing, and certainly popularizing, what became the central tenets of polyploid evolutionary thinking. Impressively, these views would remain foundational for nearly 50 yr. We identify five major themes. (1) Polyploids formed at a moderate frequency in angiosperms, for which he provided an estimate of ~30–35% of all species. (2) He considered polyploids to be very important over shallow evolutionary time but with little long-term evolutionary impact—all the evolutionary action was at the diploid level. He viewed polyploids, for the most part, as evolutionary dead-ends (Stebbins, 1950, 1971). Furthermore, strong genetic arguments, based in part on experiments with artificially produced polyploids, were posited for the lack of long-term success of polyploids. (3) Each polyploid species was thought to have formed via a single origin with concomitant limited initial genetic variation. (4) Genetic buffering, resulting from the combination of multiple parental genomes, leads to low rates of fixation of new mutations in polyploids (Stebbins, 1950). The bottleneck associated with polyploid formation, coupled with this genetic buffering, suggested that polyploids had limited genetic variation and limited potential for adaptive evolution. (5) Autopolyploids were considered to be extremely rare in nature, based on sterility estimates resulting from meiotic irregularities, and were relegated to playing a very minor role in Stebbins's view of plant evolution.

We discuss each of these topics in more detail below, first providing historical context (see also the review by Tate et al., 2005). We then revisit these themes and show how they have been collectively replaced by a new paradigm of polyploidy.

Frequency—It has long been recognized that polyploidy is a major evolutionary force in plants (e.g., Muntzing, 1936; Darlington, 1937; Clausen et al., 1945; Love and Love, 1949; Stebbins, 1950; Lewis, 1980; Grant, 1981). In fact, some of these early authors had a large impact on Stebbins and his thoughts on polyploidy. However, it long proved difficult to determine the actual frequency of the process in various plant lineages, despite numerous attempts to estimate it over the past 70 yr. The angiosperms, in particular, have received much attention regarding the occurrence of polyploidy. The standard approach was to use base chromosome numbers as a proxy for polyploidy (see below). However, only with the recent availability of genomic tools has it been possible to obtain better estimates of the frequency of successful polyploidization deeper in time.

Stebbins (1950, 1971) estimated that ~30–35% of angiosperm species had formed via polyploidy. This estimate was one of the lowest suggested by workers from that time period. For comparison, among the earliest estimates for angiosperms, Müntzing (1936) and Darlington (1937) speculated that roughly 50% of all angiosperm species were polyploid. To understand the variation in estimates among authors, it is important to understand the methodology employed. The estimates generally varied based on the cut-off chromosome number used by the author for estimating what was diploid and what was polyploid. For example, Stebbins (1971, p. 124) suggested that "all genera or families with $x = 12$ or higher have been derived originally by polyploidy..." and noted "that even the numbers $x = 10$ and $x = 11$ may often be of polyploid derivation". Grant (1981) hypothesized that flowering plants with haploid chromosome numbers of $n = 14$ or higher were of polyploid origin. With this cut-off point, he determined that 47% of all angiosperms were of polyploid origin and further proposed that 58% of monocots and 43% of "dicots" (note that eudicot was not employed at that time) were polyploid. Goldblatt (1980) maintained that this estimate was too conservative and proposed that taxa with chromosome numbers above $n = 9$ or 10 are of polyploid origin. He calculated that at least 70–80% of monocots are of polyploid origin. Lewis (1980) applied an approach similar to Goldblatt's to "dicots" and estimated that 70–80% were polyploid. Masterson (1994) used the novel approach of comparing leaf guard cell size in fossil and extant taxa from a few angiosperm families (Platanaceae, Lauraceae, Magnoliaceae) to estimate polyploid occurrence through time. With this method, she estimated that 70% of all angiosperms had experienced one or more episodes of polyploidy in their ancestry.

Polyploids as "dead-ends": Limited importance in diversification—Stebbins (1950, 1971), as well as another highly influential plant biologist of the 1900s, W. "Herb" Wagner, argued that while polyploids were frequent in plants, they had limited long-term evolutionary potential. This traditional view that both strongly promoted maintained that polyploids were "evolutionary noise" (Wagner, 1970, p. 146) unimportant to the main processes of evolution (e.g., Stebbins, 1950; Wagner, 1970). For Stebbins and other students of polyploidy from that time period, the evolutionary action was at the diploid, not the polyploid, level. For example, Stebbins (1950, p. 358) stated, "Polyploidy, therefore, may be looked upon as a process which is most effective as a means of enabling species groups which have reached a certain stage of depletion of their biotypes…to adapt themselves to new environmental conditions which arrive relatively suddenly. It is much less important in stable environments and in diploid species which are still widespread and rich in ecotypic differentiation." Stebbins (1950, p. 359) further noted, "The long-continued evolution needed to differentiate genera, families and orders, and phyla appears to have taken place chiefly on the diploid level…" Stebbins (1950, p. 366) later states "… polyploidy has appeared as a complicating force producing innumerable variations on old themes but not originating any major new departures."

These harsh views regarding the long-term evolutionary potential of polyploids rested on several assumed genetic limitations, as described in the following section.

Wagner (1970, p. 146) similarly argued that while polyploids have always existed, they have never diversified or played a major role in the evolution of plants and that the study of polyploidy has led researchers to be "carried away with side branches and blind alleys that go nowhere." The prose of Stebbins and Wagner prompted the statement, often attributed to both researchers, that polyploids were evolutionary dead-ends. Although both authors certainly implied this in their writings, neither author actually used the term "dead-end".

Despite his view that polyploids had limited long-term evolutionary potential, Stebbins (1950, p. 365) perhaps ironically inferred, over 60 yr ago, multiple cases of ancient polyploidy in angiosperms and other seed plants: "…there is some evidence that many genera and even subfamilies of seed plants have had a polyploid origin." He continued (p. 365), "…students of angiosperm phylogeny should look for traces of ancient allopolyploidy resulting from hybridization between species which were the ancestral prototypes of many of our modern families." In 1971, Stebbins (p. 124) further stated, "If this is true [that flowering plants with $x = 12$ or higher are ancient polyploids] then all of the modern species belonging to many prominent families such as Magnoliaceae, Winteraceae, Lauraceae, Monimiaceae, Fagaceae, Juglandaceae, Salicaceae, Meliaceae, Ericaceae, and Oleaceae, are derivatives of evolutionary lines which at some time in their history have undergone polyploidy." Given recent genomic insights (below) regarding the importance of ancient polyploidy in the origin of many lineages, this has proven to be a very astute inference.

Polyploids: A single origin with limited genetic potential—Stebbins viewed polyploid species as genetically depauperate with limited evolutionary potential. A new polyploid species was envisioned as forming via a single polyploidization event and would therefore exhibit a high degree of genetic uniformity across individuals. Following this model of formation, an allopolyploid would exhibit no homologous, or segregating, variation, only homeologous (nonsegregating) variation. Furthermore, if a mutation were to arise in the polyploid, its effect would be masked by either the presence of a homeologous locus (in an allotetraploid) or multiple alleles (in an autopolyploid). Although not impossible, the fixation of a new mutation is much slower in a polyploid than in its diploid parents. Stebbins (1971, p. 127) correctly noted that "…the large amount of gene duplication dilutes the effects of new mutations… polyploids have great difficulty evolving truly new adaptive gene complexes" and that "…chromosome doubling will most often have a retarding effect on evolutionary change via mutation, genetic recombination, and selection." Furthermore, this buffering effect

of multiple genomes may extend to the origins of morphological variation in a polyploid (Stebbins, 1950, 1971 [pp. 147–148]): "Very often, even in complexes on which the basis of phytogeographical evidence must be regarded as hundreds of thousands or even millions of years old, the range of morphological variability encompassed by all of the tetraploids is less than the total range of that found among the diploids…"

We now know, however, that polyploid species typically arise via multiple origins, and this mode of formation has genetic consequences that offset the limitations perceived by Stebbins. Although modern perspectives on recurrent formation of polyploid species typically trace to the work of Werth et al. (1985a, b), the concept of multiple origins of a polyploid species, and the attendant potential for enhanced genetic variation and long-term success, extends back to at least the 1950s. The work of Ownbey (1950) and Ownbey and McCollum (1953) suggested that the newly formed *Tragopogon* allopolyploids from the northwestern United States had formed multiple times. Stebbins was likely aware of Ownbey's interpretations of independent origins of both *T. mirus* and *T. miscellus*, given that he (Stebbins, 1971) briefly reviewed Ownbey's *Tragopogon* research. Perhaps because of Ownbey's work, Stebbins (1985) later seemed to recognize the potential genetic variation that might be contributed via multiple origins, and he appeared to soften his view on the long-term potential of at least some polyploids (e.g., grasses). Stebbins (1985, p. 824) stated, "The hypothesis that polyploids succeed because of their greater tolerance of severe ecological or climatic conditions is again rejected, and that which postulates secondary contacts between previously isolated populations as the principal cause for their high frequencies in some groups of angiosperms is favored." He termed this his "secondary contact hypothesis", and although he provides few details, it seems a prelude to a model in which recurrent polyploid formation produces genetically distinct lineages that subsequently cross, yielding further genetic combinations and contributing to the success of the polyploid (Soltis and Soltis, 1999).

Of course, Stebbins, Wagner, and other students of polyploidy from the second half of the 20th century could not have foreseen that the genomic revolution would reveal that polyploid genomes are highly dynamic—experiencing numerous genetic changes spurred on following polyploidization, including genomic shock and chromosomal, epigenetic, and expression-level changes. Polyploid genomes are anything but uniform.

Limited importance of autopolyploids— Allopolyploidy has historically been considered much more common than autopolyploidy in nature. That trend continues today, but it is now recognized that both are extremely important in nature (e.g., Soltis and Soltis, 1993; Ramsey and Schemske, 1998; Soltis et al., 2004; Tate et al., 2005; Wendel and Doyle, 2005). Stebbins (1950) suggested that only *Galax aphylla* (now *Galax urceolata,* Diapensiaceae) was an unambiguous example of autopolyploidy in nature. He also proposed *Sedum ternatum* and *S. pulchellum* (Crassulaceae) as additional possible examples, with *Fritillaria camschatcensis* (Liliaceae) representing "a probable autotriploid." Stebbins's view (1950) on the rarity of autopolyploids was adhered to by other giants in the field of plant evolution. For example, Grant (1981) also suggested that autopolyploids were extremely rare in nature, but his list of clear-cut autopolyploids was larger than that of Stebbins and included *Galax aphylla*, *Biscutella laevigatum* (Brassicaceae), *Dactylis glomerata* (Poaceae), and *Solanum tuberosum* (Solanaceae), as well as several "probable" autopolyploids: *Vaccinium uliginosum* (Ericaceae), *Eragrostis pallescens* (Poaceae), and *Galium mollugo* and *G. verum* (Rubiaceae).

Stebbins (1971, p. 126) provided a particularly harsh statement regarding autopolyploidy: "autopolyploidy is not a help but a hindrance" in natural populations. One section of his 1971 book (Stebbins, 1971, p. 126) is entitled, "The adaptive inferiority of raw autopolyploids and the ways in which it can be overcome." The perceived extreme rarity of natural autopolyploids was attributed to concerns about chromosome pairing and segregation. Geneticists such as Stebbins maintained that in an autotetraploid, with every chromosome represented four times, normal chromosome pairing at meiosis would be difficult, with multivalent formation leading to reduced fertility. For example, Stebbins (1950, p. 305) stated, "Of equal and perhaps greater significance from the evolutionary point of view than those on the morphology and physiology of the plants are the effects of polyploidy on fertility and genetic behavior. The most conspicuous and universal of these is the reduction of pollen and seed fertility in autopolyploids as compared with their diploid ancestors."

The above problems with autotetraploids are often noted, but Stebbins (1971) also considered the buffering effect of an additional genome to be particularly significant in autopolyploids. He employed a figure (Stebbins, 1971, his fig. 5.2, reproduced here as Fig. 1), stating (p. 127), "This figure shows the distribution of variants with respect to a quantitative character in the F_2 progeny of a cross between two parental individuals [one example is diploid and the other an autotetraploid] which differ with respect to genes at seven different loci… If inheritance is disomic, as in a diploid, the curve of distribution is the broader…" He went on, "Tetrasomic inheritance…gives the narrower more peaked curve… This diagram shows that ...with respect to quantitative characters, chromosome doubling [autopolyploidy] in the progeny tends to buffer intermediate genotypes and reduce the effects of genetic segregation." He concluded, "Hence, this desirable characteristic may also be buffered by tetrasomic inheritance."

However, adding to the complexity that is inherent in the categorization of polyploids, Stebbins (1950, p. 318) discussed several examples of what he termed "intervarietal autopolyploids." For review, the rank of variety is often used for geographical races and well-marked ecotypes within morphologically variable species. Stebbins stated, in reference to intervarietal polyploids, that "this sort may be found to be not uncommon when more polyploids are analyzed with this possibility in mind." Intervarietal autopolyploids sensu Stebbins (1950) included *Biscutella laevigatum*, *Dactylis glomerata*, *Allium schoenoprasum* (Alliaceae), *Polygonatum commutatum* (Ruscaceae), *Cuthbertia graminea* (Commelinaceae), *Eriogonum fasciculatum* (Polygonaceae), and "some of the various polyploids of *Vaccinium*" (Ericaceae). Given this definition, Stebbins was more accepting of a broadly defined autopolyploid and the importance of this mechanism in nature. In fact, as genetic data made it clear (described later) that autopolyploids were common, Stebbins later mellowed considerably in his view toward autopolyploids. In discussions with Ledyard, he indicated to us that autopolyploids, arising from crosses between genetically differentiated parents of the same species, were indeed relatively common "and that is what he had meant all along" (statement to D. and P. Soltis, International Botanical Congress, Berlin, 1987). His early concept of autopolyploidy as

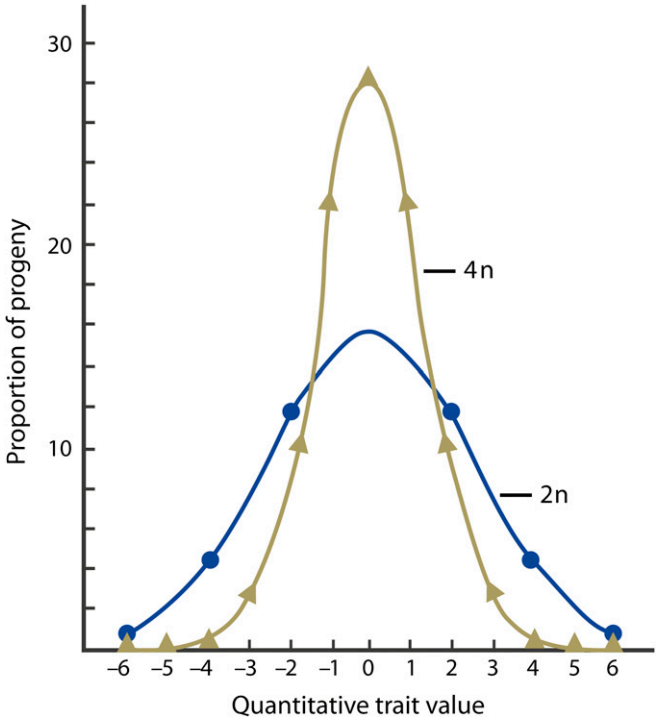


Fig. 1. The buffering effect of tetrasomic inheritance (random pairing between homologues in an autotetraploid). Depicted is the distribution of variation in F_2 progeny of a diploid (with disomic inheritance, in blue) vs. an autotetraploid (with tetrasomic inheritance, in tan). The traditional view of this "buffering effect" was that it might mask beneficial alleles and retard their fixation. Today, this same principle of genetic redundancy has been proposed, in some cases, to be adaptive in the short term, as deleterious alleles are also masked (Mable and Otto, 2001). (Redrawn from fig. 5.2 of Stebbins, 1971).

polyploidization of a single individual (Stebbins, 1950) therefore gave way to a broader perspective. Nonetheless, his strong views regarding the minor role of autopolyploidy in nature had a huge impact, hindering research into this type of polyploidy for decades.

THE NEW POLYPLOIDY PARADIGM

As early as the 1980s, new perspectives began emerging that countered many aspects of the Stebbinsian paradigm. Levin's (1983) classic paper emphasized the role of polyploidy—particularly autopolyploidy—in generating novelty at a range of organizational levels. In response to Stebbins's statement that chromosome doubling is not a help but a hindrance, Levin (1983, p. 1) stressed that "the idea that chromosome doubling per se hinders progressive evolution becomes less tenable as information on autopolyploids increases". This seminal paper was then followed by another paper challenging traditional views of autopolyploidy (e.g., Soltis and Rieseberg, 1986). Subsequent reviews compiled emerging data on topics ranging from multiple origins of polyploid species to the dynamic nature of polyploid genomes (e.g., Soltis and Soltis, 1993, 1999, 2000; Wendel, 2000; Levin, 2002). The current polyploidy paradigm benefits much from the contributions of Stebbins and others (e.g., Clausen et al., 1945; Wagner, 1970; Grant, 1981), but many earlier perceptions have been overturned: polyploidy is ubiquitous in green plants, with all angiosperms and all seed plants of ancient polyploid origin; polyploids are not "dead-ends", but instead ancient polyploidy events are often associated with major clades; genetic factors contribute to the success of polyploids—for example, polyploids typically form more than once with important long-term genetic consequences, and polyploid genome evolution is highly dynamic, with major changes that begin to occur rapidly following polyploidization; and autopolyploidy is common and a major force in plant evolution. In the second half of this paper, we revisit each of these points.

***High frequency of polyploidy*—**Recent investigations of entire genomes have dramatically altered the polyploidy paradigm. Genomic studies have shown that perhaps all eukaryotes possess genomes with considerable gene redundancy, much of which is the result of (ancient) WGD events. Ancient, as well as more recent, polyploidy events have been documented in vertebrates (e.g., Van de Peer et al., 2010; Braasch and Postlethwait, 2012; Cañestro, 2012), fungi (Hudson and Conant, 2012), and ciliates (Aury et al., 2006) and occur extensively in green plants. Within plants, the incidence of polyploidy appears to be low or absent in liverworts, hornworts, cycads, and conifers, but is frequent in lycophytes, monilophytes, and angiosperms (Husband et al., 2013). Wood et al. (2009) estimated that of speciation events, 15% for flowering plants and 31% for ferns directly involve polyploidy. Polyploidy is also prevalent in other photosynthetic lineages, such as red algae (reviewed by Husband et al., 2013).

In angiosperms, the importance of ancient polyploidy became apparent initially with the complete sequencing of the genome of *Arabidopsis thaliana*, which has a very small genome (157 Mb; Bennett et al., 2003). This species was chosen for sequencing because of its small genome, which was "undoubtedly" diploid. Nonetheless, complete genome sequencing revealed numerous duplicate genes, suggesting two or three rounds of genome duplication (Vision et al., 2000; Bowers et al., 2003). Because *A. thaliana* has only five pairs of chromosomes, it was not previously classified as a polyploid using the common "cut-off" criteria employed in typical evaluations of polyploidy (e.g., Stebbins, 1950, 1971).

Recent genomic investigations not only indicate that polyploidy is ubiquitous among angiosperms, but also suggest other major ancient WGD events (Van de Peer et al., 2009, 2010). These include an ancient WGD that preceded the origin of all extant angiosperms (Jiao et al., 2011; *Amborella* Genome Project, 2013), as well as two WGDs that occurred in close temporal succession early in eudicot evolution (Jiao et al., 2012). At least 50 independent ancient WGDs are distributed across flowering plant phylogeny (Cui et al., 2006; Soltis et al., 2009; Van de Peer et al., 2009, 2011; M. S. Barker et al., University of Arizona, personal communication). Other ancient polyploidy events occurred close to the origin of monocots, Poales, Solanales, and Lamiales. All of the angiosperm genomes sequenced to date exhibit evidence of ancient polyploidy events (Comparative Genomics [CoGe] website, http://genomevolution.org/CoGe/).

Although Stebbins did not realize the ubiquity of polyploidy, he did, however, propose that ancient polyploidy was sometimes important, suggesting that some angiosperm families may be the result of this process. In this regard, genetic/genomic data continue to provide evidence that this indeed is the case.

Isozyme data long ago showed that several families suggested by Stebbins (1971) to be ancient polyploids—Trochodendraceae, Salicaceae, Magnoliaceae, Lauraceae, and Calycanthaceae—in fact exhibited duplicate gene expression, consistent with his hypothesis (Soltis and Soltis, 1990). Genomic evidence now indicates that ancient polyploidy has played a major role in a number of additional families, including Asteraceae, Brassicaceae, Cleomaceae, Fabaceae, Poaceae, and Solanaceae (reviewed by Soltis et al., 2009).

Extant seed plants also share an additional round of ancient polyploidy (Jiao et al., 2011), with evidence for additional genome duplication events in ferns and other tracheophytes (Barker and Wolf, 2010). Wood et al. (2009) estimated that ~35% of extant flowering plant species are of recent polyploid origin. As a result, a large fraction of genes, perhaps as many as 67% in some species, may be directly derived from ancient WGD (Barker et al., 2012).

A new look at polyploidy and diversification— The identification of ancient WGD events at many points in angiosperm phylogeny provides the opportunity to assess the correspondence between inferred genome duplication events and major diversifications—the role of polyploidy in "macrodiversification." Many ancient WGDs are associated with key diversification events in angiosperm evolution, such as the origins of angiosperms, eudicots, and monocots.

Examination of polyploidy events in Brassicaceae, Poaceae, and Solanaceae suggests that ancient WGD was followed by a burst in species richness, typically a few nodes after the WGD (Soltis et al., 2009). Ancient polyploidy also seems to be associated with increases in plant diversity in Asteraceae, Brassicaceae, Cleomaceae, and Fabaceae (Soltis et al., 2009; Doyle, 2012; Schranz et al., 2012). Within most of these clades, there is phylogenetic asymmetry "with a species-rich crown group and a species-poor sister clade" (Schranz et al., 2012, p. 147). Moreover, there may be a lag-time or delay between the WGD event and subsequent radiations (Fig. 2). Schranz et al. (2012, p. 147) further proposed that "ultimate success of the crown group does not only involve the WGD and novel key traits, but largely subsequent evolutionary phenomena including later migration events, changing environmental conditions and/or differential extinction rates."

Mike Barker et al. (University of Arizona, personal communication) found that roughly half of the 59 ancient WGD events that they examined are associated with diversification. In addition, using a large phylogenetic tree for angiosperms, Tank et al. (2012) demonstrated statistically that several major ancient polyploidy events closely coincide with bursts in diversification, but with these radiations typically occurring a few nodes after the ancient WGD events.

Other evidence indicates increases in biological diversity and/or complexity in polyploid lineages (De Smet and Van de Peer, 2012). Phylogenetic dating analyses of several ancient WGD events suggest an association between the Cretaceous–Tertiary (KT) extinction and WGD (Fawcett et al., 2009; Vanneste et al., 2014): polyploidy may have contributed to lineage survival

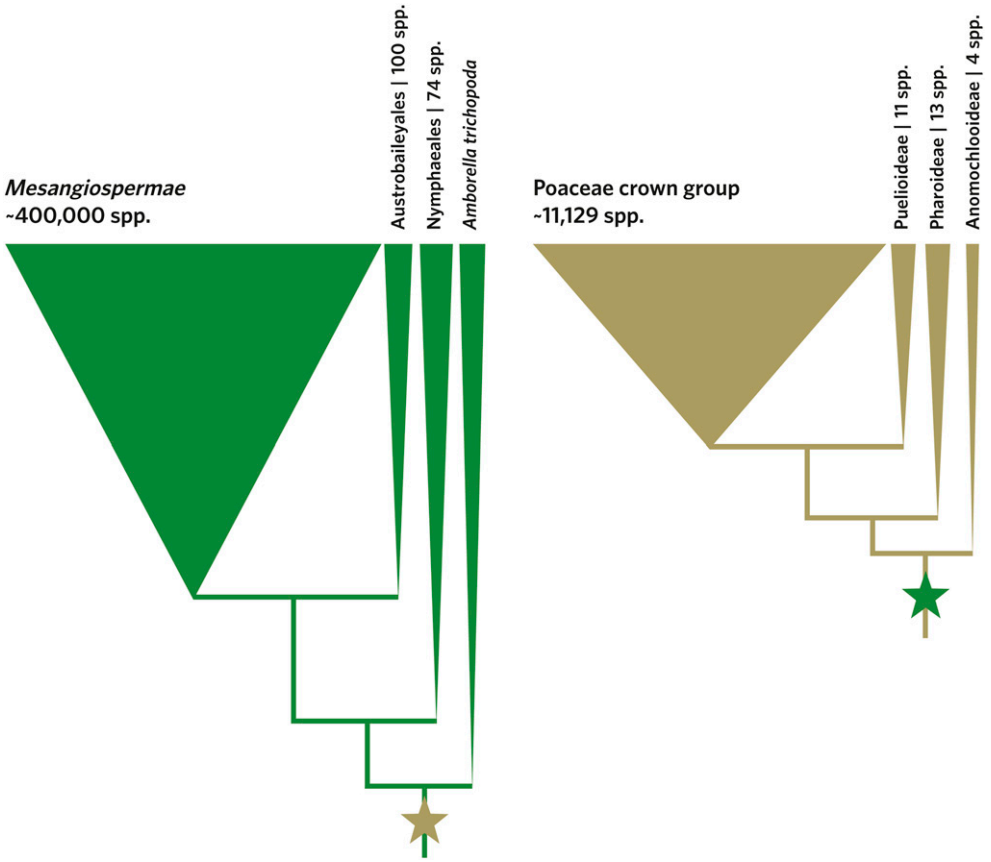


Fig. 2. Following a whole genome duplication (represented as stars), there appears to be a lag-time before diversification (modified from Schranz et al., 2012). Trees drawn following the topologies of Soltis et al. (2012) and Stevens (2001 onward).

following the KT mass extinction, a compelling hypothesis that requires more investigation (Soltis and Burleigh, 2009). In an interesting twist, rather than searching for "advantages" of polyploids to explain their high frequency, Meyers and Levin (2006, p. 1198) hypothesized that the abundance of polyploidy may be the result of "a simple ratcheting process that does not require evolutionary advantages due to the biological properties of organisms." They show that the average ploidal level within a lineage can continue to increase to the levels seen today, "even if there are ecological or physiological disadvantages to higher ploidy."

Recent reanalyses of data for ferns and angiosperms revived the concept of polyploids as evolutionary dead-ends, indeed using this very word (Mayrose et al., 2011; see also Arrigo and Barker, 2012). Mayrose et al. (2011) argued that polyploids have higher extinction rates than diploids and are therefore often "dead-ends" that do not leave a legacy. Although it is likely that most new polyploids go extinct soon after formation, a number of computational, methodological, and statistical limitations raise serious questions about the results of these studies and whether polyploids do in fact diversify less than diploids (Soltis et al., 2014).

Genetic variation in polyploids of multiple origin—Speciation via cladogenesis, regardless of mode (e.g., allopatric, sympatric, or saltational speciation; reviewed by Grant [1981], Futuyma [1998], and Levin [2000]), yields sister species that are (eventually) reciprocally monophyletic, even if viewed as paraphyletic following species formation (Rieseberg and Brouillet, 1994). However, polyphyletic local origins of polyploid species have been recognized for over 60 yr (e.g., Ownbey, 1950) and are today considered the rule for polyploid species (e.g., Werth et al., 1985a, b). Interestingly, this view of recurrent polyploid species formation is not presented in any of the highly influential reviews of polyploidy from the mid-1900s, including those by Stebbins (1950, 1971) and Grant (1971, 1981). It is now well established, based on several lines of evidence, that individual polyploid plant, as well as animal, species typically form multiple times (reviewed by Soltis and Soltis [1993, 1999, 2000]).

It is puzzling that the concept of multiple origins of polyploid species did not gain more traction with Stebbins, who reviewed the ancestries of *Tragopogon mirus* and *T. miscellus* (Asteraceae) in his 1971 book (Stebbins, 1971). Ownbey (1950) and Ownbey and McCollum (1953) reported that each of the newly formed allotetraploid *Tragopogon* species likely formed at least twice. Likewise, although Grant (1981) did not mention recurrent polyploidization, his own research on *Gilia* (Polemoniaceae) suggested that this process occurred (Grant, 2002). Other examples of recurrent polyploidy from the premolecular literature include species of *Madia* (Asteraceae) (Clausen et al., 1945), *Gutierrezia* (Asteraceae) (Solbrig, 1971), *Mimulus* (Phrymaceae) (Mia et al., 1964), and *Rubus* (Rosaceae) (Rozanova, 1938; see Mavrodiev and Soltis, 2001).

Nearly all polyploids that have been investigated with genetic markers show evidence of recurrent formation, and the estimated number of independent polyploidization events typically increases as data are gathered for additional populations and for increasingly sensitive markers. For example, autotetraploid *Heuchera grossulariifolia* (Saxifragaceae) may have five origins (Segraves et al., 1999). Allohexaploid *Draba norvegica* (Brassicaceae) has formed at least 13 times in a small area of Scandinavia (Brochmann et al., 1992). *Glycine tabacina* (Fabaceae), an allopolyploid, has formed at least six times in Australia (Doyle et al., 2003). *Tragopogon miscellus* and *T. mirus* may have formed over 20 and 10 times, respectively, in eastern Washington and adjacent Idaho (USA) in just the past 80 yr—multiple polyploidizations have even occurred within a single small town (Symonds et al., 2010; Soltis et al., 2012). Exceptions in which polyploidy appears to have occurred only once in the formation of a species include salt marsh grass, *Spartina anglica* (see Ainouche et al., 2012), and peanut, *Arachis hypogaea* (Kochert et al., 1996). Therefore, multiple origins are now considered to be the rule in polyploid evolution (Soltis and Soltis, 1993, 1999).

Recurrent polyploidization has important implications for concepts of genetic diversity within polyploid species. One of the key arguments Stebbins (1950) made against the long-term evolutionary importance of polyploid species was their lack of genetic diversity as a result of the bottleneck associated with their formation. The general view among systematists today is that independently formed lineages may over time produce a tokogenetic (that is, reticulating genealogical) network, incorporating genetic variation from genetically differentiated parental individuals and generating new genotypes through gene flow and recombination (Fig. 3; Soltis and Soltis, 1999; Tate et al., 2005; Soltis et al., 2014). The notion of recurrent polyploidization has shattered earlier perceptions of polyploids as genetically depauperate species of uniform genotype that represent evolutionary dead-ends.

A question of great interest is: Can populations of independent origin interbreed, or do they represent reproductively isolated lineages? Experimental demonstration of such interbreeding among polyploid lineages of separate origin is still rare. Recent work on *Mimulus* indicates that polyploid populations of separate origin are interfertile (Sweigart et al., 2008). A mixture of results is apparent for populations of *Tragopogon* polyploids of separate origin; some populations appear to be interfertile, whereas some combinations are sterile (Ownbey and McCollum, 1953; M. Chester et al., University of Oxford, unpublished data). This is clearly an area of research that requires more investigation.

The dynamic nature of polyploid genomes—Polyploid genomes are highly dynamic, beyond anything that Stebbins and his contemporaries could have predicted. Not only are polyploids ubiquitous in nature, polyploidy itself has played a central role in shaping and restructuring plant genomes. Rapid changes post-polyploid formation occur in genome structure, gene content, gene expression, and methylation and other epigenetic regulators (Fig. 4), and we briefly review these topics here. These features yield variation within polyploid species—in contrast to the prediction of genetic uniformity—and contribute to evolutionary novelty and possibly long-term persistence of polyploid species.

Genome structure and chromosomal changes—Molecular cytogenetic techniques allow for in-depth analysis of genome restructuring following polyploidy. For example, fluorescent in situ hybridization (FISH) and genomic in situ hybridization (GISH) revealed that the allotetraploid *T. miscellus* has extensive chromosomal variability (Lim et al., 2008; Chester et al., 2012). None of the populations examined was fixed for a particular karyotype, 76% of the individuals showed intergenomic translocations, and 69% exhibited aneuploidy for one or more chromosomes. Similar results were recently obtained for *T. mirus* although compensated aneuploidy was not as frequent in this recent polyploid (Chester et al., in press). The extensive chromosomal variation still present after ca. 40 generations in *T. mirus* and *T. miscellus* suggests that substantial and prolonged

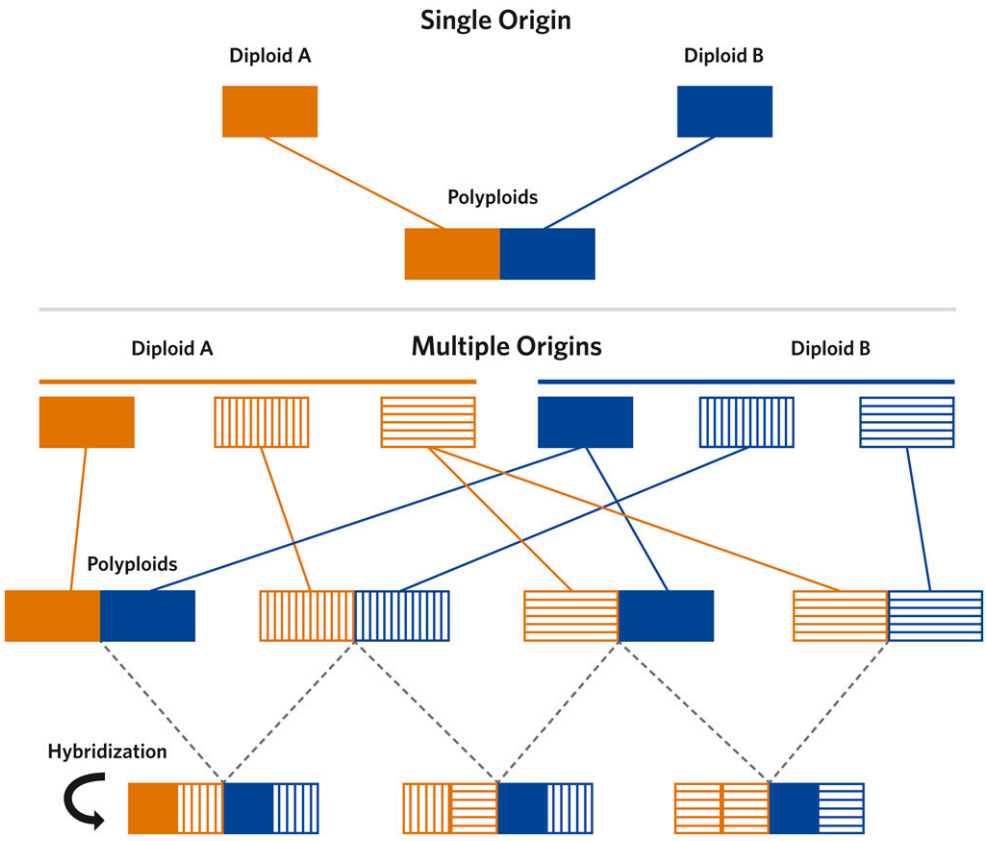


Fig. 3. Contrasting viewpoints of polyploid formation and frequency (modified from Soltis and Soltis, 1999). The traditional view (top) considered polyploidy events rare and considered most polyploids to be of single origin with low genetic diversity. The current view (bottom) is one of multiple origins and high genetic diversity, of which only a subset is represented here. Colors represent parental genomes (homeologues), and patterns represent different alleles.

chromosomal instability might be common in natural populations after WGD (Fig. 4). Extensive chromosomal variation, including translocations and compensated aneuploidy, was also observed in synthetic lines of the allotetraploid *Brassica napus* (rapeseed; Gaeta et al., 2007; Xiong et al., 2011). However, such variation is not present in cultivated *B. napus*, a result attributed to selection for genomic stability through less frequent homeologous pairing (Udall et al., 2005; Gaeta and Pires, 2010). Whereas selection seems to limit genome dynamics and stabilize genome structure fairly soon after polyploid formation in *B. napus*, *Nicotiana* allopolyploids of various ages continue accumulating genomic rearrangements for much longer periods of time (~4.5 million years [Myr] since formation; Lim et al., 2007).

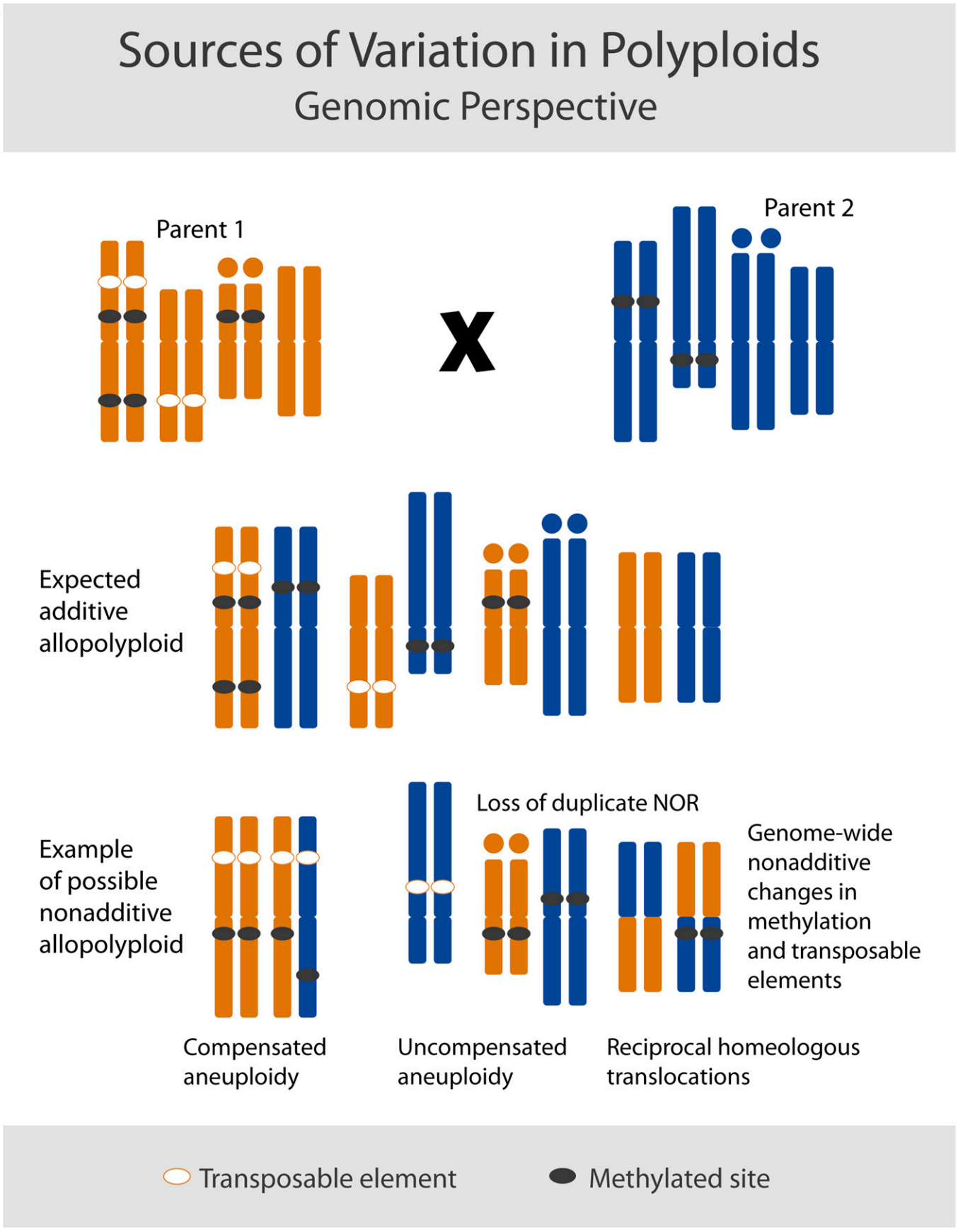
In contrast, allopolyploid *Gossypium* has maintained a strikingly stable genome since formation (approximately 1–2 my ago [Ma]) (Liu et al., 2001). Due to the divergence between *Gossypium* parental chromosomes (~5–10 Ma), homeologous pairing is uncommon, resulting in relatively few exchanges between parental genomes (Hendrix and Stewart, 2005; Salmon et al., 2010; Wang et al., 2010). Likewise, after as few as 150 yr following formation, genomic stability in allopolyploid *Spartina anglica* has also been reported, perhaps because, as in cotton, the parental genomes diverged several million years ago (~3 Ma) (Ainouche et al., 2004, 2012). Allopolyploid *Cardamine flexuosa* represents an interesting system, with recent investigation revealing synteny between homeologues (indicating low divergence between parental genomes, and an expectation of frequent homeologous exchange), though only one homeologous translocation appears to have occurred (Mandáková et al., 2014).

Natural and synthetic allopolyploid *Arabidopis suecica* and one of its progenitors, autotetraploid *A. arenosa*, maintain somatic aneuploid mosaics (intraindividual variation in some,

→

Fig. 4. A nonexhaustive example of potential sources of variation in an allopolyploid due to the merging of two parental genomes (homeologues, differentiated by blue and orange). (A) Variation at the genomic level, including major changes to the karyotype, and nonadditive global methylation/transposable element patterns. (B) Variation at the genetic level, comprising homeologue-specific loss/exchange/conversion and the repeatability (or lack thereof) of these across multiple lineages. (C) Variation at the transcriptomic level can take the form of changes to expression level (the volume of transcript produced by both homeologous gene copies), expression bias (higher expression of one homeologue), tissue-specific expression, and the interaction of regulatory elements between homeologous genomes.

A


Sources of Variation in Polyploids
Genomic Perspective
Parent 1
X
Parent 2
Expected additive allopolyploid
Example of possible nonadditive allopolyploid
Loss of duplicate NOR
Genome-wide nonadditive changes in methylation and transposable elements
Compensated aneuploidy
Uncompensated aneuploidy
Reciprocal homeologous translocations
Transposable element
Methylated site

B

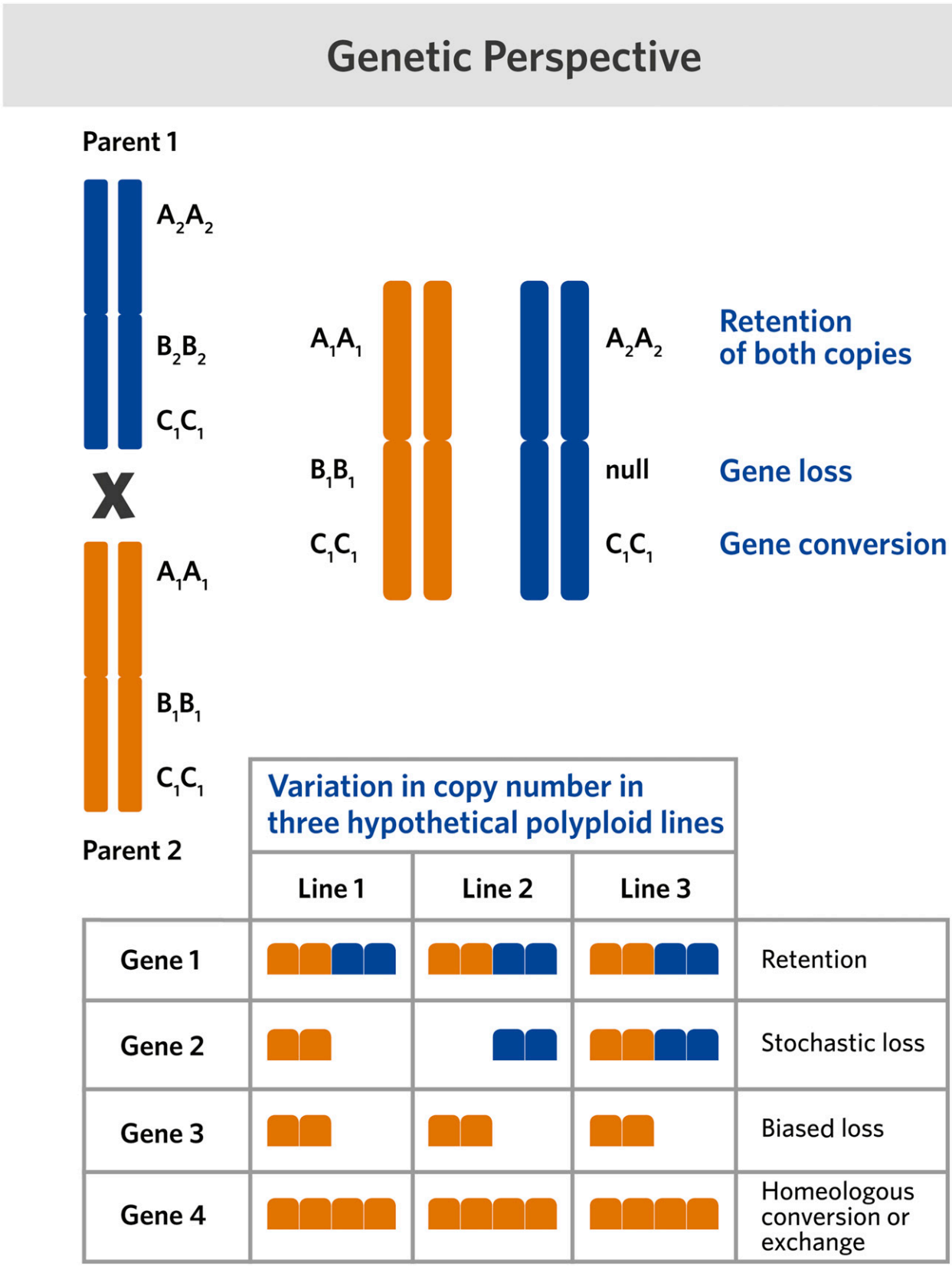


Fig. 4. Continued.

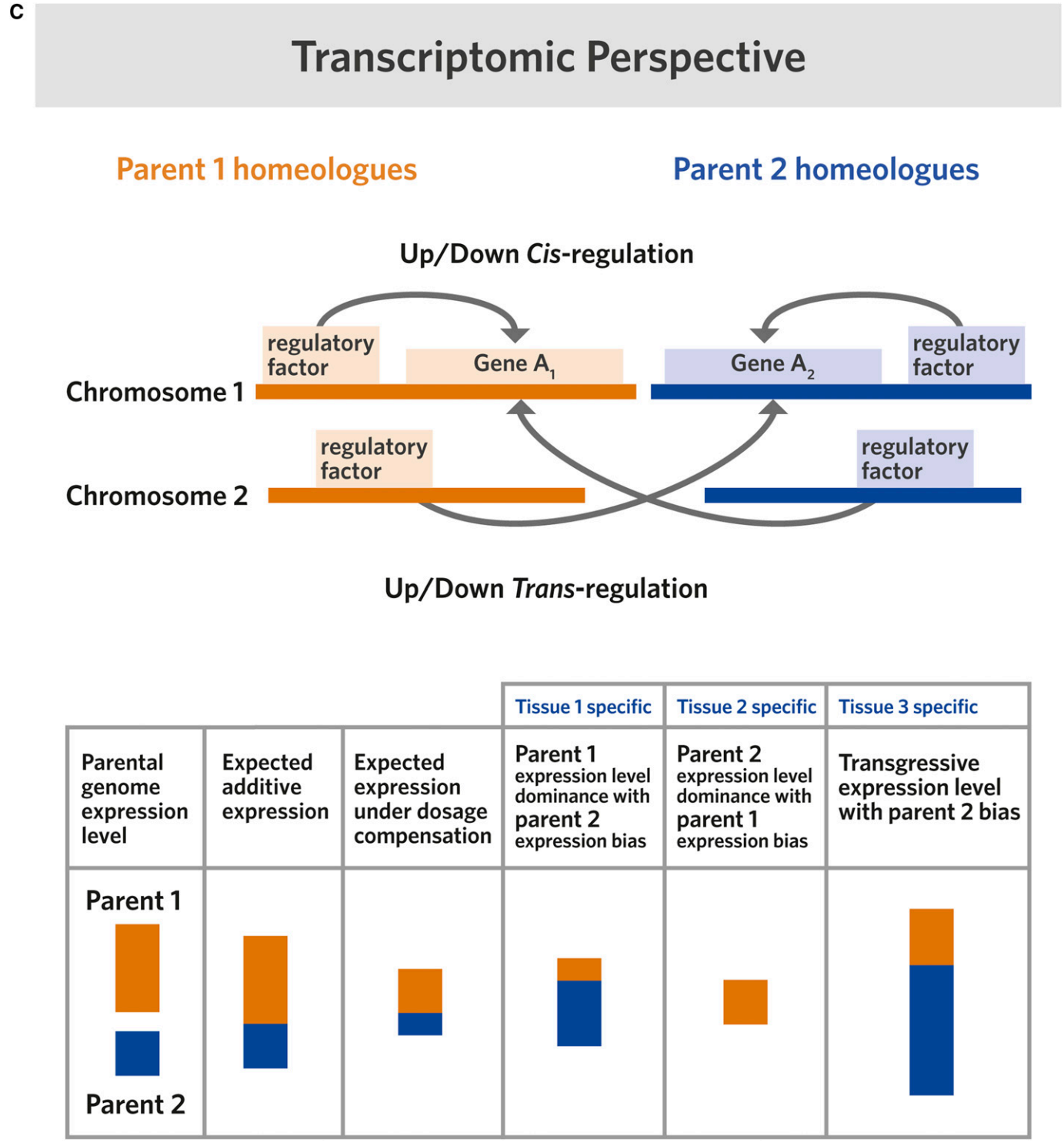


Fig. 4. Continued.

but not all, of the chromosome complement) in surprisingly high frequency (up to 20% and 34% in natural and synthetic plants, respectively), while the other progenitor, autotetraploid *A. thaliana*, exhibits much lower frequencies (4%), with diploid *A. thaliana* having 0% (Wright et al., 2009). Genome duplication in *Arabidopsis*, both auto- and allopolyploidy, appears to increase tolerance of within-individual aneuploid mosaicism, as even the least tolerant tetraploid *A. thaliana* is more tolerant than its diploid progenitor. Synthetic *A. suecica* also undergoes rapid genomic stabilization of the nucleolar organizing and 5S rDNA regions through loss and/or homeologous rearrangement; this has also been documented in natural accessions

(Pontes et al., 2004). *Arabidopsis* neopolyploid lines (*A. thaliana* [2*x*] × *A. suecica* [4*x*]) not only display aneuploidy in somatic tissue but also give rise to aneuploid offspring (similar to *Brassica,* above); aneuploidy was also found to correlate with phenotypic change (Matsushita et al., 2012).

These chromosomal analyses demonstrate that plant species respond differently to polyploidy. Species of *Tragopogon*, *Brassica*, and *Nicotiana* exhibit extensive structural variation, whereas polyploids in *Gossypium*, *Spartina*, and *Cardamine* have undergone little to no genome restructuring. This variation in the extent of chromosomal variation indicates that more work is needed before we can understand why some polyploid genomes rearrange and others do not.

Gene loss—Upon formation, allopolyploids have duplicate genes at all loci, and these extra loci may be maintained, modified, or lost, with the latter comprising both true physical loss of DNA and homeologous gene conversions (Fig. 4; Wang and Paterson, 2011). Losses of one duplicate gene copy have occurred over short time scales, in both synthetic and natural allopolyploids (Kashkush et al., 2002; Nie et al., 2008; Anssour et al., 2009; Buggs et al., 2010; Koh et al., 2010). Gene loss can occur immediately following polyploidization, as demonstrated by Nie et al. (2008) in S_1 synthetic hexaploid *Triticum*. In other cases, however, gene losses only occur in later generations following WGD (Song et al., 1995; Buggs et al., 2009). In young polyploids, these losses appear to occur frequently, as was shown in *Tragopogon miscellus* with high interpopulation and interindividual variation displayed with respect to homeologus losses (Tate et al., 2009; Buggs et al., 2012). That is not to say that all gene loss is random, however. Repeated patterns of homeolog loss and retention have been reported across multiple origins of both *T. mirus* and *T. miscellus* (Tate et al., 2006, 2009; Koh et al., 2010; Buggs et al., 2012). Furthermore, in *T. miscellus*, loci belonging to certain gene ontology (GO) categories were disproportionately more likely to be lost, and patterns of loss and retention after 40 generations in this young polyploid were similar to those discovered for much older (40 Myr) WGDs in Asteraceae (Barker et al., 2008). Over longer evolutionary time, patterns of duplicate gene retention and loss appear to be related to gene function (e.g., Paterson et al., 2006; Barker et al., 2008; Severin et al., 2011; De Smet et al., 2013). Taken together, given enough time, many of the seemingly stochastic processes associated with neopolyploids eventually converge on a pattern of single vs. duplicate gene retention.

Changes in gene expression—In addition to structural changes to the genome and changes in gene content, recent research has shown plasticity and transgression in allopolyploid gene expression patterns (Fig. 4), indicating that polyploids are not the sum of their parental genes. Instead, many polyploids deviate from expectations in which parental gene expression patterns are combined in the allopolyploid, i.e., midparent expression levels. Homeologous silencing and nonadditive up- or downregulation may explain these deviations, although these changes are not necessarily consistent across the genome and are not always associated with chromosome doubling per se (Hegarty et al., 2005, 2006, 2012; Buggs et al., 2009, 2011; Chelaifa et al., 2010; Ainouche et al., 2012). For example, *Spartina townsendii*, a homoploid hybrid of *S. maritima* and *S. alterniflora* (themselves both polyploid), exhibits gene expression patterns similar to those of *S. alterniflora* (Chelaifa et al., 2010). The natural allopolyploid derivative of *S. maritima* and *S. alterniflora*, *S. anglica*, deviates slightly from the homoploid hybrid in expression by exhibiting more balanced parental expression levels (Chelaifa et al., 2010; Ainouche et al., 2012). However, because expression patterns in *S. anglica* are similar to those of the homoploid hybrid, it appears that hybridization had a greater impact than genome doubling on gene expression. Such expression-level dominance has also been reported in polyploids in *Gossypium* and *Arabidopsis* (Wang et al., 2006b; Chang et al., 2010; Flagel and Wendel, 2010; Yoo et al., 2013), among others. Whether expression biases occur as a result of hybridization, polyploidization, or subsequent evolution over time, and if they are conserved across separate origins of polyploids, appears to vary among taxa. Moreover, the underlying mechanisms responsible for biased gene expression require further investigation (see Yoo et al., 2013; M.-J. Yoo et al., Florida Museum of Natural History, unpublished manuscript).

In addition to gene silencing, genetic changes in polyploids may lead to functional diversification of the homeologs, creating genes of new function (neofunctionalization) or a partitioning of gene function (subfunctionalization) (e.g., Ohno, 1970; Lynch and Conery, 2000; Lynch and Force, 2000; Prince and Pickett, 2002). One of the most exciting areas of discovery in allopolyploids is the documentation of organ-specific subfunctionalization of gene expression, a process that may be a major contributor to the success of polyploids. Subfunctionalization has been particularly well studied in cotton (e.g., Adams et al., 2003, 2004; Adams and Wendel, 2004, 2005). Based on studies of recent polyploids in *Tragopogon*, it is also apparent that subfunctionalization may begin to occur soon after polyploidization (Buggs et al., 2011).

Epigenetics—Beyond genomic and genetic attributes of polyploids, epigenetic properties may also contribute to variation and novelty in polyploids. Chromatin modification, DNA methylation, and *cis-/trans*-acting regulatory interactions may generate nonadditive expression patterns such as those described above (Fig. 4). In fact, ecological and physiological novelty has been linked to epigenetic modifications in polyploids (Osborn et al., 2003). The term "genomic shock" (McClintock, 1984) refers to genomic stress of any kind, including hybridization and polyploidization, prompting major genomic change and associated epigenetic effects. Investigations into the epigenetic effects involved in polyploidy are still in their infancy, with most research predominantly investigating methylation.

DNA methylation exhibits nonadditive patterns following both auto- and allopolyploidization (Salmon et al., 2005; Kraitshtein et al., 2010; Zhao et al., 2011; Lavania et al., 2012). Salmon et al. (2005) teased apart the role played by hybridization and genome duplication per se, indicating that genome merger and not polyploidy was largely responsible for nonadditive methylation patterns in *Spartina* (see also Parisod et al., 2009). However, alterations to methylation patterns do not always accompany hybridization or polyploidization, as Liu et al. (2001) reported for allopolyploid *Gossypium.* Likewise, divergent regulatory factors, particularly *trans* factors acting between parental genomes, also influence gene expression in allopolyploids and are capable of silencing, upregulating, or downregulating homeologous loci (Wang et al., 2006a; Shi et al., 2012; and reviewed in Buggs et al., 2014). For example, in the allotetraploid *Arabidopsis suecica*, a gene (*FRI*) from the *A. arenosa* parental subgenome downregulates the *A. thaliana* copy of another gene (*FLC*) in the flowering time pathway to yield a much later flowering time in the polyploid than in either parent. Studies of such well-described

pathways make it clear that epigenetic factors may control expression patterns in polyploids and can potentially serve as dynamic mechanisms contributing to polyploid evolution.

Autopolyploidy is common—Allopolyploidy is still considered to be more common than autopolyploidy (e.g., Soltis and Soltis, 1993; Ramsey and Schemske, 1998; Soltis et al., 2004; Tate et al., 2005; Wendel and Doyle, 2005), but increasing importance is given to autopolyploidy, although we likely continue to underestimate both the prevalence and role of autopolyploidy in ecology and evolution. The perceived rarity of natural autopolyploids historically was attributed in part to sterility resulting from irregular chromosome pairing at meiosis. Because every chromosome is represented four times in an autotetraploid, multivalent formation can lead to reduced fertility. However, chromosome pairing in even-numbered polyploids may be stable and does not necessarily interfere with the ability of a polyploid to reproduce. Chromosome pairing in wheat is under simple genetic control (Sears, 1976). Several genes (*Pairing homoeologous*, *Ph* genes) control chromosome pairing in wheat, but the strongest effect is associated with a gene on the long arm of chromosome 5B, *Phl* (Ji and Langridge, 1990; Griffiths et al., 2006). Rapid sequence elimination in newly formed wheat polyploids (Shaked et al., 2001) suggests that differential elimination of genome-specific sequences may facilitate homologous chromosome pairing. Simulations also suggest mechanisms for autopolyploids that may also facilitate a move from multivalent formation and polysomic inheritance to disomic inheritance (Le Comber et al., 2010).

Because a major criterion for recognition of an autopolyploid has been polysomic inheritance (e.g., Muller, 1914; Haldane, 1930), detection of autopolyploids was long hampered by lack of easy tools for assessing genetic diversity and inheritance patterns. Inference of disomic vs. polysomic inheritance from allozyme (see Tate et al., 2005) and other genetic markers (e.g., microsatellites; Landergott et al., 2006; Stift et al., 2008) revolutionized the study of autopolyploidy. Based on allozyme electrophoresis, studies of diverse plants revealed a number of previously unrecognized autopolyploids (reviewed by Soltis and Soltis [1993, 1999]; and Tate et al. [2005]), including *Tolmiea menziesii* (Saxifragaceae), *Heuchera micrantha* and *H. grossulariifolia* (Saxifragaceae), *Turnera ulmifolia* var. *elegans* and var. *intermedia* (Turneraceae), and *Allium nevii* (Alliaceae). Other genetic markers, including microsatellites, have revealed many additional examples. We have searched the literature from the past 25 yr and provide an updated list of possible autopolyploids (Table 1).

Numerous studies suggest that autopolyloids are frequently generated, but may either quickly be lost or persist undetected. For example, Ramsey and Schemske (1998) estimated that the rate of autotetraploid formation is high—comparable to the genic mutation rate. Although most certainly do not survive, even a small success rate ultimately yields a high number of autopolyploid species. Certainly most of the cytotypes recognized as intraspecific chromosomal series are autopolyploids, based on morphological similarity among cytotypes—many may be unrecognized distinct lineages (e.g., species). Furthermore, autopolyploidy may be more prevalent in some plant groups than others. For example, autopolyploids have often been documented in Saxifragaceae (Soltis and Soltis, 1993) and Cactaceae (see Hamrick et al., 2002; Arakaki et al., 2007; Majure et al., 2012). Most known polyploids in mosses appear to be autopolyploids (Wyatt et al., 1989; Husband et al., 2013).

Insight into the possible high frequency of autopolyploidy, as well as the number of unnamed polyploid species, has been provided using the California flora as a database (J. Ramsey and B. C. Husband, personal communication; reviewed by Soltis et al. [2007]). Of 2647 species from 346 genera in 62 angiosperm families, 334 species (13%) have multiple cytotypes (clear 3*x*, 4*x*, or higher multiples of the base chromosome number for a given genus). Most of these cytotypes are presumed to be autopolyploids, but all would require careful study to clarify their origin. Nonetheless, we will assume for purposes of this example that these are autopolyploids. Because some of these 334 chromosomally polymorphic taxonomic species actually have more than two cytotypes, if each cytotype represented a distinct species, the total number of unrecognized species is actually 483. Even if only 50% are autopolyploids, the point is clear—we have grossly underestimated the importance of autopolyploids in nature (see Soltis et al., 2007). Furthermore, this or any estimation of the occurrence of multiple cytotypes from the literature (e.g., from any regional flora) could be a low minimum estimate.

The proposed reasons for the success of autopolyploids are several and involve tetrasomic (in an autotetraploid) or higher-level polysomic inheritance (Soltis and Rieseberg, 1986; Soltis and Soltis, 1989a). This results in increased heterozygosity compared to diploids (see Moody et al., 1993) and up to four different alleles per locus in a single autotetraploid plant (Soltis and Soltis, 1993). Parisod et al. (2010) note that although few autopolyploids have been examined in any detail, autopolyploids do not seem to experience major genome restructuring or major changes of gene expression during the first generations following genome doubling, However, over longer periods of evolutionary time, these processes are likely to become more important. They hypothesize that polysomic inheritance provides a short-term evolutionary advantage for an autopolyploid compared to its diploid progenitor. Recently, computer simulations indicted that autopolyploids may also be capable of escaping polysomic inheritance and regaining disomic inheritance, opening the door to neo- and subfunctionalization (Le Comber et al., 2010; see review above).

Biogeographic and niche modeling analyses have begun to investigate the possible role of niche divergence in the establishment and persistence of both autopolyploids and allopolyploids. Although establishment of an autopolyploid may be particularly susceptible to minority cytotype exclusion (Levin, 1975), many autopolyploids have nonetheless become established and persist, perhaps due to early divergence in habitat requirements. Few studies have empirically shown autopolyploids to occupy novel niche space following formation. One of the best examples of niche divergence promoting the establishment of a newly originated autopolyploid is in *Achillea* (Ramsey, 2011; see Levin, 2011); this study provides evidence of a neohexaploid being ecologically divergent from its tetraploid parent at the time of formation. Although the above work stands as an example of the ideal method for demonstrating niche divergence, it can be exceedingly difficult and time-consuming. Given the large number of polyploids in nature, ecological niche modeling using readily available locality data from herbarium records and other sources can offer broad insights into patterns of polyploidy and novelty. A new literature is emerging on the distribution of polyploids and their diploid progenitors. Here we review the handful of autopolyploids that have been examined with this approach (niche differentiation in allopolyploids is covered in a later section).

TABLE 1. Presently recognized autopolyploids and the type of evidence used to support their mode of origin. Included are the results of previous such tables compiled by Soltis and Soltis (1993), Soltis et al. (2007), Parisod et al. (2009), and Arnold et al. (2012).

Taxon	Ploidy	Type of evidence	Source
Acacia nilotica	4*x*	segregation pattern	Mandal et al., 1994
Actinidia chinensis var. *deliciosa*	4*x*	segregation pattern and meiotic associations	Mertten et al., 2012; Huang et al., 1997
Adansonia digitata	4*x*	segregation pattern	Larsen et al., 2009
Allium nevii	4*x*	segregation pattern	Rieseberg and Doyle, 1989
Arabidopsis lyrata	4*x*	segregation pattern	Mable et al., 2004
Aster amellus	6*x*	morphology and lack of fixed heterozygosity	Mándaková and Münzbergová, 2008
Biscutella laevigata	4*x*	segregation pattern	Tremetsberger et al., 2002
Centaurea jacea	4*x*	segregation pattern	Hardy et al., 2001
Chamerion angustifolium	4*x*	segregation pattern	Husband and Schemske, 1997
Chrysanthemum morifolium	6*x*	morphological segregation	Langton, 1980
Dactylis glomerata	4*x*	segregation pattern	Lumaret, 1987
Dahlia variabilis	4*x*	morphology	Lawrence, 1931
Dioscorea alata	4*x*	segregation pattern	Nemorin et al., 2012
Dioscorea trifida	4*x*	segregation patterns	Bousalem et al., 2006
Galax urceolata	4x	chemistry and lack of fixed heterozygosity	Soltis et al., 1983; Epes and Soltis, 1984
Galium anisophyllum	4*x*	morphology	Ehrendorfer, 1965
Haplopappus spinulosus	4*x*	segregation pattern	Hauber, 1986
Heuchera cylindrica	4*x*	segregation pattern	R. A. Ruppel and K. A. Segraves, unpublished data
Heuchera grossulariifolia	4*x*	segregation pattern	Wolf et al., 1989
Heuchera micrantha	4*x*	segregation pattern	Soltis and Soltis, 1989b
Lotus corniculatus	4*x*	segregation pattern	Fjellstrom et al., 2001
Lythrum salicaria	4*x*	morphological segregation	Fisher, 1943; Fisher, 1949
Maclura pomifera	4*x*	segregation pattern	Laushman et al., 1996
Medicago falcata	4*x*	morphology and segregation pattern	Quiros, 1982; Stanford, 1951
Medicago sativa	4*x*	segregation pattern	Quiros, 1982; Stanford, 1951
Pachycereus pringlei	4*x*	segregation pattern	Murawski et al., 1994
Panicum virgatum	8*x*	segregation pattern	Okada et al., 2011
Paspalum notatum	4*x*	segregation pattern	Stein et al., 2004
Paspalum simplex	4*x*	segregation pattern	Pupilli et al., 1997
Phleum pratense	6*x*	morphology	Nordenskiold, 1953
Prunus spinosa	4*x*	segregation pattern	Leinemann, 2000
Rorippa amphibia	4*x*	segregation pattern	Stift et al., 2008
Rorippa sylvestris	4*x*	segregation pattern	Stift et al., 2008
Rutidosis leptorrhynchoides	4*x*	segregation pattern	Brown and Young, 2000
Solanum tuberosum	4*x*	morphology and segregation pattern	Howard, 1970; Martinez-Zapater and Oliver, 1984; Quiros and McHale, 1985
Thymus praecox	4*x*	segregation pattern	Landergott et al., 2006
Tolmiea menziesii	4*x*	segregation pattern	Soltis and Soltis, 1988
Turnera sidoides complex	2*x*–8*x*	meiotic associations	Kovalsky and Solis Neffa, 2012
Turnera ulmifolia var. *elegans*	4*x*	segregation pattern	Shore and Barrett, 1987; Shore, 1991
Turnera ulmifolia var. *intermedia*	4*x*	morphology and segregation pattern	Shore and Barrett, 1987; Shore, 1991
Vaccinium corymbosum	4*x*	segregation pattern	Krebs and Hancock, 1989

Diploid and autotetraploid cytotypes of *Heuchera cylindrica* inhabit separate ranges but were found not to have diverged in niche requirements (Godsoe et al., 2013). Conversely, in *Claytonia*, three species, each comprising a cryptic ploidal series including both auto- and allopolyploids, were shown to have undergone divergence in niche space between the diploids and polyploids, though tetraploid and hexaploid niches were found in some cases to overlap with one another (McIntyre, 2012). *Tolmiea menziesii*, an autotetraploid, appears to be both ecologically and geographically distinct from its progenitor, *T. diplomenziesii* (Soltis, 1984; C. J. Visger et al., unpublished data). In *Houstonia*, divergence between diploid and tetraploid cytotypes was found in *H. longifolia*, but lack of divergence was observed for *H. purpurea* (Glennon et al., 2012). In *Primula* sect. *Aleuritia*, three polyploid species—most likely autopolyploids—and their diploid progenitor, *P. farinosa*, all occupy distinct ranges and ecological niches (Theodoridis et al., 2013). The greatest similarity in distribution is between *P. farinosa* and the autotetraploid, *P. halleri*, with disjunct distributions for the hexaploid (*P. scotica* [= *P. farinosa* × *P. halleri*], northern Scotland) and octoploid (*P. scandinavica* [= *P. farinosa* × *P. scotica*], mostly Norway). Although *P. scotica* and *P. scandinavica* are considered allopolyploids, they are ultimately derived from only *P. farinosa*, suggesting they may actually be complex autopolyploids. In this complex, niche breadth has decreased with each round of polyploidization. Together, these studies suggest that in some cases, autopolyploid formation is associated with a shift in habitat requirements, but other times, no such shift has occurred.

Ecology—Stebbins (1950) considered that successful establishment of a polyploid required ecological divergence from its parents. Studies to date on allopolyploids provide mixed results (niche differentiation in autopolyploids was discussed above). Some allopolyploids occupy a niche intermediate to their parents, others inhabit areas similar to one parent, and some occupy a unique niche relative to the parents (e.g., Martin and Husband, 2009; Theodoridis et al., 2013; Glennon et al., 2014; Harbert et al., 2014; B. Marchant et al., University of Florida, unpublished data; see Soltis et al., 2014). However, unlike Ramsey's (2011) results for autopolyploid *Achillea*, there is currently no equivalent published

evidence of a newly formed allopolyploid species being ecologically divergent from its parents (see Abbott et al., 2013).

Genome duplication has shaped not only speciation, but also the phenotypic and ecological diversity of plants, altering habitat use, life histories, competitive abilities, interactions with herbivores and pathogens, and pollinator-mediated reproduction (Thompson et al., 2004; Oswald and Nuismer, 2007; Thompson and Merg, 2008; Arvanitis et al., 2010; Boalt et al., 2010; Ramsey, 2011; Martin and Husband, 2013; Strong and Ayres, 2013; Ramsey and Ramsey, 2014). Segraves and Thompson (1999) found that natural autopolyploid populations of *Heuchera grossulariifolia* (Saxifragaceae) differ in floral features and flowering time from diploid populations and that these differences are associated with different suites of pollinators (relevant to isolating mechanisms, below). Similarly, Boalt et al. (2010) found an association between ploidy and herbivory tolerance in *Cardamine*.

Physiology—Stebbins (1971) proposed that physiological changes associated with polyploidy may be key to the success of these plants and occupation of new habitats, and Levin (1983) eloquently elaborated on this suggestion. As first proposed in several now-classic papers, many physiological and developmental processes are affected by increases in ploidy, including gas exchange rates, gene activity, hormone levels, photosynthetic rates, and water balance (Levin, 1983, 2002; Warner and Edwards, 1993). Although more physiological analyses are needed, recent physiological data clearly indicate that diverse changes accompany genome doubling, and these could be beneficial to the new polyploid species (e.g., Coate et al., 2012, 2013; Wang et al., 2013). For example, polyploidy has affected the response to salt stress in polyploid *Robinia* (Wang et al., 2013) and photosynthetic response in polyploid *Glycine* (Coate et al., 2012).

Reproduction and isolating mechanisms—The establishment and persistence of a newly formed polyploid are clearly crucial for the success or failure of a polyploid species, and Stebbins (1950) addressed these processes, particularly in light of isolating mechanisms between diploids and polyploids. It is now clear that a number of features may contribute to the reproductive success of a neopolyploid and therefore its establishment and persistence. These include perenniality or a propensity toward apomixis or self-compatibility. Additionally, changes in morphological features (namely in floral characteristics) following polyploidization may reinforce the postzygotic reproductive barriers that prevent mating between cytotypes (e.g., Tate et al., 2005).

A new polyploid may be reproductively isolated from its diploid progenitors, not only as a result of its multiplied chromosome number, but also because the physiological and morphological changes that follow or accompany polyploidization may alter its reproductive biology. Reproductive barriers may be prezygotic (e.g., geographic isolation, flowering phenology differences, pollinator consistency) or postzygotic (e.g., triploid hybrid inviability, inbreeding depression). A breakdown of genetic incompatibility systems often accompanies polyploid formation (Richards, 1997) and leads to self-fertilization, which can isolate a new polyploid from its diploid parent(s) and promote establishment of the new polyploid. This change occurs in species with a single-locus gametophytic self-incompatibility (GSI) system, but is not known to occur in species with multigenic GSI or sporophytic self-incompatibility (SSI) systems (de Nettancourt, 2001; Ramsey and Schemske, 2002).

Husband and Sabara (2003) showed that autotetraploid individuals of *Chamerion angustifolium* (Onagraceae) were reproductively isolated from the diploids by geographic distance, flowering asynchrony, pollinator fidelity, self pollination, and gametic selection, with geographic isolation (41%) and pollinator fidelity (44%) representing the greatest proportions of these mechanisms. They also proposed that the emphasis previously placed on postzygotic factors, such as triploid sterility/inviability, may actually be secondary to prezygotic isolating mechanisms, but this assumes sufficient time for prezygotic barriers to evolve.

Morphological changes resulting from polyploidization can also have an effect on the reproductive biology of a neopolyploid species. Segraves and Thompson (1999) found that natural autopolyploid populations of *Heuchera grossulariifolia* (Saxifragaceae) not only have larger flowers than the diploid populations, but also different floral shapes and flowering times. The suites of pollinators visiting sympatric diploid and tetraploid plants differed proportionally when the flowering time of the two cytotypes was synchronous. Moreover, the independently generated autotetraploid populations differed in a number of floral characters (Segraves and Thompson, 1999).

NEW DIRECTIONS

Plant biologists and plant geneticists have now taken polyploid research into new directions that could not have been anticipated even 20 yr ago, let alone during the time of Stebbins. Modern research into the consequences of polyploidy now includes studies of the proteome, microRNAs, and the impact of alternative splicing (AS). We cover several of these topics below and point readers to relevant reviews. Following the report of Levin (1983) and others, perhaps the most important conclusion from such ongoing studies is that polyploidy could propel a population into a new adaptive sphere, given the myriad changes that accompany genome doubling and lead to novelty (e.g., Soltis et al., 2014).

Despite great progress in documenting the genomic and transcriptomic changes in polyploids relative to their diploid parents, we know little about the impact of WGD on the proteome (e.g., Albertin et al., 2006, 2007; Gancel et al., 2006; Carpentier et al., 2011; Hu et al., 2011, 2013; Kong et al., 2011; Koh et al., 2012; Ng et al., 2012). Given that the functional states of proteins in a proteome directly affect molecular and biochemical events in cells that determine phenotype, investigating how changes in gene expression profiles and AS events relate to protein-level changes is essential for understanding the molecular and evolutionary consequences of polyploidy, including molecular, biochemical, and physiological mechanisms that ultimately result in evolutionary change. Despite only a handful of proteomic studies of polyploids and their parents, some have revealed that the proteome of the polyploid does not always match the results predicted from the transcriptome alone; furthermore, novel proteins not found in either parent may be produced. These data point to the complexity of cellular-level plant processes, as well as the need for additional comparative analyses of the proteomes of polyploids and their diploid progenitor(s) (e.g., Gancel et al., 2006; Hu et al., 2011, 2013; Kong et al., 2011; Koh et al., 2012; Ng et al., 2012).

Although the important role of AS is now appreciated in eukaryotes, including plants (Reddy et al., 2012, 2013; Syed et al., 2012), few studies have analyzed the impact of polyploidy on AS (M. J. Yoo et al., Florida Museum of Natural History, unpublished manuscript). Fractionation, neofunctionalization (Ohno, 1970), and subfunctionalization (Hughes, 1994; Force et al., 1999) are all important processes that occur

following polyploidy, but the combined impact of these processes coupled with AS following WGD is unknown. Of the few studies conducted on this topic, some suggest that there is little or no correlation between AS and gene and genome duplication (Talavera et al., 2007; Roux and Robinson-Rechavi, 2011). Others, however, suggested a negative correlation between AS and duplication, and that alternatively spliced isoforms between duplicates may differ dramatically (Su et al., 2006; Chen et al., 2011). Zhang et al. (2009) found that exonic splicing enhancers and exonic splicing silencers rapidly diverge after gene duplication, while Santos et al. (2011) presented evidence of isoform loss and neofunctionalization after duplication. These findings agree with the hypothesis that gene duplication at least may impact AS. But less is known about genome-wide duplication and AS. Zhang et al. (2010) provided evidence of divergence of AS patterns following gene and genome duplication in *Arabidopsis*; interestingly, some of the differences reported occur in an organ- or stress-specific manner. Hence, an important new set of questions arises: Given that AS increases proteomic flexibility, are both parental AS profiles maintained in an allopolyploid? Does one parental AS pattern dominate? How much novel AS occurs following genome doubling?

Still another important new area of research involves the interplay of many of the genomic phenomena discussed above. As recently reviewed, an important requirement of polyploids is the need to retain dosage balance following gene duplication (Conant et al., 2014). These authors argue that elucidating these dosage effects represents "one aspect of an emerging pluralistic framework" in the study of polyploid evolution.

CONCLUSIONS

The first half of the 20th century witnessed tremendous advances in the collective understanding of plant genetics and of the role of genetics in evolution. Within a few short decades, the discovery of chromosomes, the "rediscovery" of Mendel's work, and the integration of genetics, systematics, and population biology of plants revolutionized perspectives on plant evolution. Despite outstanding, vital contributions by a host of excellent plant biologists, the Modern Synthesis as applied to plants was both largely developed and championed by Ledyard Stebbins (Smocovitis, 1997, 2001), and in no specific area was his influence greater than in the study of polyploidy. As should be clear from this review, Stebbins (1950) shaped the community's thinking on polyploidy (and many other topics) for nearly half a century, and in many aspects, still has valuable gems to impart. Stebbins himself was revolutionary, pulling together disparate fields to provide a cohesive view of polyploid evolution. Stebbinsian legend has it that he specifically tackled the polyploidy question in the 1920s because it was a nearly empty niche and he thought he could make a name for himself!

Just as plants undergo cycles of polyploidization and diploidization (e.g., Haufler, 1987, 2002), scientific topics move in and out of popularity, and so it has been with polyploidy. Despite tremendous research activity for several decades, interest in polyploidy, at least in the United States, waned during the last 20 yr of the 1900s. Perhaps ironically, approximately 100 yr after the discovery of chromosomes, genomic tools began to reveal the complex, duplicated nature of plant genomes—even small, apparently simple genomes like that of *Arabidopsis thaliana* (Vision et al., 2000; Bowers et al., 2003). The sudden ability to gather genomic and transcriptomic data has revolutionized the study of polyploidy once again—this time through a technical revolution rather than through the lens of a visionary—but the result is the same, with polyploidy once again a lively topic of research and discussion, with facets ranging from the subgenomic to ecosystem levels. Indeed, given recent and current research avenues, it appears that Stebbins's contributions to concepts such as ancient polyploidy and ecological niches are as relevant today as they were over 60 yr ago.

Ancient WGD is no longer a startling outcome of genome sequencing and assembly, but the number of inferred WGDs may be. Fortunately, as the number of sequenced plant genomes continues to increase, inferences of genome duplication, synteny, and fractionation become increasingly feasible. For example, comparison of the genome of *Amborella trichopoda* (the sister to all other extant angiosperms) with a set of eudicots demonstrated syntenic relationships maintained over vast phylogenetic distances and provided further evidence for two WGDs early in eudicot evolution (*Amborella* Genome Project, 2013). Ancient polyploidy—and its role in both genome evolution and organismal diversification—will continue to be an important topic for many years to come (Jiao and Paterson, 2014).

As Stebbins noted repeatedly (including Stebbins, 1985; Bayer et al., 1991), polyploids are most successful when they originate from genetically different (and therefore typically geographically separated) parents. Despite scores of studies debating whether polyploids have broader ecological amplitudes than their parental species, and the role of polyploidy in postglacial recolonization, relatively few studies are actually based on data. The application of ecological niche modeling, as described above for autopolyploids and their diploid progenitors as well as for allopolyploids and the origin of ecological novelty (Soltis et al., 2014), provides new landscape perspectives on an old problem, using locality data that, in some cases, have been under our noses for centuries. Digitization of herbarium records and their deposition in GBIF, iDigBio, or BISON are providing immense new sources of data for exploring the distributions of polyploids and for formulating ecological hypotheses.

As we celebrate a century of the *American Journal of Botany*, we also celebrate the unparalleled contributions, many of which appeared in *AJB*, of Ledyard Stebbins to our understanding of polyploidy and plant evolution. We hope that this review will stimulate new research on unanswered questions raised by Stebbins, his predecessors and contemporaries, and those who have come since, and on new topics unimaginable even a decade ago.

LITERATURE CITED

Abbott, R., D. Albach, S. Ansell, J. W. Arntzen, S. J. E. Baird, N. Bierne, J. Boughman, et al. 2013. Hybridization and speciation. *Journal of Evolutionary Biology* 26: 229–246.

Adams, K. L., R. Cronn, R. Percifield, and J. F. Wendel. 2003. Genes duplicated by polyploidy show unequal contributions to the transcriptome and organ-specific reciprocal silencing. *Proceedings of the National Academy of Sciences, USA* 100: 4649–4654.

Adams, K. L., R. Percifield, and J. F. Wendel. 2004. Organ-specific silencing of duplicated genes in a newly synthesized cotton allotetraploid. *Genetics* 168: 2217–2226.

Adams, K. L., and J. F. Wendel. 2004. Exploring the genomic mysteries of polyploidy in cotton. *Biological Journal of the Linnean Society* 82: 573–581.

Adams, K. L., and J. F. Wendel. 2005. Novel patterns of gene expression in polyploid plants. *Trends in Genetics* 21: 539–543.

Ainouche, M. L., A. Baumel, and A. Salmon. 2004. *Spartina anglica* C. E. Hubbard: A natural model system for analysing early evolutionary changes that affect allopolyploid genomes. *Biological Journal of the Linnean Society* 82: 475–484.

AINOUCHE, M. L., H. CHELAIFA, J. FERREIRA, S. BELLOT, A. AINOUCHE, AND A. SALMON. 2012. Polyploid evolution in *Spartina*: Dealing with highly redundant hybrid genomes. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 225–243. Springer, New York, New York, USA.

ALBERTIN, W., K. ALIX, T. BALLIAU, P. BRABANT, M. DAVANTURE, C. MALOSSE, B. VALOT, AND H. THIELLEMENT. 2006. Numerous and rapid nonstochastic modifications of gene products in newly synthesized *Brassica napus* allotetraploids. *Genetics* 173: 1101–1113.

ALBERTIN, W., K. ALIX, T. BALLIAU, P. BRABANT, M. DAVANTURE, C. MALOSSE, B. VALOT, AND H. THIELLEMENT. 2007. Differential regulation of gene products in newly synthesized *Brassica napus* allotetraploids is not related to protein function nor subcellular localization. *BMC Genomics* 8: 56.

AMBORELLA GENOME PROJECT. 2013. The *Amborella* genome and the evolution of flowering plants. *Science* 342: 1241089.

ANSSOUR, S., T. KRÜGEL, T. F. SHARBEL, H. P. SALUZ, G. BONAVENTURE, AND I. T. BALDWIN. 2009. Phenotypic, genetic and genomic consequences of natural and synthetic polyploidization of *Nicotiana attenuata* and *Nicotiana obtusifolia*. *Annals of Botany* 103: 1207–1217.

ARAKAKI, M., D. E. SOLTIS, AND P. SPERANZA. 2007. New chromosome counts and evidence of polyploidy in *Haageocereus* and related genera in tribe Trichocereeae and other tribes of Cactaceae. *Brittonia* 59: 290–297.

ARNOLD, B., K. BOMBLIES, AND J. WAKELEY. 2012. Extending coalescent theory to autotetraploids. *Genetics* 192: 195–204.

ARRIGO, N., AND M. S. BARKER. 2012. Rarely successful polyploids and their legacy in plant genomes. *Current Opinion in Plant Biology* 15: 140–146.

ARVANITIS, L., C. WIKLUND, Z. MÜNZBERGOVA, J. P. DAHLGREN, AND J. EHRLÉN. 2010. Novel antagonistic interactions associated with plant polyploidization influence trait selection and habitat preference. *Ecology Letters* 13: 330–337.

AURY, J. M., O. JAILLON, L. DURET, B. NOEL, C. JUBIN, B. M. PORCEL, B. SÉGURENS, ET AL. 2006. Global trends of whole-genome duplications revealed by the ciliate *Paramecium tetraurelia*. *Nature* 444: 171–178.

BARKER, M. S., G. J. BAUTE, AND S. L. LIU. 2012. Duplications and turnover in plant genomes. *In* J. F. Wendel, J. Greilhuber, J. Dolezel, and I. J. Leitch [eds.], Plant genome diversity, vol. 1, 155–169. Springer, Vienna, Austria.

BARKER, M. S., N. C. KANE, M. MATVIENKO, A. KOZIK, R. W. MICHELMORE, S. J. KNAPP, AND L. H. RIESEBERG. 2008. Multiple paleopolyploidizations during the evolution of the Compositae reveal parallel patterns of duplicate gene retention after millions of years. *Molecular Biology and Evolution* 25: 2445–2455.

BARKER, M. S., AND P. G. WOLF. 2010. Unfurling fern biology in the genomics age. *BioScience* 60: 177–185.

BAYER, R. J., B. G. PURDY, AND D. G. LEBEDYK. 1991. Niche differentiation among eight sexual species of *Antennaria gaertner* (Asteraceae: Inuleae) and *A. rosea*, their allopolyploid derivative. *Evolutionary Trends in Plants* 5: 109–123.

BAYER, R. J., AND G. L. STEBBINS JR. 1981. Chromosome numbers of North American species of *Antennaria gaertner* (Asteraceae: Inuleae). *American Journal of Botany* 68: 1342.

BEASLEY, J. O. 1940. The origin of American tetraploid *Gossypium* species. *American Naturalist* 74: 285.

BENNETT, M. D., I. J. LEITCH, H. J. PRICE, AND J. S. JOHNSTON. 2003. Comparisons with *Caenorhabditis* (~100 Mb) and Drosophila (~175 Mb) using flow cytometry show genome size in Arabidopsis to be ~157 Mb and thus ~25% larger than the Arabidopsis Genome Initiative estimate. *Annals of Botany* 91: 547–557.

BOALT, E., L. ARVANITIS, K. LEHTILÄ, AND J. EHRLÉN. 2010. The association among herbivory tolerance, ploidy level, and herbivory pressure in *Cardamine pratensis*. *Evolutionary Ecology* 24: 1101–1113.

BOUSALEM, M., G. ARNAU, I. HOCHU, R. ARNOLIN, V. VIADER, S. SANTONI, AND J. DAVID. 2006. Microsatellite segregation analysis and cytogenetic evidence for tetrasomic inheritance in the American yam *Dioscorea trifida* and a new basic chromosome number in the Dioscoreae. *Theoretical and Applied Genetics* 113: 439–451.

BOWERS, J. E., B. A. CHAPMAN, J. RONG, AND A. H. PATERSON. 2003. Unravelling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. *Nature* 422: 433–438.

BRAASCH, I., AND J. H. POSTLETHWAIT. 2012. Polyploidy in fish and the teleost genome duplication. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 341–383. Springer, New York, New York, USA.

BROCHMANN, C., P. S. SOLTIS, AND D. E. SOLTIS. 1992. Recurrent formation and polyphyly of nordic polyploids in *Draba* (Brassicaceae). *American Journal of Botany* 79: 673–688.

BROWN, A. H., AND A. G. YOUNG. 2000. Genetic diversity in tetraploid populations of the endangered daisy *Rutidosis leptorrhynchoides* and implications for its conservation. *Heredity* 85: 122–129.

BUGGS, R. J. A., S. CHAMALA, W. WU, L. GAO, G. D. MAY, P. S. SCHNABLE, D. E. SOLTIS, ET AL. 2010. Characterization of duplicate gene evolution in the recent natural allopolyploid *Tragopogon miscellus* by next-generation sequencing and Sequenom iPLEX MassARRAY genotyping. *Molecular Ecology* 19: 132–146.

BUGGS, R. J., S. CHAMALA, W. WU, J. A. TATE, P. S. SCHNABLE, D. E. SOLTIS, P. S. SOLTIS, AND W. B. BARBAZUK. 2012. Rapid, repeated, and clustered loss of duplicate genes in allopolyploid plant populations of independent origin. *Current Biology* 22: 248–252.

BUGGS, R. J., N. DOUST, J. TATE, J. KOH, K. SOLTIS, F. FELTUS, H. PATERSON, ET AL. 2009. Gene loss and silencing in *Tragopogon miscellus* (Asteraceae): Comparison of natural and synthetic allotetraploids. *Heredity* 103: 73–81.

BUGGS, R. J., L. ZHANG, N. MILES, J. TATE, L. GAO, W. WEI, P. S. SCHNABLE, ET AL. 2011. Transcriptomic shock generates evolutionary novelty in a newly formed, natural allopolyploid plant. *Current Biology : CB* 21: 551–556.

BUGGS, R. J .A., J. F. WENDEL, J. J. DOYLE, D. E. SOLTIS, P. S. SOLTIS, AND J. E. COATE. 2014. The legacy of diploid progenitors in allopolyploid gene expression patterns. *Philosophical Transactions of the Royal Society of London. Series B* 369: 20130354.

CAÑESTRO, C. 2012. Two rounds of whole genome duplication: Evidence and impact on the evolution of vertebrate innovations. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 309–340. Springer, New York, New York, USA.

CARPENTIER, S. C., B. PANIS, J. RENAUT, B. SAMYN, A. VERTOMMEN, A. C. VANHOVE, R. SWENNEN, AND K. SERGEANT. 2011. The use of 2D-electrophoresis and de novo sequencing to characterize inter- and intra-cultivar protein polymorphisms in an allopolyploid crop. *Phytochemistry* 72: 1243–1250.

CHANG, P. L., B. P. DILKES, M. MCMAHON, L. COMAI, AND S. V. NUZHDIN. 2010. Homoeolog-specific retention and use in allotetraploid *Arabidopsis suecica* depends on parent of origin and network partners. *Genome Biology* 11: R125.

CHELAIFA, H., A. MONNIER, AND M. AINOUCHE. 2010. Transcriptomic changes following recent natural hybridization and allopolyploidy in the salt marsh species *Spartina* × *townsendii* and *Spartina anglica* (Poaceae). *New Phytologist* 186: 161–174.

CHEN, T. W., T. H. WU, W. V. NG, AND W.-C. LIN. 2011. Interrogation of alternative splicing events in duplicated genes during evolution. *BMC Genomics* 12 (supplement 3): S16.

CHESTER, M., J. P. GALLAGHER, V. V. SYMONDS, A. V. CRUZ DA SILVA, E. V. MAVRODIEV, A. R. LEITCH, P. S. SOLTIS, AND D. E. SOLTIS. 2012. Extensive chromosomal variation in a recently formed natural allopolyploid species, *Tragopogon miscellus* (Asteraceae). *Proceedings of the National Academy of Sciences, USA* 109: 1176–1181.

CHESTER, M., R. K. RILEY, P. S. SOLTIS, AND D. E. SOLTIS. In press. Patterns of chromosomal variation in natural populations of the neoallotetraploid *Tragopogon mirus* (Asteraceae). *Heredity*.

CLAUSEN, J., D. D. KECK, AND W. M. HIESEY. 1945. Experimental studies on the nature of species II. Plant evolution through amphiploidy and autopolyploidy, with examples from the Madiinae. Carnegie Institute of Washington, Washington, D.C., USA.

CLAUSEN, R. E., AND T. H. GOODSPEED. 1925. Interspecific hybridization in *Nicotiana*. II. A tetraploid *glutinosa-tabacum* hybrid, an experimental verification of Winge's hypothesis. *Genetics* 10: 278–284.

COATE, J. E., A. K. LUCIANO, V. SERALATHAN, K. J. MINCHEW, T. G. OWENS, AND J. J. DOYLE. 2012. Anatomical, biochemical, and photosynthetic responses to recent allopolyploidy in *Glycine dolichocarpa* (Fabaceae). *American Journal of Botany* 99: 55–67.

COATE, J. E., A. F. POWELL, T. G. OWENS, AND J. J. DOYLE. 2013. Transgressive physiological and transcriptomic responses to light stress in allopolyploid *Glycine dolichocarpa* (Leguminosae). *Heredity* 110: 160–170.

CONANT, G. C., J. A. BIRCHLER, AND J. C. PIRES. 2014. Dosage, duplication, and diploidization: clarifying the interplay of multiple models for duplicate gene evolution over time. *Current Opinion in Plant Biology* 19:91–98.

CUI, L., P. K. WALL, J. H. LEEBENS-MACK, B. G. LINDSAY, D. E. SOLTIS, J. J. DOYLE, P. S. SOLTIS, ET AL. 2006. Widespread genome duplications throughout the history of flowering plants. *Genome Research* 16: 738–749.

DARLINGTON, C. D. 1937. Recent advances in cytology. J. & A. Churchill, London, UK.

DE NETTANCOURT, D. 2001. Incompatibility and incongruity in wild and cultivated plants, 2nd ed. Springer Verlag, Berlin, Germany.

DE SMET, R., K. L. ADAMS, K. VANDEPOELE, M. C. E. VAN MONTAGU, S. MAERE, AND Y. VAN DE PEER. 2013. Convergent gene loss following gene and genome duplications creates single-copy families in flowering plants. *Proceedings of the National Academy of Sciences, USA* 110: 2898–2903.

DE SMET, R., AND Y. VAN DE PEER. 2012. Redundancy and rewiring of genetic networks following genome-wide duplication events. *Current Opinion in Plant Biology* 15: 168–176.

DIGBY, L. 1912. The cytology of *Primula kewensis* and of other related *Primula* hybrids. *Annals of Botany* 26: 357–388.

DOYLE, J. J. 2012. Polyploidy in Legumes. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 147–180. Springer, New York, New York, USA.

DOYLE, J. J., J. L. DOYLE, J. T. RAUSCHER, AND A. H. D. BROWN. 2003. Diploid and polyploid reticulate evolution throughout the history of the perennial soybeans (*Glycine* subgenus *Glycine*). *New Phytologist* 161: 121–132.

EHRENDORFER, F. 1965. Dispersal mechanisms, genetic systems, and colonizing abilities in some flowering plant families. *In* H. G. Baker and G. L. Stebbins Jr. [eds.], The genetics of colonizing species, 331–352. Academic Press, New York, New York, USA.

EPES, D. A., AND D. E. SOLTIS. 1984. An electrophoretic investigation of Galax urceolata (Diapensiaceae). Abstract. *American Journal of Botany* 71: 165.

FAWCETT, J. A., S. MAERE, AND Y. VAN DE PEER. 2009. Plants with double genomes might have had a better chance to survive the Cretaceous-Tertiary extinction event. *Proceedings of the National Academy of Sciences, USA* 106: 5737–5742.

FISHER, R. A. 1943. Allowance for double reduction in the calculation of genotype frequencies with polysomic inheritance. *Annals of Eugenics* 12: 169–171.

FISHER, R. A. 1949. The linkage problem in a tetrasomic wild plant, *Lythrum salicaria. Hereditas* 35: 225–233.

FJELLSTROM, R. G., P. R. BEUSELINCK, AND J. J. STEINER. 2001. RFLP marker analysis supports tetrasomic inheritance in *Lotus corniculatus* L. *Theoretical and Applied Genetics* 102: 718–725.

FLAGEL, L. E., AND J. F. WENDEL. 2010. Evolutionary rate variation, genomic dominance and duplicate gene expression evolution during allotetraploid cotton speciation. *New Phytologist* 186: 184–193.

FORCE, A., M. LYNCH, F. B. PICKETT, A. AMORES, Y. YAN, AND J. POSTLETHWAIT. 1999. Preservation of duplicate genes by complementary, degenerative mutations. *Genetics* 151: 1531–1545.

FUTUYMA, D. J. 1998. Evolutionary biology, 3rd ed. Sinauer, Sunderland, Massachusetts, USA.

GAETA, R. T., AND J. C. PIRES. 2010. Homoeologous recombination in allopolyploids: The polyploid ratchet. *New Phytologist* 186: 18–28.

GAETA, R. T., J. C. PIRES, F. INIGUEZ-LUY, E. LEON, AND T. C. OSBORN. 2007. Genomic changes in resynthesized *Brassica napus* and their effect on gene expression and phenotype. *Plant Cell* 19: 3403–3417.

GANCEL, A.-L., J. GRIMPLET, F.-X. SAUVAGE, P. OLLITRAULT, AND J.-M. BRILLOUET. 2006. Predominant expression of diploid mandarin leaf proteome in two citrus mandarin-derived somatic allotetraploid hybrids. *Journal of Agricultural and Food Chemistry* 54: 6212–6218.

GATES, R. R. 1909. The stature and chromosomes of *Oenothera gigas* De Vries. *Zeitschrift fur Induktive Abstammungs- und Vererbungslehre* 3: 525–552.

GLENNON, K. L., L. J. RISSLER, AND S. A. CHURCH. 2012. Ecogeographic isolation: A reproductive barrier between species and between cytotypes in *Houstonia* (Rubiaceae). *Evolutionary Ecology* 26: 909–926.

GLENNON, K. L., M. E. RITCHIE, AND K. A. SEGRAVES. 2014. Evidence for shared broad-scale climatic niches of diploid and polyploid plants. *Ecology Letters* 17: 574–582.

GODSOE, W., M. A. LARSON, K. L. GLENNON, AND K. A. SEGRAVES. 2013. Polyploidization in *Heuchera cylindrica* (Saxifragaceae) did not result in a shift in climatic requirements. *American Journal of Botany* 100: 496–508.

GOLDBLATT, P. 1980. Polyploidy in angiosperms: Monocotyledons. *In* W. H. Lewis [ed.], Polyploidy: Biological relevance, 219–239. Plenum Press, New York, New York, USA.

GOODSPEED, T. H., AND R. E. CLAUSEN. 1928. Interspecific hybridization in *Nicotiana*. VIII. The *sylvestris-tomentose-tabacum* hybrid triangle and its bearing on the origin of *tabacum. University of California Publications in Botany* 2: 245–256.

GRANT, V. 1971. Plant speciation. Columbia University Press, New York, New York, USA.

GRANT, V. 1981. Plant speciation, 2nd ed. Columbia University Press, New York, New York, USA.

GRANT, V. 2002. Frequency of spontaneous amphiploids in *Gilia* (Polemoniaceae) hybrids. *American Journal of Botany* 89: 1197–1202.

GREGORY, R. T., AND B. K. MABLE. 2005. Polyploidy in animals. *In* T. R. Gregory [ed.], The evolution of the genome, 427–517. Elsevier, San Diego, California, USA.

GRIFFITHS, S., R. SHARP, T. N. FOOTE, I. BERTIN, M. WANOUS, S. READER, I. COLAS, AND G. MOORE. 2006. Molecular characterization of *Ph1* as a major chromosome pairing locus in polyploid wheat. *Nature* 439: 749–752.

HALDANE, J. B. S. 1930. Theoretical genetics of autopolyploids. *Journal of Genetics* 22: 359–372.

HAMRICK, J. L., J. D. NASON, T. H. FLEMING, AND J. M. NASSAR. 2002. Genetic diversity in columnar cacti. *In* T. H. Fleming and A. Valiente-Banet [eds.], Columnar cacti and their mutualists: Evolution, ecology, and conservation, 122–133. University of Arizona Press, Tuscon, Arizona, USA.

HARBERT, R. S., A. H. D. BROWN, AND J. J. DOYLE. 2014. Climate niche modeling in the perennial *Glycine* (Leguminosae) allopolyploid complex. *American Journal of Botany* 101: 710–721.

HARDY, O. J., M. DE LOOSE, X. VEKEMANS, AND P. MEERTS. 2001. Allozyme segregation and inter-cytotype reproductive barriers in the polyploid complex *Centaurea jacea*. *Heredity* 87: 136–145.

HAUBER, D. P. 1986. Autotetraploidy in *Haplopappus spinulosus* hybrids: Evidence from natural and synthetic tetraploids. *American Journal of Botany* 73: 1595–1606.

HAUFLER, C. H. 1987. Electrophoresis is modifying our concepts of evolution in homosporous pteridophytes. *American Journal of Botany* 74: 953–966.

HAUFLER, C. H. 2002. Homospory 2002: An odyssey of progress in pteridophyte genetics and evolutionary biology. *Bioscience* 52: 1081–1093.

HEGARTY, M. J., R. J. ABBOTT, AND S. J. HISCOCK. 2012. Allopolyploid speciation in action: The origins and evolution of *Senecio cambrensis. In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 245–270. Springer, New York, New York, USA.

HEGARTY, M. J., G. L. BARKER, I. D. WILSON, R. J. ABBOTT, K. J. EDWARDS, AND S. J. HISCOCK. 2006. Transcriptome shock after interspecific hybridization in *Senecio* is ameliorated by genome duplication. *Current Biology* 16: 1652–1659.

HEGARTY, M. J. M., J. M. J. JONES, I. I. D. WILSON, G. L. BARKER, J. A. COGHILL, P. SANCHEZ-BARACALDO, G. LIU, ET AL. 2005. Development of anonymous cDNA microarrays to study changes to the *Senecio* floral transcriptome during hybrid speciation. *Molecular Ecology* 14: 2493–2510.

HENDRIX, B., AND J. M. STEWART. 2005. Estimation of the nuclear DNA content of *Gossypium* species. *Annals of Botany* 95: 789–797.

HICKS, G. C., AND G. L. STEBBINS JR. 1934. Meiosis in some species and a hybrid of *Paeonia. American Journal of Botany* 21: 228.

HOWARD, H. M. 1970. Genetics of the potato *Solanum tuberosum*. Logos Press, London, UK.

HU, G., N. L. HOUSTON, D. PATHAK, L. SCHMIDT, J. J. THELEN, AND J. F. WENDEL. 2011. Genomically biased accumulation of seed storage proteins in allopolyploid cotton. *Genetics* 189: 1103–1115.

HU, G., J. KOH, M.-J. YOO, K. GRUPP, S. CHEN, AND J. F. WENDEL. 2013. Genomically biased accumulation of seed storage proteins in allopolyploid cotton. *New Phytologist* 200: 570–582.

HUANG, H., F. DANE, Z. WANG, Z. JIANG, R. HUANG, AND S. WANG. 1997. Isozyme inheritance and variation in *Actindia. Heredity* 78: 328–336.

HUDSON, C. M., AND G. C. CONANT. 2012. Yeast as a window into changes in genome complexity due to polyploidization. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 293–308, Springer, New York, New York, USA.

HUGHES, A. L. 1994. The evolution of functionally novel proteins after gene duplication. *Proceedings of the Royal Society, B, Biological Sciences* 256: 119–124.

HUSBAND, B. C., S. J. BALDWIN, AND J. SUDA. 2013. The incidence of polyploidy in natural plant populations: Major patterns and evolutionary processes. *In* J. Greilhuber, J. Dolezel, and J. F. Wendel [eds.], Plant genome diversity, 255–276. Springer Vienna, Austria.

HUSBAND, B. C., AND H. A. SABARA. 2003. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, *Chamerion angustifolium* (Onagraceae). *New Phytologist* 161: 703–713.

HUSBAND, B. C., AND D. W. SCHEMSKE. 1997. The effect of inbreeding in diploid and tetraploid populations of *Epilobium angustifolium* (Onagraceae): Implications for the genetic basis of inbreeding depression. *Evolution* 51: 737.

JI, L.-H., AND P. LANGRIDGE. 1990. The genetic control of chromosome pairing in wheat. *Australian Journal of Plant Physiology* 17: 239–251.

JIAO, Y., J. LEEBENS-MACK, S. AYYAMPALAYAM, J. E. BOWERS, M. R. MCKAIN, J. MCNEAL, M. ROLF, ET AL. 2012. A genome triplication associated with early diversification of the core eudicots. *Genome Biology* 13: R3.

JIAO, Y. AND A. H. PATERSON. 2014. Review article: Polyploidy-associated genome modifications during land plant evolution. *Philosophical Transactions of the Royal Society B* 369 20130355.

JIAO, Y., N. J. WICKETT, S. AYYAMPALAYAM, A. S. CHANDERBALI, L. LANDHERR, P. E. RALPH, L. P. TOMSHO, ET AL. 2011. Ancestral polyploidy in seed plants and angiosperms. *Nature* 473: 97–100.

KASHKUSH, K., M. FELDMAN AND A. A. LEVY. 2002. Gene loss, silencing and activation in a newly synthesized wheat allotetraploid. *Genetics* 160: 1651–1659.

KELLIS, M., B. W. BIRREN, AND E. S. LANDER. 2004. Proof and evolutionary analysis of ancient genome duplication in the yeast *Saccharomyces cerevisiae. Nature* 428: 617–624.

KIHARA, H., AND T. ONO. 1926. Chromosomenzahlen und systematische Gruppierun der Rumex-Arten. *Zeitschrift für Zellforschung und mikroskopiche Anatomie (Vienna, Austria)* 4: 474–481.

KOCHERT, G., H. T. STALKER, M. GIMENES, L. GALGARO, C. R. LOPES, AND K. MOORE. 1996. RFLP and cytogenetic evidence on the origin and evolution of allotetraploid domesticated peanut, *Arachis hypogaea* (Leguminosae). *American Journal of Botany* 83: 1282–1291.

KOH, J., S. CHEN, N. ZHU, F. YU, P. S. SOLTIS, AND D. E. SOLTIS. 2012. Comparative proteomics of the recently and recurrently formed natural allopolyploid *Tragopogon mirus* (Asteraceae) and its parents. *New Phytologist* 196: 292–305.

KOH, J., P. S. SOLTIS, AND D. E. SOLTIS. 2010. Homeolog loss and expression changes in natural populations of the recently and repeatedly formed allotetraploid *Tragopogon mirus* (Asteraceae). *BMC Genomics* 11: 97.

KONG, F., S. MAO, J. JIANG, J. WANG, X. FANG, AND Y. WANG. 2011. Proteomic changes in newly synthesized *Brassica napus* allotetraploids and their early generations. *Plant Molecular Biology Reporter* 29: 927–935.

KOVALSKY, I. E., AND V. G. SOLÍS NEFFA. 2012. Evidence of 2*n* microspore production in a natural diploid population of *Turnera sidoides* subsp. *carnea* and its relevance in the evolution of the *T. sidoides* (Turneraceae) autopolyploid complex. *Journal of Plant Research* 125: 725–734.

KRAITSHTEIN, Z., B. YAAKOV, V. KHASDAN, AND K. KASHKUSH. 2010. Genetic and epigenetic dynamics of a retrotransposon after allopolyploidization of wheat. *Genetics* 186: 801–812.

KREBS, S. L., AND J. F. HANCOCK. 1989. Tetrasomic inheritance of isoenzyme markers in the highbush blueberry, *Vaccinium corymbosum* L.1. *Heredity* 63: 11–18.

KUWADA, Y. 1911. Meiosis in the pollen mother cells of *Zea mays* L. *Botanical Magazine* 25: 163–181.

LANDERGOTT, U., Y. NACIRI, J. J. SCHNELLER, AND R. HOLDEREGGER. 2006. Allelic configuration and polysomic inheritance of highly variable microsatellites in tetraploid gynodioecious *Thymus praecox* agg. *Theoretical and Applied Genetics* 113: 453–465.

LANGTON, F. A. 1980. Chimerical structure and carotenoid inheritance in *Chrysanthemum morifolium* (Ramat.) [sic]. *Euphytica* 29: 807–812.

LARSEN, A. S., A. VAILLANT, D. VERHAEGEN, AND E. D. KJÆR. 2009. Eighteen SSR-primers for tetraploid *Adansonia digitata* and its relatives. *Conservation Genetics Resources* 1: 325–328.

LAUSHMAN, R. H., A. SCHNABLE, J. L. HAMRICK, AND H. LAUSHMAN. 1996. Electrophoretic evidence for tetrasomic inheritance in the dioecious tree *Maclura pomifera* (Raf.) Schneid. *Journal of Heredity* 87: 469–473.

LAVANIA, U. C., S. SRIVASTAVA, S. LAVANIA, S. BASU, N. K. MISRA, AND Y. MUKAI. 2012. Autopolyploidy differentially influences body size in plants, but facilitates enhanced accumulation of secondary metabolites, causing increased cytosine methylation. *Plant Journal* 71: 539–549.

LAWRENCE, W. J. C. 1931. The genetics and cytology of *Dahlia variabilis*. *Journal of Genetics* 24: 257–306.

LE COMBER, S. C., M. L. AINOUCHE, A. KOVARIK, AND A. R. LEITCH. 2010. Making a functional diploid: From polysomic to disomic inheritance. *New Phytologist* 186: 113–122.

LEINEMANN, L. 2000. Inheritance analysis of isozyme phenotypes in tetraploid species using single plant progenies. An example in black thorn (*Prunus spinosa* L.). *Forest Genetics* 7: 205–209.

LEVIN, D. 2011. Polyploidy and ecological transfiguration in *Achillea. Proceedings of the National Academy of Sciences, USA* 108: 6697–6698.

LEVIN, D. A. 1975. Minority cytotype exclusion in local plant populatons. *Taxon* 24: 35–43.

LEVIN, D. A. 1983. Polyploidy and novelty in flowering plants. *American Naturalist* 122: 1–25.

LEVIN, D. A. 2000. The origin, expansion, and demise of plant species. Oxford University Press, New York, New York, USA.

LEVIN, D. A. 2002. The role of chromosomal change in plant evolution. Oxford University Press, New York, New York, USA.

LEWIS, W. H. 1980. Polyploidy in angiosperms: Dicotyledons. *In* W. Lewis [ed.], Polyploidy, 241–268. Springer, New York, New York, USA.

LIM, K. Y., A. KOVARIK, R. MATYASEK, M. W. CHASE, J. J. CLARKSON, M. A. GRANDBASTIEN, AND A. R. LEITCH. 2007. Sequence of events leading to near-complete genome turnover in allopolyploid *Nicotiana* within five million years. *New Phytologist* 175: 756–763.

LIM, K. Y., D. E. SOLTIS, P. S. SOLTIS, J. TATE, R. MATYASEK, H. SRUBAROVA, A. KOVARIK, ET AL. 2008. Rapid chromosome evolution in recently formed polyploids in *Tragopogon* (Asteraceae). *PLoS ONE* 3: e3353.

LIU, B., C. L. BRUBAKER, G. MERGEAI, R. C. CRONN, AND J. F. WENDEL. 2001. Polyploid formation in cotton is not accompanied by rapid genomic changes. *Genome* 44: 321–330.

LÖVE, Á., AND D. LÖVE. 1949. The geobotanical significance of polyploidy: 1. Polyploidy and latitude. Instituto Botânica da Facultad de Ciências, Coimbra, Portugal.

LUMARET, R., J.-L. GUILLERM, J. DELAY, A. AIT LAJ LOUTFI, J. IZCO, AND M. JAY. 1987. Polyploidy and habitat differentiation in *Dactylis glomerata* L. from Galicia (Spain). *Oecologia* 73: 436–446.

LUTZ, A. M. 1907. A preliminary note on the chromosomes of *Œnothera lamarckiana* and one of its mutants, *O. gigas. Science* 26: 151–152.

LYNCH, M., AND J. S. CONERY. 2000. The evolutionary fate and consequences of duplicate genes. *Science* 290: 1151–1155.

LYNCH, M., AND A. FORCE. 2000. The probability of duplicate gene preservation by subfunctionalization. *Genetics* 154: 459–473.

MABLE, B. 2003. Breaking down taxonomic barriers in polyploidy research. *Trends in Plant Science* 8: 582–590.

MABLE, B. K., J. BELAND, AND C. DI BERARDO. 2004. Inheritance and dominance of self-incompatibility alleles in polyploid *Arabidopsis lyrata. Heredity* 93: 476–486.

MABLE, B. K., AND S. P. OTTO. 2001. Masking and purging mutations following EMS treatment in haploid, diploid and tetraploid yeast (*Saccharomyces cerevisiae*). *Genetical Research* 77: 9–26.

MAJURE, L. C., W. S. JUDD, P. S. SOLTIS, AND D. E. SOLTIS. 2012. Cytogeography of the *Humifusa* clade of *Opuntia* s.s. Mill. 1754 (Cactaceae, Opuntioideae, Opuntieae): Correlations with pleistocene refugia and morphological traits in a polyploid complex. *Comparative Cytogenetics* 6: 53–77.

MANDÁKOVÁ, T., K. MARHOLD, AND M. A. LYSAK. 2014. The widespread crucifer species *Cardamine flexuosa* is an allotetraploid with a conserved subgenomic structure. *New Phytologist* 201: 982–992.

MANDÁKOVÁ, T., AND Z. MÜNZBERGOVÁ. 2008. Morphometric and genetic differentiation of diploid and hexaploid populations of *Aster amellus* agg. in a contact zone. *Plant Systematics and Evolution* 274: 155–170.

MANDAL, A. K., R. A. ENNOS, AND C. W. FAGG. 1994. Mating system analysis in a natural population of *Acacia nilotica* subspecies *leiocarpa. Theoretical and Applied Genetics* 89: 931–935.

MARTIN, S. L., AND B. C. HUSBAND. 2009. Influence of phylogeny and ploidy on species ranges of North American angiosperms. *Journal of Ecology* 97: 913–922.

MARTIN, S. L., AND B. C. HUSBAND. 2013. Adaptation of diploid and tetraploid *Chamerion angustifolium* to elevation but not local environment. *Evolution* 67: 1780–1791.

MARTINEZ-ZAPATER, J. M., AND J. L. OLIVER. 1984. Genetic analysis of isozyme loci in tetraploid potatoes (*Solanum tuberosum* L.). *Genetics* 108: 669–679.

MASTERSON, J. 1994. Stomatal size in fossil plants: Evidence for polyploidy in majority of angiosperms. *Science* 264: 421–424.

MATSUSHITA, S. C., A. P. TYAGI, G. M. THORNTON, J. C. PIRES, AND A. MADLUNG. 2012. Allopolyploidization lays the foundation for evolution of distinct populations: Evidence from analysis of synthetic *Arabidopsis* allohexaploids. *Genetics* 191: 535–547.

MAVRODIEV, E. V., AND D. E. SOLTIS. 2001. Recurring polyploid formation: An early account from the Russian literature. *Taxon* 50: 469–474.

MAYROSE, I., S. H. ZHAN, C. J. ROTHFELS, K. MAGNUSON-FORD, M. S. BARKER, L. H. RIESEBERG, AND S. P. OTTO. 2011. Recently formed polyploid plants diversify at lower rates. *Science* 333: 1257.

MCCLINTOCK, B. 1984. The significance of responses of the genome to challenge. *Science* 226: 792–801.

MCFADDEN, E. S., AND E. R. SEARS. 1946. The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *Journal of Heredity* 37: 81–107.

MCINTYRE, P. J. 2012. Polyploidy associated with altered and broader ecological niches in the *Claytonia perfoliata* (Portulacaceae) species complex. *American Journal of Botany* 99: 655–662.

MERTTEN, D., G. K. TSANG, K. I. MANAKO, M. A. MCNEILAGE, AND P. M. DATSON. 2012. Meiotic chromosome pairing in *Actinidia chinensis* var. *deliciosa. Genetica* 140: 455–462.

MEYERS, L. A., AND D. A. LEVIN. 2006. On the abundance of polyploids in flowering plants. *Evolution* 60: 1198–1206.

MIA, M. M., B. B. MUKHERJEE, AND R. K. VICKERY. 1964. Chromosome counts in section *Simuolus* of the genus *Mimulus* (Scrophulariaceae). VI. New numbers in *M. guttatus*, *M. tigrinus*, and *M. glabratus*. *Madroño* 17: 156–160.

MOODY, M. E., L. D. MUELLER, AND D. E. SOLTIS. 1993. Genetic variation and random drift in autotetraploid populations. *Genetics* 154: 649–657.

MULLER, H. J. 1914. A new mode of segregation in Gregory's tetraploid primulas. *American Naturalist* 48: 508–512.

MÜNTZING, A. 1930. Übber Chromosomenvermehrung in Galeopsis-Kreuzungen und ihre phylogenetische bedeutung. *Hereditas* 14: 153–172.

MÜNTZING, A. 1936. The evolutionary significance of autopolyploidy. *Hereditas* 21: 363–378.

MURAWSKI, D. A., T. H. FLEMING, K. RITLAND, AND J. L. HAMRICK. 1994. Mating system of *Pachycereus pringlei*: An autotetraploid cactus. *Heredity* 72: 86–94.

NEMORIN, A., K. ABRAHAM, J. DAVID, AND G. ARNAU. 2012. Inheritance pattern of tetraploid *Dioscorea alata* and evidence of double reduction using microsatellite marker segregation analysis. *Molecular Breeding* 30: 1657–1667.

NG, D. W.-K., C. ZHANG, M. MILLER, Z. SHEN, S. P. BRIGGS, AND Z. J. CHEN. 2012. Proteomic divergence in *Arabidopsis* autopolyploids and allopolyploids and their progenitors. *Heredity* 108: 419–430.

NIE, L., Z. HAN, L. LU, Y. YAO, Q. SUN, AND Z. NI. 2008. Genomic and genic sequence variation in synthetic hexaploid wheat (AABBDD) as compared to their parental species. *Progress in Natural Science* 18: 533–538.

NORDENSKIOLD, H. 1953. A genetical study in the mode of segregation in hexaploid *Phleum pratense*. *Hereditas* 39: 469–488.

OHNO, S. 1970. Evolution by gene duplication. Springer-Verlag, New York, New York, USA.

OKADA, M., C. LANZATELLA, AND C. M. TOBIAS. 2011. Single-locus EST-SSR markers for characterization of population genetic diversity and structure across ploidy levels in switchgrass (*Panicum virgatum* L.). *Genetic Resources and Crop Evolution* 58: 919–931.

OSBORN, T. C., J. C. PIRES, J. A. BIRCHLER, D. L. AUGER, J. Z. CHEN, H. LEE, L. COMAI, ET AL. 2003. Understanding mechanisms of novel gene expression in polyploids. *Trends in Genetics* 19: 141–147.

OSWALD, B. P., AND S. L. NUISMER. 2007. Neopolyploidy and pathogen resistance. *Proceedings of the Royal Society, B, Biological Sciences* 274: 2393–2397.

OWNBEY, M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon. American Journal of Botany* 37: 487–499.

OWNBEY, M., AND G. D. MCCOLLUM. 1953. Cytoplasmic inheritance and reciprocal amphiploidy in *Tragopogon. American Journal of Botany* 40: 788–796.

PARISOD, C., R. HOLDEREGGER, AND C. BROCHMANN. 2010. Evolutionary consequences of autopolyploidy. *New Phytologist* 186: 5–17.

PARISOD, C., A. SALMON, T. ZERJAL, M. TENAILLON, M. A. GRANDBASTIEN, AND M. AINOUCHE. 2009. Rapid structural and epigenetic reorganization near transposable elements in hybrid and allopolyploid genomes in *Spartina. New Phytologist* 184: 1003–1015.

PATERSON, A. H., B. A. CHAPMAN, J. C. KISSINGER, J. E. BOWERS, F. A. FELTUS, AND J. C. ESTILL. 2006. Many gene and domain families have convergent fates following independent whole-genome duplication events in *Arabidopsis*, *Oryza*, *Saccharomyces* and *Tetraodon. Trends in Genetics* 22: 597–602.

PONTES, O., N. NEVES, M. SILVA, M. S. LEWIS, A. MADLUNG, L. COMAI, W. VIEGAS, AND C. S. PIKAARD. 2004. Chromosomal locus rearrangements are a rapid response to formation of the allotetraploid *Arabidopsis suecica* genome. *Proceedings of the National Academy of Sciences, USA* 101: 18240–18245.

PRINCE, V. E., AND F. B. PICKETT. 2002. Splitting pairs: The diverging fates of duplicated genes. *Nature Reviews Genetics* 3: 827–837.

PUPILLI, F., M. E. CACERES, S. ARCIONI, AND C. L. QUARIN. 1997. Segregation analysis of RFLP markers reveals a tetrasomic inheritance in apomictic *Paspalum* simplex. *Genome* 40: 822–828.

QUIROS, C. F. 1982. Tetrasomic segregation for multiple alleles in alfalfa. *Genetics* 101: 117–127.

QUIROS, C. F., AND N. MCHALE. 1985. Genetic analysis of isozyme variants in diploid and tetraploid potatoes. *Genetics* 111: 131–145.

RAMSEY, J. 2011. Polyploidy and ecological adaptation in wild yarrow. *Proceedings of the National Academy of Sciences, USA* 108: 7096–7101.

RAMSEY, J., AND D. W. SCHEMSKE. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29: 467–501.

RAMSEY, J., AND D. W. SCHEMSKE. 2002. Neopolyploidy in flowering plants. *Annual Review of Ecology and Systematics* 33: 589–639.

RAMSEY, J., AND T. S. RAMSEY. 2014. Review article: Ecological studies of polyploidy in the 100 years following its discovery. *Philosophical Transactions of the Royal Society B* 369 20130352.

RAVEN, P. H. 2000. G. Ledyard Stebbins (1906–2000): An appreciation. *Proceedings of the National Academy of Sciences, USA* 97: 6945–6946.

REDDY, A. S. N., Y. MARQUEZ, M. KALYNA, AND A. BARTA. 2013. Complexity of the alternative splicing landscape in plants. *Plant Cell* 25: 3657–3683.

REDDY, A. S. N., M. F. ROGERS, D. N. RICHARDSON, M. HAMILTON, AND A. BEN-HUR. 2012. Deciphering the plant splicing code: Experimental and computational approaches for predicting alternative splicing and splicing regulatory elements. *Frontiers in Plant Science* 3: 18.

RICHARDS, A. J. 1997. Plant breeding systems, 2nd ed. Springer, Chapman, & Hall, London, UK.

RIESEBERG, L. H., AND L. BROUILLET. 1994. Are many plant species paraphyletic? *Taxon* 43: 21–32.

RIESEBERG, L. H., AND M. F. DOYLE. 1989. Tetrasomic segregation in the naturally occurring autotetraploid *Allium nevii* (Alliaceae). *Hereditas* 111: 31–36.

ROUX, J., AND M. ROBINSON-RECHAVI. 2011. Age-dependent gain of alternative splice forms and biased duplication explain the relation between splicing and duplication. *Genome Research* 21: 357–363.

ROZANOVA, M. A. 1938. On polymorphic type of species origin. *Comptes Rendus de l'Academie des Sciences de l'URRS* 18: 677–680.

SALMON, A., M. L. AINOUCHE, AND J. F. WENDEL. 2005. Genetic and epigenetic consequences of recent hybridization and polyploidy in *Spartina* (Poaceae). *Molecular Ecology* 14: 1163–1175.

SALMON, A., L. FLAGEL, B. YING, J. A. UDALL, AND J. F. WENDEL. 2010. Homoeologous nonreciprocal recombination in polyploid cotton. *New Phytologist* 186: 123–134.

SANTOS, M. E., A. ATHANASIADIS, A. B. LEITÃO, L. DUPASQUIER, AND E. SUCENA. 2011. Alternative splicing and gene duplication in the evolution of the *FoxP* gene subfamily. *Molecular Biology and Evolution* 28: 237–247.

SARKAR, P., AND G. L. STEBBINS. 1956. Morphological evidence concerning the origin of the B genome in wheat. *American Journal of Botany* 43: 297–304.

SCHRANZ, M. E., S. MOHAMMADIN, AND P. P. EDGER. 2012. Ancient whole genome duplications, novelty and diversification: The WGD radiation lag-time model. *Current Opinion in Plant Biology* 15: 147–153.

SEARS, E. R. 1976. Genetic control of chromosome pairing in wheat. *Annual Review of Genetics* 10: 31–51.

SEGRAVES, K. A., AND J. N. THOMPSON. 1999. Plant polyploidy and pollination: Floral traits and insect visits to diploid and tetraploid *Heuchera grossulariifolia. Evolution* 53: 1114–1127.

SEGRAVES, K. A., J. N. THOMPSON, P. S. SOLTIS, AND D. E. SOLTIS. 1999. Multiple origins of polyploidy and the geographic structure of *Heuchera grossulariifolia. Molecular Ecology* 8: 253–262.

SEVERIN, A. J., S. B. CANNON, M. M. GRAHAM, D. GRANT, AND R. C. SHOEMAKER. 2011. Changes in twelve homoeologous genomic regions in soybean following three rounds of polyploidy. *Plant Cell* 23: 3129–3136.

SHAKED, H., K. KASHKUSH, H. OZKAN, M. FELDMAN, AND A. LEVY. 2001. Sequence elimination and cytosine methylation are rapid and reproducible responses of the genome to wide hybridization and allopolyploidy in wheat. *Plant Cell* 13: 1749–1759.

SHI, X., D. W.-K. NG, C. ZHANG, L. COMAI, W. YE, AND Z. J. CHEN. 2012. *Cis-* and *trans*-regulatory divergence between progenitor species determines gene-expression novelty in Arabidopsis allopolyploids. *Nature Communications* 3: 950.

SHORE, J. S. 1991. Tetrasomic inheritance and isozyme variation in *Turnera ulmifolia* vars. *elegans* Urb. and *intermedia* Urb. (Turneraceae). *Heredity* 66: 305–312.

SHORE, J. S., AND S. C. H. BARRETT. 1987. Inheritance of floral and isozyme polymorphisms in *Turnera ulmifolia* L. *Heredity* 78: 44–48.

SMOCOVITIS, V. B. 1997. G. Ledyard Stebbins, Jr. and the evolutionary synthesis (1924–1950). *American Journal of Botany* 84: 1625–1637.

SMOCOVITIS, V. B. 2001. G. Ledyard Stebbins and the evolutionary synthesis. *Annual Review of Genetics* 35: 803–814.

SOLBRIG, O. 1971. Polyphyletic origin of tetraploid populations of *Gutierrezia sarothrae* (Compositae). *Madroño* 21: 20–25.

SOLTIS, D. E. 1984. Autopolyploidy in *Tolmiea menziesii* (Saxifragaceae). *American Journal of Botany* 71: 1171–1174.

SOLTIS, D. E., V. A. ALBERT, J. LEEBENS-MACK, C. D. BELL, A. H. PATERSON, C. ZHENG, D. SANKOFF, ET AL. 2009. Polyploidy and angiosperm diversification. *American Journal of Botany* 96: 336–348.

SOLTIS, D. E., B. A. BOHM, AND G. L. NESOM. 1983. Flavonoid Chemistry of cytotypes in Galax (Diapensiaceae). *Systematic Botany* 8: 15–23.

SOLTIS, D. E., R. J. A. BUGGS, B. BARBAZUK, S. CHAMALA, M. CHESTER, J. P. GALLAGHER, P. S. SCHNABLE, AND P. S. SOLTIS. 2012. The early stages of polyploidy: Rapid and repeated evolution in *Tragopogon*. *In* P. S. Soltis and D. E. Soltis [eds.], Polyploidy and genome evolution, 271–292. Springer, New York, New York, USA.

SOLTIS, D. E., AND J. G. BURLEIGH. 2009. Surviving the K-T mass extinction: New perspectives of polyploidization in angiosperms. *Proceedings of the National Academy of Sciences, USA* 106: 5455–5456.

SOLTIS, D. E., AND L. H. RIESEBERG. 1986. Autopolyploidy in *Tolmiea menziesii* (Saxifragaceae): Genetic insights from enzyme electrophoresis. *American Journal of Botany* 73: 310.

SOLTIS, D. E., AND P. S. SOLTIS. 1988. Electrophoretic evidence for tetrasomic segregation in *Tolmiea menziesii* (Saxifragaceae). *Heredity* 60: 375–382.

SOLTIS, D. E., AND P. S. SOLTIS. 1989a. Genetic consequences of autopolyploidy in *Tolmiea* (Saxifragaceae). *Evolution* 43: 586–594.

SOLTIS, D. E., AND P. S. SOLTIS. 1989b. Tetrasomic inheritance in *Heuchera micrantha* (Saxifragaceae). *Heredity* 80: 123–126.

SOLTIS, D. E., AND P. S. SOLTIS. 1990. Isozyme evidence for ancient polyploidy in primitive angiosperms. *Systematic Botany* 15: 328–337.

SOLTIS, D. E., AND P. S. SOLTIS. 1993. Molecular data facilitate a reevaluation of traditional tenets of polyploid evolution. *Critical Reviews in Plant Sciences* 12: 243–273.

SOLTIS, D. E., AND P. S. SOLTIS. 1999. Polyploidy: Recurrent formation and genome evolution. *Trends in Ecology & Evolution* 14: 348–352.

SOLTIS, D. E., P. S. SOLTIS, D. W. SCHEMSKE, J. F. HANCOCK, J. N. THOMPSON, B. C. HUSBAND, AND W. S. JUDD. 2007. Autopolyploidy in angiosperms: Have we grossly underestimated the number of species? *Taxon* 56: 13–30.

SOLTIS, D. E., P. S. SOLTIS, AND J. A. TATE. 2004. Advances in the study of polyploidy since plant speciation. *New Phytologist* 161: 173–191.

SOLTIS, P. S., X. LIU, D. B. MARCHANT, C. J. VISGER, AND D. E. SOLTIS. 2014. Polyploidy and novelty: Gottlieb's legacy. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 369: 1648.

SOLTIS, P. S., AND D. E. SOLTIS. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proceedings of the National Academy of Sciences, USA* 97: 7051–7057.

SONG, K., P. LU, K. TANG, AND T. C. OSBORN. 1995. Rapid genome change in synthetic polyploids of *Brassica* and its implications for polyploid evolution. *Proceedings of the National Academy of Sciences, USA* 92: 7719–7723.

STANFORD, E. H. 1951. Tetrasomic inheritance in alfalfa. *Agronomy Journal* 43: 222.

STEBBINS, G. L. 1929. Further additions to the Mt. Desert flora. *Rhodora Journal of the New England Botanical Club* 31: 81–88.

STEBBINS, G. L. 1938. Cytological characteristics associated with the different growth habits in the dicotyledons. *American Journal of Botany* 25: 189.

STEBBINS, G. L. JR. 1940. The significance of polyploidy in plant evolution. *American Naturalist* 74: 54–66.

STEBBINS, G. L. 1947. Types of polyploids: Their classification and significance. *Advances in Genetics* 1: 403–429.

STEBBINS, G. L. 1950. Variation and evolution in plants. Oxford University Press, London, UK.

STEBBINS, G. L. 1956. Cytogenetics and evolution of the grass family. *American Journal of Botany* 43: 890–905.

STEBBINS, G. L. 1964. Four basic questions of plant biology. *American Journal of Botany* 51: 220–230.

STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold, London, UK.

STEBBINS, G. L. 1985. Polyploidy, hybridization, and the invasion of new habitats. *Annals of the Missouri Botanical Garden* 72: 824–832.

STEBBINS, G. L. 1992. Comparative aspects of plant morphogenesis: A cellular, molecular, and evolutionary approach. *American Journal of Botany* 79: 589.

STEBBINS, G. L. 1999. A brief summary of my ideas on evolution. *American Journal of Botany* 86: 1207.

STEBBINS, G. L., B. L. HARVEY, E. L. COX, J. N. RUTGER, G. JELENCOVIC, AND E. YAGIL. 1963. Identification of the ancestry of an amphiploid *Viola* with the aid of paper chromatography. *American Journal of Botany* 50: 830–839.

STEBBINS, G. L., J. I. VALENCIA, AND R. M. VALENCIA. 1946. Artificial and natural hybrids in the Gramineae, tribe Hordeae I. *Elymus, Sitanion*, and *Agropyron. American Journal of Botany* 33: 338.

STEBBINS, G. L., AND E. YAGIL. 1966. The morphogenetic effects of the hooded gene in barley. I. The course of development in hooded and awned genotypes. *Genetics* 54: 727–741.

STEIN, J., C. L. QUARIN, E. J. MARTÍNEZ, S. C. PESSINO, AND J. P. A. ORTIZ. 2004. Tetraploid races of *Paspalum notatum* show polysomic inheritance and preferential chromosome pairing around the apospory-controlling locus. *Theoretical and Applied Genetics* 109: 186–191.

STEVENS, P. F. 2001 onward. Angiosperm Phylogeny Website, version 12, July 2012 [and more or less continuously updated since]. Available at http://www.mobot.org/MOBOT/research/APweb/

STIFT, M., C. BERENOS, P. KUPERUS, AND P. H. VAN TIENDEREN. 2008. Segregation models for disomic, tetrasomic and intermediate inheritance in tetraploids: A general procedure applied to *Rorippa* (yellow cress) microsatellite data. *Genetics* 179: 2113–2123.

STRONG, D. R., AND D. R. AYRES. 2013. Ecological and evolutionary misadventures of *Spartina*. *Annual Review of Ecology, Evolution, and Systematics* 44: 389–410.

SU, Z., J. WANG, J. YU, X. HUANG, AND X. GU. 2006. Evolution of alternative splicing after gene duplication. *Genome Research* 16: 182–189.

SWEIGART, A. L., N. H. MARTIN, AND J. H. WILLIS. 2008. Patterns of nucleotide variation and reproductive isolation between a *Mimulus* allotetraploid and its progenitor species. *Molecular Ecology* 17: 2089–2100.

SYED, N. H., M. KALYNA, Y. MARQUEZ, A. BARTA, AND J. W. S. BROWN. 2012. Alternative splicing in plants—Coming of age. *Trends in Plant Science* 17: 616–623.

SYMONDS, V. V., P. S. SOLTIS, AND D. E. SOLTIS. 2010. Dynamics of polyploid formation in *Tragopogon* (Asteraceae): Recurrent formation, gene flow, and population structure. *Evolution* 64: 1984–2003.

TALAVERA, D., C. VOGEL, M. OROZCO, S. A. TEICHMANN, AND X. DE LA CRUZ. 2007. The (in)dependence of alternative splicing and gene duplication. *PLoS Computational Biology* 3: e33.

TANK, D., J. EASTMAN, M. PENNELL, AND L. HARMON. 2012. Progressive radiations and the pulse of angiosperm diversification. Botany 2012: Annual Meeting of the Botanical Society of America, Columbus, Ohio, USA [online abstract]. Website http://2012.botanyconference.org/engine/search/index.php?func=detail&aid=732.

TATE, J. A., P. JOSHI, K. A. SOLTIS, P. S. SOLTIS, AND D. E. SOLTIS. 2009. On the road to diploidization? Homoeolog loss in independently formed populations of the allopolyploid *Tragopogon miscellus* (Asteraceae). *BMC Plant Biology* 9: 80.

TATE, J. A., Z. NI, A. C. SCHEEN, J. KOH, C. A. GILBERT, Z. J. CHEN, P. S. SOLTIS, AND D. E. SOLTIS. 2006. Evolution and expression of homoeologous loci in *Tragopogon miscellus* (Asteraceae), a recent and reciprocally formed allopolyploid. *Genetics* 173: 1599–1611.

TATE, J. A., D. E. SOLTIS, AND P. S. SOLTIS. 2005. Polyploidy in plants. *In* T. R. Gregory [ed.], The evolution of the genome, 371–426. Elsevier, San Diego, California, USA.

THEODORIDIS, S., C. RANDIN, O. BROENNIMANN, T. PATSIOU, AND E. CONTI. 2013. Divergent and narrower climatic niches characterize polyploid species of European primroses in *Primula* sect. *Aleuritia*. *Journal of Biogeography* 40: 1278–1289.

THOMPSON, J. N., AND K. F. MERG. 2008. Evolution of polyploidy and the diversification of plant–pollinator interactions. *Ecology* 89: 2197–2206.

THOMPSON, J. N., S. L. NUISMER, AND K. F. MERG. 2004. Plant polyploidy and the evolutionary ecology of plant/animal interactions. *Biological Journal of the Linnean Society* 82: 511–519.

TREMETSBERGER, K., C. KÖNIG, R. SAMUEL, W. PINSKER, AND T. F. STUESSY. 2002. Infraspecific genetic variation in *Biscutella laevigata* (Brassicaceae): New focus on Irene Manton's hypothesis. *Plant Systematics and Evolution* 233: 163–181.

UDALL, J. A., P. A. QUIJADA, AND T. C. OSBORN. 2005. Detection of chromosomal rearrangements derived from homologous recombination in four mapping populations of *Brassica napus* L. *Genetics* 169: 967–979.

VAN DE PEER, Y. 2011. A mystery unveiled. *Genome Biology* 12: 113.

VAN DE PEER, Y., J. A. FAWCETT, S. PROOST, L. STERCK, AND K. VANDEPOELE. 2009. The flowering world: A tale of duplications. *Trends in Plant Science* 14: 680–688.

VAN DE PEER, Y., S. MAERE, AND A. MEYER. 2010. 2R or not 2R is not the question anymore. *Nature Reviews Genetics* 11: 166.

VANNESTE, K., S. MAERE, AND Y. VAN DE PEER. 2014. Review article: Tangled up in two: a burst of genome duplications at the end of the Cretaceous and the consequences for plant evolution. *Philosophical Transactions of the Royal Society B* 369, 20130353.

VISION, T. J., D. G. BROWN, AND S. D. TANKSLEY. 2000. The origins of genomic duplications in *Arabidopsis*. *Science* 290: 2114–2117.

WAGNER, W. JR.1970. Biosystematics and evolutionary noise. *Taxon* 19: 146–151.

WANG, J., L. TIAN, H.-S. LEE, AND Z. J. CHEN. 2006a. Nonadditive regulation of FRI and FLC loci mediates flowering-time variation in *Arabidopsis allopolyploids*. *Genetics* 173: 965–974.

WANG, J., L. TIAN, H. LEE, N. WEI, H. JIANG, B. WATSON, A. MADLUNG, ET AL. 2006b. Genomewide nonadditive gene regulation in *Arabidopsis* allotetraploids. *Genetics* 172: 507–517.

WANG, K., W. GUO, Z. YANG, Y. HU, AND W. ZHANG. 2010. Structure and size variations between 12A and 12D homoeologous chromosomes based on high-resolution cytogenetic map in allotetraploid cotton. *Chromosoma* 119: 255–266.

WANG, X.-Y., AND A. H. PATERSON. 2011. Gene conversion in angiosperm genomes with an emphasis on genes duplicated by polyploidization. *Genes* 2: 1–20.

WANG, Z., M. WANG, L. LIU, AND F. MENG. 2013. Physiological and proteomic responses of diploid and tetraploid black locust (*Robinia pseudoacacia* L.) subjected to salt stress. *International Journal of Molecular Sciences* 14: 20299–20325.

WARNER, D. A., AND G. E. EDWARDS. 1993. Effects of polyploidy on photosynthesis. *Photosynthesis Research* 35: 135–147.

WENDEL, J. 2000. Genome evolution in polyploids. *Plant Molecular Biology* 42: 225–249.

WENDEL, J. F., AND J. J. DOYLE. 2005. Polyploidy and evolution in plants. *In* R. J. Henry [ed.], Plant diversity and evolution: Genotypic and phenotypic variation in higher plants, 97–117. CABI, Wallingford, UK.

WERTH, C. R., S. I. GUTTMAN, AND W. H. ESHBAUGH. 1985a. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. *Systematic Botany* 10: 184–192.

WERTH, C. R., S. I. GUTTMAN, AND W. H. ESHBAUGH. 1985b. Recurring origins of allopolyploid species in *Asplenium*. *Science* 228: 731–733.

WINGE, O. 1917. The chromsomes: Their number and general importance. *In* R. C. Jackson and D. Hauber [eds.], Polyploidy, 131–275. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

WINKLER, H. 1916. Uber die experimentelle Erzeugung von Pflanzen mit abweichenden. *Chromosomenzahlen. Zeitschrift für Botanik* 8: 417–531.

WOLF, P. G., P. S. SOLTIS, AND D. E. SOLTIS. 1989. Tetrasomic inheritance and chromosome pairing behaviour in the naturally occurring autotetraploid *Heuchera grossulariifolia* (Saxifragaceae). *Genome* 32: 655–659.

WOOD, T. E., N. TAKEBAYASHI, M. S. BARKER, I. MAYROSE, P. B. GREENSPOON, AND L. H. RIESEBERG. 2009. The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences, USA* 106: 13875–13879.

WRIGHT, K. M., J. C. PIRES, AND A. MADLUNG. 2009. Mitotic instability in resynthesized and natural polyploids of the genus *Arabidopsis* (Brassicaceae). *American Journal of Botany* 96: 1656–1664.

WYATT, R., A. STONEBURNER, AND I. J. ODRZYKOSKI. 1989. Bryophyte isozymes: Systematic and evolutionary implications. *In* D. E. Soltis and P. S. Soltis [eds.], Isozymes in plant biology, 221–240. Dioscorides, Portland, Oregon, USA.

XIONG, Z., R. T. GAETA, AND J. C. PIRES. 2011. Homoeologous shuffling and chromosome compensation maintain genome balance in resynthesized allopolyploid *Brassica napus*. *Proceedings of the National Academy of Sciences, USA* 108: 7908–7913.

YOO, M., E. SZADKOWSKI, AND J. WENDEL. 2013. Homoeolog expression bias and expression level dominance in allopolyploid cotton. *Heredity* 110: 171–180.

ZEIGER, E., AND G. L. STEBBINS. 1972. Developmental genetics in barley: A mutant for stomatal development. *American Journal of Botany* 59: 143–148.

ZHANG, P. G., S. Z. HUANG, A.-L. PIN, AND K. L. ADAMS. 2010. Extensive divergence in alternative splicing patterns after gene and genome duplication during the evolutionary history of *Arabidopsis*. *Molecular Biology and Evolution* 27: 1686–1697.

ZHANG, Z., L. ZHOU, P. WANG, Y. LIU, X. CHEN, L. HU, AND X. KONG. 2009. Divergence of exonic splicing elements after gene duplication and the impact on gene structures. *Genome Biology* 10: R120.

ZHAO, N., B. ZHU, M. LI, L. WANG, L. XU, H. ZHANG, S. ZHENG, ET AL. 2011. Extensive and heritable epigenetic remodeling and genetic stability accompany allohexaploidization of wheat. *Genetics* 188: 499–510.