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NEOPOLYPLOIDY IN FLOWERING PLANTS

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■ **Abstract** Here we review the biology of early generation neopolyploids and discuss the profound changes that accompany their formation. Newly formed auto- and allopolyploids exhibit considerable meiotic complexity, including multivalent pairing, multisomic inheritance, and the production of unbalanced gametes. The cytogenetic behavior of allopolyploids and autopolyploids differ statistically, but are more similar than commonly believed. The progeny of neopolyploids include a high frequency of aneuploids, pseudoeuploids and homeologue-recombinant genotypes that may contribute to the phenotypic variability observed in early generation polyploids. We find no evidence to support the traditional view that autopolyploids possess lower fertility than allopolyploids, casting doubt on the paradigm that allopolyploids should be more frequent due to their inherent fertility. The fertility of early generation polyploids increases rapidly, owing largely to selection against meiotic configurations that generate unbalanced gametes. Neopolyploids are commonly differentiated from progenitors by a combination of morphological, phenological and life-history characteristics. Further progress toward understanding polyploid evolution will require studies in natural populations that can evaluate the demographic and larger ecological significance of the cytogenetic and phenotypic character of neopolyploids.

INTRODUCTION

Polyploidy, the genome-wide multiplication of chromosome number, is a key feature in plant evolution. It is estimated that between 47 and 70% of flowering plants are the descendants of polyploid ancestors (Masterson 1994). Differences in ploidy are commonly observed among closely related plant species and among populations within species (Lewis 1980a), and recent molecular studies have revealed that polyploid taxa often have multiple origins (Soltis & Soltis 1993, 1999). These observations demonstrate that polyploidy in plants is a dynamic process. Polyploids generally differ markedly from their progenitors in morphological, ecological, physiological and cytological characteristics (Levin 1983, 2002; Lumaret 1988)

that can contribute both to exploitation of a new niche and to reproductive isolation. Thus, polyploidy is a major mechanism of adaptation and speciation in plants (Clausen et al. 1945, Stebbins 1950, Grant 1981, Otto & Whitton 2000, Levin 2002).

In spite of the importance of polyploidy, the factors contributing to polyploid evolution are poorly understood (Thompson & Lumaret 1992). There are two early stages of polyploid evolution: formation of new cytotypes and their demographic establishment. To understand the process of polyploid formation requires information on the pathways, cytological mechanisms, and rates of polyploid formation. To assess the likelihood that a new polyploid will successfully establish requires information on the viability and fertility of new cytotypes, as well as their phenotypic characteristics and fitness in different environments. A review of polyploid formation is provided in a companion *Annual Review of Ecology and Systematics* chapter (Ramsey & Schemske 1998). Here we review the literature regarding newly formed polyploids to answer the following questions: 1. What are the cytogenetic characteristics of neopolyploids, and how do these relate to the viability, fertility, and stability of polyploids? 2. What are the phenotypic consequences of polyploidy, and by what genetic means are they induced?

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INFERENCE IN POLYPLOID RESEARCH

Despite an enormous literature concerning the biological characteristics of polyploids and their progenitors, most investigations compare naturally occuring established cytotypes. This approach may confound phenotypic differences attributable to ploidy per se with those that result from evolution since the time of polyploid formation (Bretagnolle & Lumaret 1995, De Kovel & De Jong 2000). For example, Smith (1946) documented substantial differences in the morphology, size, flowering phenology, and drought tolerance of diploid, tetraploid, and hexaploid "races" of *Sedum pulchellum*. Without comparative information from closely related homoploid taxa, we have no way of ascribing the divergence observed among cytotypes to polyploidy versus genic differentiation via natural selection, genetic drift, interspecific hybridization, or other mechanisms. It is also common practice to compare the geographic distribution of different cytotypes in an effort to identify the ecological consequences of polyploidy (Lewis 1980b). For example, Mosquin (1966) showed that diploids, tetraploids, and hexaploids of *Epilobium angustifolium* occupy very different geographic regions, an observation consistent with the hypothesis that polyploidy promotes ecological diversification. Yet, in most plants, profound ecological and geographic differentiation is perhaps just as frequent without changes in ploidy (Clausen et al. 1940).

This chapter is focused on the origins and demographic establishment of polyploids, phenomenon dependent on the characteristics of polyploids at the time of origin. One approach that minimizes the confounding effects of postformation evolution involves the comparison of diploid progenitors with newly formed polyploids (neopolyploids). For example, Müntzing (1951) induced autotetraploids in

three varieties of rye and directly compared the growth, tillering, phenology, yield, and baking properties of tetraploids and progenitor diploids. In this way, the biological attributes of the early generation polyploids can be compared directly to those of their progenitor cytotypes. As a rule, we include only neopolyploids in our analyses here, though the characteristics of naturally established and cultivated polyploids are sometimes discussed.

In addition to elucidating the process of polyploid establishment, studies of neopolyploids provide insights into the nature of polyploidy as an adaptation. The difficulty of determining the role of polyploidy per se in creating cytotype differences hampers investigations of naturally occurring polyploids: What fraction of the phenotypic differences between related cytotypes are a direct consequence of polyploidy rather than incidental differentiation accrued via genic differentiation in allopatry? Three hypotheses may be posed to explain observed cytotype adaptation in natural populations. First, phenotypic differentiation may be driven by polyploidy per se, through the combined effects of increased cell size, gene dosage effects, allelic diversity and other mechanisms (Levin 1983, 2002; Lumaret 1988). Second, postzygotic reproductive isolation of cytotypes may facilitate ecotypic differentiation, either through reinforcement (Petit et al. 1999) or liberation from gene flow that may slow the process of local adaptation and range expansion (Kirkpatrick & Barton 1997). Finally, cytotype differences may simply represent allelic differences accumulated via conventional evolutionary processes that operate in both diploid and polyploid populations. Clearly, comparisons of neopolyploids and established cytotypes in natural polyploid complexes will play an important role in evaluating the role of polyploidy in adaptation and speciation. Where relevant, we discuss the implications of our results for both demographic establishment and the larger evolutionary significance of polyploidy.

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APPROACH AND TERMINOLOGY

A major motivation for this review is to synthesize the diverse literature on early generation polyploids and thereby provide a resource for the development of future research on polyploid establishment. To this end, we have tabulated data from ~250 published studies and made this information available on the Annual Reviews web site (http://www.annualreviews.org; see Supplementary Materials). We summarize these data throughout the text and identify the location of each database on the web site. Textual citations generally include only the most comprehensive studies.

By necessity, most of the plants considered in this review are agricultural or horticultural cultivars, as well as classic genetic systems (e.g., *Datura* and *Nicotiana*). These studies provide insights into neopolyploids in natural populations, but we caution that further investigations are needed to test our results. First, polyploids generated in domesticated, highly modified and inbred cultivars may not always be representative of neopolyploids in natural populations. Second, many surveyed polyploids were induced by experimental treatments such as heat shock and

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colchicine. These methods provide a practical advantage in allowing researchers to generate large numbers of neopolyploids from diverse plant material, but also induce occasional chromosomal rearrangements, chromosome substitutions, aneuploidy and, in some cases, apparent genic mutations (Randolph 1932, Bergner et al. 1940, Smith 1943, Sanders & Franzke 1964, Salanki & Parameswarappa 1968). Induced neopolyploids, which are formed by somatic doubling, may also be less heterozygous than spontaneous neopolyploids, which are hypothesized to arise primarily via unreduced gametes (see Bretagnolle & Thompson 1995). The origin of all surveyed polyploids is documented in Web Tables. Finally, naturally occurring polyploids are unknown in some of the taxa included here. Inasmuch as some species (and species hybrids) may be predisposed to generate demographically successful neopolyploids, these data represent a random sample of newly formed polyploids rather than a sample of successful polyploids. As discussed below, there is a general need for studies of neopolyploidy in natural polyploid complexes.

Our surveys include a wide range of plant families, genera, and species, but because of limited sample size we do not interpret our results in a phylogenetic framework. As a general rule, data collected from related congeneric and conspecific varieties were as variable as those observed in distant relatives. Hence, data from related congeners, hybrid combinations, and different strains or populations of a single species are treated as independent. Most datasets incorporate data from numerous taxa, including one to several species or accessions per genus. Complete datasets are online in Supplementary Materials.

In this chapter, $2n$ refers to the somatic chromosome number and n to the gametic chromosome number regardless of the degree of polyploidy, while x is the most probable base number. This gives the following cytological designations: diploids ($2n = 2x$), triploids ($2n = 3x$), tetraploids ($2n = 4x$), etc. As summarized in Ramsey & Schemske (1998), the terms autopolyploid and allopolyploid have a complex history. We believe that the primary criterion for classifying a polyploid is its mode of origin. In this chapter we use the term autopolyploid to denote a polyploid arising within or between populations of a single species, and allopolyploid to indicate polyploids derived from hybrids between species, where species are defined according to their degree of pre- and post-zygotic reproductive isolation (biological species concept). Alternate definitions of polyploid types will be discussed in later sections.

MEIOTIC BEHAVIOR OF NEOPOLYPLOIDS

Chromosomes that are structurally similar and pair normally at meiosis are termed homologous. Parental diploid species have two sets of homologous chromosomes, and an autotetraploid has four sets. Allopolyploids possess chromosome complements from two or more evolutionary lineages. These chromosomes are differentiated to some degree by (*a*) DNA sequence (e.g., allelic differences caused by nucleotide substitutions or indels); (*b*) structure and gene order (e.g., chromosomal rearrangements); and/or (*c*) total number. Partially homologous

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chromosomes are called homeologous. For example, the chromosomes of the diploid species *Collinsia concolor* and *C. sparsiflora* ($x = 7$) are distinguished by reciprocal translocations and paracentric inversions as well as numerous gene differences (Garber & Gorsic 1956, Garber & Dhillon 1962). The diploid F1 hybrid has two sets of chromosomes that are homeologous, and can be assigned the genomic formula CS; at meiosis, the F1 exhibits interchange complexes, dicentric bridges and fragments, and a high frequency of unpaired chromosomes (univalents). Allotetraploid *Collinsia concolor* × *sparsiflora* (CCSS) has both homologous (C-C, S-S) and homeologous (C-S) chromosomes. At meiosis the allotetraploid exhibits no complexes, bridges or fragments, and few univalents.

At a basic level, meiosis can be understood as three sequential processes: chromosome pairing (synapsis), crossing over (chiasma formation), and chromosome distribution (Sybenga 1975; Singh 1993). Pairing occurs during prophase I. In polyploids, associations between homologous or homeologous chromosomes are determined at synapsis; hence, chromosome pairing determines broad patterns of genetic recombination and chromosome distribution at anaphase. At metaphase I, synapsed homologues and homeologues usually cross over and form chiasmata, exchanges of chromatid segments, leading to genetic recombination. The frequency and distribution of chiasmata determine the configurations of chromosomes during metaphase and anaphase. Finally, pairing partners, whether homologous or homeologous, are distributed to opposite poles of mother cells during anaphase I.

Autopolyploids possess only homologous chromosomes, while allotetraploids possess two or more sets of homeologous chromosomes. This has led to the prediction that meiosis and inheritance should differ between the two types of polyploids (Müntzing 1932, 1936; Winge 1932; Darlington 1937; Stebbins 1950; Soltis & Rieseberg 1986). In autopolyploids, the four or more sets of homologous chromosomes of autopolyploids should pair randomly during prophase (autosyndesis). These homologues should form groups of two (bivalent configuration), three (trivalent configuration), four (quadrivalent configuration) or more during metaphase. Hence, alleles at a given locus on the homologous chromosomes of autopolyploids should segregate at random; unlike diploids, autopolyploids should be characterized by multisomic inheritance. In allopolyploids, chromosomes are expected to pair nonrandomly, with homologous pairing (autosyndesis) occurring to the exclusion of homeologous pairing (allosyndesis). Homologous chromosomes of allopolyploids should then form only balanced pairs (bivalent configuration) during metaphase. Hence, alleles at a given locus on homeologous chromosomes of allopolyploids should segregate independently; like diploids, allopolyploids should be characterized by disomic inheritance. Examples of typical meiotic configurations in diploids and polyploids are shown in Figure 1.

In effect, autopolyploids are considered to represent cytogenetically complex, multisomic parental diploids, while allopolyploids represent fixed, disomic species hybrids. To test these hypotheses, we surveyed the literature regarding the meiotic behavior of neoauto- and neoallopolyploids. In these sections, we consider only

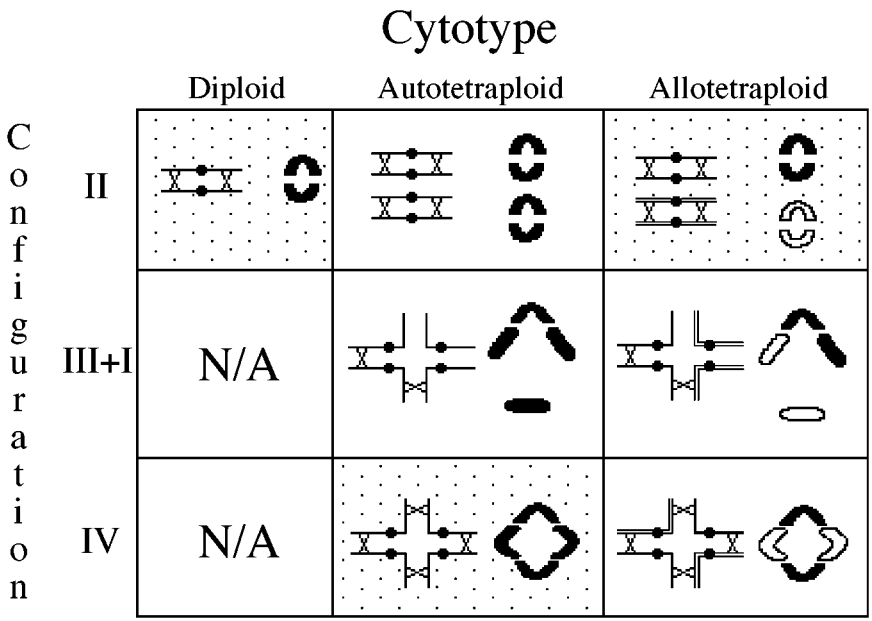

Figure 1 Univalent (I), bivalent (II), trivalent (III), and quadrivalent (IV) associations of homologous and homeologous metacentric chromosomes in diploids, autotetraploids and allotetraploids. Theoretical derivations (*left*) and resulting meiotic figures (*right*) are illustrated for each configuration and cytotype. Crossover events are shown by an "X," and centromeres by a dot (•). Configurations commonly hypothesized to be "normal" for a given cytotype are highlighted with stippled background. The formation of configurations in diploids and polyploids is dependent upon the distribution and number of chiasmata formed between homologous/homeologous chromosomes, hence illustrated associations represent a subset of all possible configurations. A comprehensive review of meiotic configurations is provided by Sybenga (1975).

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even-ploidy cytotypes, i.e., tetraploids, hexaploids, and octoploids. The meiosis and progeny of triploids are evaluated in Ramsey & Schemske 1998.

Auto- and Allosyndesis

The major hypotheses regarding the character of hybrid and nonhybrid polyploids are predicated on the assumptions that autopolyploids exhibit random pairing of homologues and allopolyploids lack homeologous pairing. There are, however, few direct observations of auto- and allosyndetic pairing. Markers for distinguishing homologs at meiotic prophase and metaphase are often unavailable, preempting evaluation of preferential pairing in autopolyploids. Morphological differences between homeologous chromosomes of some taxa enable determinations of heteromorphic pairing in allopolyploids (e.g., Lindstrom & Humphrey 1933), but

not systematic estimates of the frequency of auto- and allosyndesis. Homologous and homeologous pairing can be inferred from meiotic configurations and from inheritance data (see below), though indirect estimates do not assess pairing that is gamete- or sporophyte-lethal. This factor may explain the phenotypic stability of allopolyploids that have multivalent pairing and other meiotic irregularities (e.g., Brown 1951). In this scenario, allosyndesis contributes to the lowered fertility of polyploids.

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Meiotic Configurations

In a simple model, one might predict that autopolyploids would exhibit 100% multivalent configurations, while allopolyploids would have 100% bivalent pairings. To evaluate the chromosome associations of auto- and allopolyploids we surveyed the occurrence of univalents, bivalents, trivalents and quadrivalents during late prophase (diakinesis) and metaphase I of neopolyploids. It should be noted that chiasma formation and configurations at diakenesis and metaphase are not always indicative of synapsis during prophase, because paired chromosomes sometimes fail to cross over (Sybenga 1975, Jackson 1976). Hence, metaphase configurations represent successful pairings that result in genetic recombination. Metaphase associations are standard cytological inference, and the only widely available index of meiotic pairing in polyploids.

In our survey, the mean percent occurrence of multivalents (trivalents and quadrivalents) is significantly higher in autopolyploids (28.8%, N = 93 studies) than in allopolyploids (8.0%, N = 78 studies) (Mann-Whitney U test, $P < 0.001$) (Figure 2; see Web Table 1). This result supports the hypothesis of differential chromosome behavior of auto- and allopolyploids, but also raises several issues. First, in autopolyploids, the occurrence of bivalent pairing is higher (mean 63.7%, range 12 to 98.2), and quadrivalent pairing lower (mean 26.8%, range 1.8 to 69.1), than what theoretically might be expected from homologous chromosomes (e.g., 0% bivalents and 100% quadrivalents). For example, induced autotetraploids of *Lolium perenne* exhibited 1% trivalent and 20% quadrivalent configurations at metaphase I (Simonsen 1973), while autotetraploid tomato had almost no trivalents and 19% quadrivalents (Upcott 1935).

Two mechanisms could limit bivalent pairing in first and early generation autopolyploids that have not been fertility-selected: (*a*) nonrandom chromosome associations among some homologues, and (*b*) existence of physical limitations or genetic factors limiting multivalent pairing between randomly associating homologous chromosomes. The former hypothesis is unlikely. "Diploidization" of autopolyploids is hypothesized to occur by the gradual accumulation of structural differences in homologous chromosomes (Doyle 1963, Sybenga 1969) as well as the evolution of genic factors that enforce preferential pairing in established polyploid populations. Moreover, the numbers of multivalents occurring per mother cell (0, 1, 2, 3, . . . x) in new autopolyploids generally follows a binomial distribution, suggesting that the probability of quadrivalent formation is the same for each

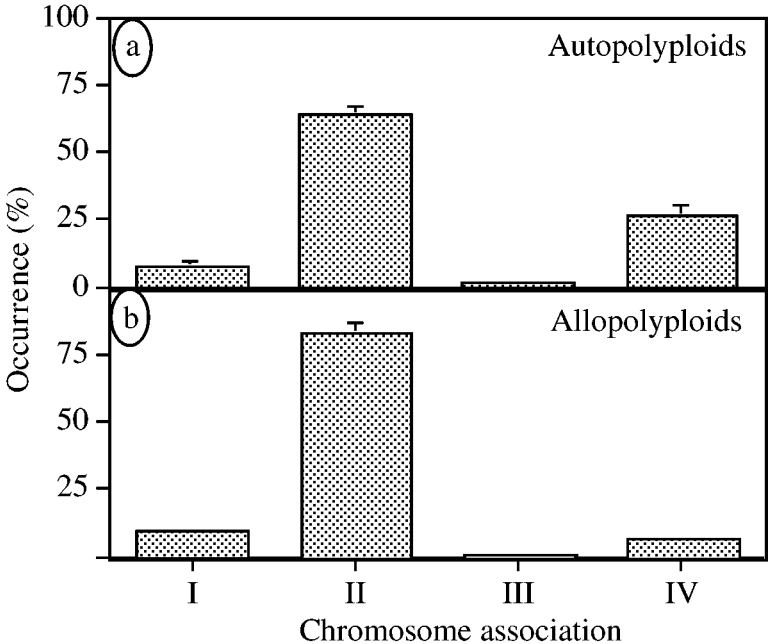

Figure 2 Mean percent occurrence (± 2 SE) of univalent (I), bivalent (II), trivalent (III) and quadrivalent (IV) chromosome associations during metaphase I of newly formed (*a*) autopolyploids (N = 93) and (*b*) allopolyploids (N = 78). Data from Web Table 1.

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set of homologous chromosomes (McCollum 1958, Morrison & Rajhathy 1960a, Simonsen 1973, Sybenga 1996).

Most cytogeneticists hypothesize that the frequency and distribution of chiasmata dictate the occurrence of multivalents in autopolyploids (Kostoff 1940, McCollum 1958, Hazarika & Rees 1967, Sybenga 1975). As an illustration, consider a single parameter, number of chiasma initiation sites per chromosome. Pairing behavior in diploids is robust to the manner of pairing initiation because 100% bivalent pairing will result if chiasma can initiate at one or more sites, and if each chromosome has at least one crossover. In contrast, configurations of polyploids are strongly influenced by chiasma initiation. In an autotetraploid, if pairing is initiated at only one chromosomal location, no more than two bivalents will form from each set of four homologues. If pairing is initiated at two chromosomal locations, two thirds of resulting configurations will be quadrivalents, while one third will be bivalents (John & Henderson 1962, Sved 1966). Assuming pairing initiation at two or more sites, other factors could decrease or increase multivalent frequencies (Sybenga 1975, Lavania 1986). For example, polyploids may tend to exhibit reduced chiasma formation compared to progenitor diploids (e.g., Hazarika & Rees 1967), perhaps because complex chromosome associations interfere with pairing and crossover. Polyploids may thus exhibit fewer or altered chiasma, and

hence fewer multivalents, than observations of diploids would lead one to expect. Some chromosomes may be structurally incapable of forming all possible chiasmata between four or more homologues (Sybenga 1975).

The observation that the occurrence of two chiasma initiation points per chromosome leads to an expected 66% frequency of multivalents, coupled with early cytological surveys suggesting occurrences of multivalents range from 50% to 80% (Morrison & Rajhathy 1960a,b), led some cytogeneticists to hypothesize that two thirds of chromosome associations in "good" autopolyploids should be multivalents (Sved 1966; Jackson 1976). Our survey revealed that quadrivalent frequency of neoautotetraploids (mean 29%, range 2 to 69) is significantly different than 66% (One-Sample test, $P < 0.0001$). In the absence of cytological data regarding chiasma formation, there does not appear to be a reliable a priori expectation regarding the configurations of autopolyploids.

Another unexpected result of this survey is the common occurrence of multivalents in allopolyploids (see Web Table 1). Trivalents and quadrivalents were observed in 80% of surveyed allopolyploids, and percent occurrence is significantly different than zero (One-sample Sign Test, $P < 0.0001$). The mean frequency of multivalent pairing observed in allopolyploids (mean 8.0%, range 0 to 52) is approximately one quarter the occurrence in autopolyploids (mean 28.8%, range 2 to 69). Multivalents are reported in polyploids generated by wide crosses (e.g., Howard 1938, Stebbins & Vaarama 1954, Phillips 1964) and in many classic textbook polyploids. For example, *Primula kewensis*, the famous allopolyploid derived by somatic doubling of sterile diploid F1 *P. floribunda* × *verticillata*, exhibited 18% multivalent pairing at metaphase I (Upcott 1940).

Multivalent pairing in allopolyploids is biologically significant for two reasons. First, homeologous pairing in bivalents and multivalents will lead to the production of genically unbalanced euploid chromosomes, and hence reduced fertility (Howard 1938; see below). Second, the occurrence of multivalents provides evidence of intergenomic recombination in allopolyploids. Sved (1966) estimated the relationship between multivalent and recombination frequencies for allotetraploids with two pairing initiation sites per chromosome but differing degrees of preferential pairing. The relationship between quadrivalent occurrence and segregation frequency (indexed as the frequency of homozygous *aa* recessive gametes produced by the heterozygote *aaAA* parent) is approximately linear. For the mean frequency of quadrivalents in our survey, the expected segregation frequency is 1.2%. In comparison, 16.7% segregation would be expected in an autopolyploid (Sved 1966).

Patterns of Inheritance in Neopolyploids

It is commonly believed that strict autosyndesis in allopolyploids leads to independent segregation of alleles on homeologous chromosomes, and hence "fixed heterozygosity" inherited in a disomic manner (Winge 1932, Roose & Gottlieb 1976, Soltis & Soltis 1993). Consider an allotetraploid with the duplex heterozygote genotype *AAaa*, where one pair of homeologs carries the *A* allele, and the other has the *a* allele. Autosyndesis leads to a single arrangement of bivalent pairings,

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and all gametes will be heterozygous *Aa* (Sybenga 1969). In contrast, pairing of duplicate chromosomes in autopolyploids is hypothesized to occur at random during meiotic prophase I. Crossover may involve any homologue, and segregation at a given locus can involve as many alleles as there are homologous chromosomes. If the above-described heterozygote *AAaa* was an autopolyploid, 12 quadrivalent and bivalent associations could occur during meiosis. Although the heterozygous gamete *Aa* would be the most frequent product of meiosis, ~30–45% of the gametes would be completely homozygous. The exact outcome is dependent upon the frequency of recombination between the marker locus and the centromere and the occurrence of multivalents (Little 1945, Burnham 1962, Bever & Felber 1992).

The chromatid segregation model postulates that recombination can occur between a locus and the centromere. Hence, sister chromatids of homologs associated as multivalents will sometimes end up with different alleles, depending on the structure of the multivalent and the crossover frequency. By chance, anaphase II may reunite identical alleles initially held on sister chromatids but recombined to separate homologs by chiasma during metaphase I, a phenomenon termed double reduction. Assuming 100% quadrivalent configurations and the consistent presence of one chiasma between the *A* locus and the centromere, the chromatid segregation model would predict gametic ratios of 2 *aa*:5 *Aa*:2 *AA* from the *AAaa* sporophyte (Burnham 1962, Jackson & Jackson 1996). In the chromosome segregation model, there would be no crossing over between the *A* locus and the centromere, for example because the locus is located near the centromere. Chromatids of homologs associated as quadrivalents will possess the same allele, and double reduction is not possible. Segregation ratios are thus robust to the frequency of multivalents and total gamete ratios will be 1 *aa*:4 *Aa*:1 *AA* (Sybenga 1969, Jackson & Jackson 1996). Segregation rates of most loci in autopolyploids are probably intermediate between those predicted by chromatid and chromosome segregation models of multisomic inheritance. Also, the frequent occurrence of aneuploids in the progeny of neopolyploids alters realized segregation rates.

Available studies of spontaneous and induced autopolyploids are all consistent with the hypothesis of multisomic inheritance (see Web Table 2; N = 14 loci in 7 species), thus supporting the hypothesis of random association of homologues in nonhybrid polyploids. For example, flower color in diploid Jimsonweed (*Datura*) is determined by two alleles at a single locus, with purple (*P*) dominant to white (*p*). In autotetraploids, backcrosses of duplex heterozygotes (*PPpp*) to homozygous recessives (*pppp*) generated 905 purple-flowered individuals and 179 white-flowered individuals, frequencies that correspond to an expected 5:1 ratio. Crosses of induced autotetraploid *Tradescantia paludosa* that were duplex heterozygous for self-incompatibility alleles (i.e., S1133 × S2244) generated 10% di-allelic, 40% tri-allelic, and 50% tetra-allelic progeny, frequencies consistent with the chromosome segregation model of multisomic inheritance (Annerstedt & Lundqvist 1967).

Segregation ratios in allopolyploids vary dramatically across taxa, sometimes approaching disomic inheritance but more typically multisomic inheritance (see

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Web Table 2; N = 58 loci in 23 species). The most comprehensive data involve *Gossypium* species. A variety of monogenic characters are known from the cultivated cottons, *G. hirsutum* and *G. barbadense*, and their wild relatives. Gerstel & Phillips (1958) used marker alleles to test segregation patterns in polyploids derived from congeners of varying phylogenetic affinity. *G. hirsutum* and *G. barbadense* are stable allopolyploids derived from distant relatives; extant accessions are characterized by bivalent pairing and disomic inheritance, and are assigned the genome formula AADD. Strains of tetraploid cotton that were homozygous for dominant marker alleles on the D or A genomes were crossed to a variety of natural diploid D and A genome species, and the converse. These crosses generated triploid hybrids (AD_1D_2 and A_1A_2D), which were treated with colchicine to induce allohexaploids ($AAD_1D_1D_2D_2$ and $A_1A_1A_2A_2DD$). Depending upon the occurrence of homeologous pairing of D and A chromosomes during meiosis, hexaploids would generate either (*a*) gametes that were always heterozygous for the dominant marker (AD_1D_2 and A_1A_2D), or (*b*) a combination of heterozygous and homozygous gametes (AD_1D_1, AD_1D_2, and AD_2D_2, or A_1A_1D, A_1A_2D, and A_2A_2D). The latter possibility is manifest as the occurrence of recessive (wild-type) individuals in a test cross, in which hexaploids were backcrossed to diploid parentals to form tetraploids. A multisomic chromosome segregation model would predict a 1:5 occurrence of recessives, which would never occur under conditions of strict disomic inheritance. Segregation rates varied widely between crosses, and were correlated with frequencies of multivalents at meiotic metaphase (Figure 3) (Phillips 1962, 1964). For example, segregation of recessives in *G. hirsutum* × *arboreum* averaged 5.1:1, approximately the frequency expected with polysomic inheritance, while *G. barbadense* × *gossypioides* averaged 72:1 (Figure 3). The latter value is less than that predicted by multisomic inheritance, but very different from the predicted value of 0 for disomic inheritance.

Because the diploid progenitors of most neoallopolyploids are morphologically distinct, it is possible to evaluate allosyndesis and the breakdown of disomic inheritance in a general way by comparing the phenotypic characteristics of parentals and primary allopolyploids with those of successive allopolyploid generations. For example, Grant (1954) described segregation of leaf width, pubescence, calyx lobe shape, corolla length, filament length, and other traits in progeny of the spontaneous allopolyploid *Gilia millefoliata* × *achilleaefolia*. We found that 31 of 42 studies of neopolyploid accessions identified substantial segregation for morphological characteristics, marker alleles and fertility (see Web Table 3). It should be noted that segregation in spontaneous neopolyploids may be caused by recombination in unreduced gametes produced by progenitor F1 hybrids and triploid intermediates in addition to allosyndesis in the neopolyploid itself (Howard 1938, Müntzing 1932). Also, aneuploidy and gene silencing can generate patterns of phenotypic variability that may be confused with intergenomic recombination.

Nonetheless, the combined data on inheritance and segregation in allopolyploids (see Web Tables 2, 3) clearly suggest that (*a*) variation in the frequency of allosyndesis is expected for different pairwise combinations of species, and

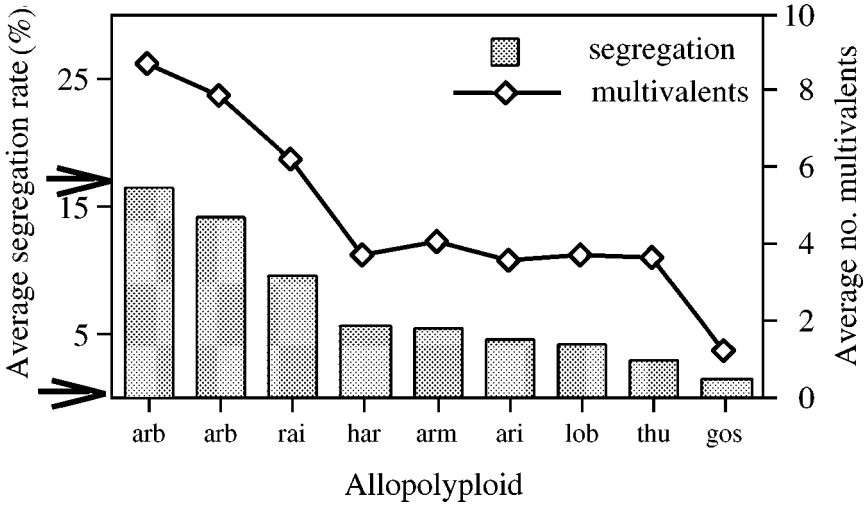

Figure 3 Segregation of recessive genotypes (*zzzz*) from crosses of duplex heterozygotes (*ZZzz*) to recessive testers (*zzzz*) (*left axis, columns*), and percent occurrence of multivalents at meiotic metaphase I (*right axis, line*), in allopolyploids involving cotton (*Gossypium hirsutum* or *G. barbadense*) and wild relatives (*G. arboreum, G. raimondii, G. harknessii, G. armourianum, G. aridum, G. lobatum, G. thurberi,* and *G. gossypioides*). Arrows show expected segregation for multisomic inheritance (chromosome segregation) and disomic inheritance. Data from Phillips (1962, 1964).

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(*b*) except in wide crosses, the mean frequency of allosyndesis is considerably greater than zero (Goodspeed & Bradley 1942, Grant 1975). The long-term evolutionary consequences of intergenomic segregation are unknown (Sybenga 1969, 1996). Rapid evolution of chromosome structure and genic control of chromosome pairing (see below) may lead to strict homologue pairing and disomic inheritance, though possibly after considerable recombination between homeologues. Alternatively, allosyndesis may result in chance fixation of chromosome segments from one homeologue or the other, generating hybrid polyploids that are multisomic for individual chromosomes or chromosome regions (Stebbins 1950). Models suggest that in the absence of mitigating factors, even occasional multivalent pairing can rapidly deteriorate to a system of multisomic inheritance (Sybenga 1996). As discussed below, these possibilities challenge the perception of allopolyploids as "constant species hybrids" (Winge 1932).

ANEUPLOIDY

Aneuploidy, defined as the possession of chromosome numbers either greater or less than an exact multiple of the base chromosome number *x*, is common in flowering plants (Grant 1981). Aneuploidy is hypothesized to contribute to

phenotypic evolution and speciation in some genera, and may, in some cases, enable transitions between euploid chromosome numbers. Some polyploid lineages have a high occurrence of aneuploid variation. For example, some taxa exhibit polyploid drop, aneuploid reduction at the polyploid chromosome number (Darlington 1963). Here we examine the origin and maintenance of aneuploid cytotypes in neopolyploid populations.

Polyploids Generate a High Frequency of Aneuploid Gametes

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The occurrence of univalents and multivalents during polyploid meiosis complicates the orderly separation of homologs/homeologues. Univalents and trivalents by necessity divide unequally during anaphase I because there is no mechanism to evenly divide the chromosomes of an odd-number configuration (though by chance, unbalanced divisions may compensate each other, for example by a 2–1 separation of a trivalent, and a 0–1 division of a univalent). The divisions of tetraploids are more complicated to assess. Some ten types of quadrivalent configurations can be formed, depending on which homologous/homeologous chromosomes happen to cross over (Sybenga 1975, Singh 1993). Quadrivalent configurations can broadly be divided into ring configurations (each homolog/homeolog forming two chiasma) and chain configurations (each homolog/homeolog forms one or two chiasma), analogous to the ring and rod configurations of diploids. Among ring and chain configurations, one may distinguish alternate orientations (proximate homologs/homeologs oriented in opposite directions) and adjacent orientations (proximate homologs/homeologs oriented, to varying degrees, in the same direction). Alternate quadrivalent orientations, sometimes called zigzag orientations, are believed to nearly always generate equal (2–2) chromosome disjunctions (Garber 1955, McCollum 1958), whereas disjunctions from adjacent orientations will include both balanced and unbalanced separations. Orientation frequencies are dependent upon the initial likelihood of formation, and stability during the transition from metaphase to anaphase; reorientation of individual configurations is probably frequent (Sybenga 1975). Frequencies of alternate quadrivalent frequencies vary among polyploid species (Myers & Hill 1940, Garber 1954, Jones 1956, McCollum 1958), so the contributions of quadrivalents to unbalanced meiotic divisions may vary across taxa. The evolution of increased zigzag quadrivalent orientations may be an important mechanism increasing fertility of neopolyploid lineages.

To evaluate the extent of aneuploidy in the gametes of neopolyploids we summarized the literature on anaphase I and metaphase II chromosome distributions in pollen mother cells, as well as chromosome counts in maturing pollen grains. Chromosome compositions determined at later stages of development (e.g., pollen mitoses) more accurately reflect actual pollen cytotypes than determinations made early in development (e.g., anaphase I). There was no clear influence of stage of development on the frequency of aneuploidy in our dataset (see Web Table 4; Gulcan

& Sybenga 1967), but where more than one stage was investigated in a study we included later measurements. No data on megaspore mother cells and ovules were available.

Occurrences of aneuploid pollen in auto- and allopolyploids were not significantly different (mean 36.0 versus 43.1%, Mann Whitney U test, $P = 0.6173$; see Web Table 4), so we pooled polyploid types for consideration of specific cytotypes. Euploid (n) pollen were most frequent (mean 62.5%, range 31.1 to 78.5, N = 26 studies), followed by $n - 1$ and $n + 1$ cytotypes (mean 16.4 and 13.2%, respectively) (Figure 4*a*; see Web Table 4). Pollen lacking or gaining three or

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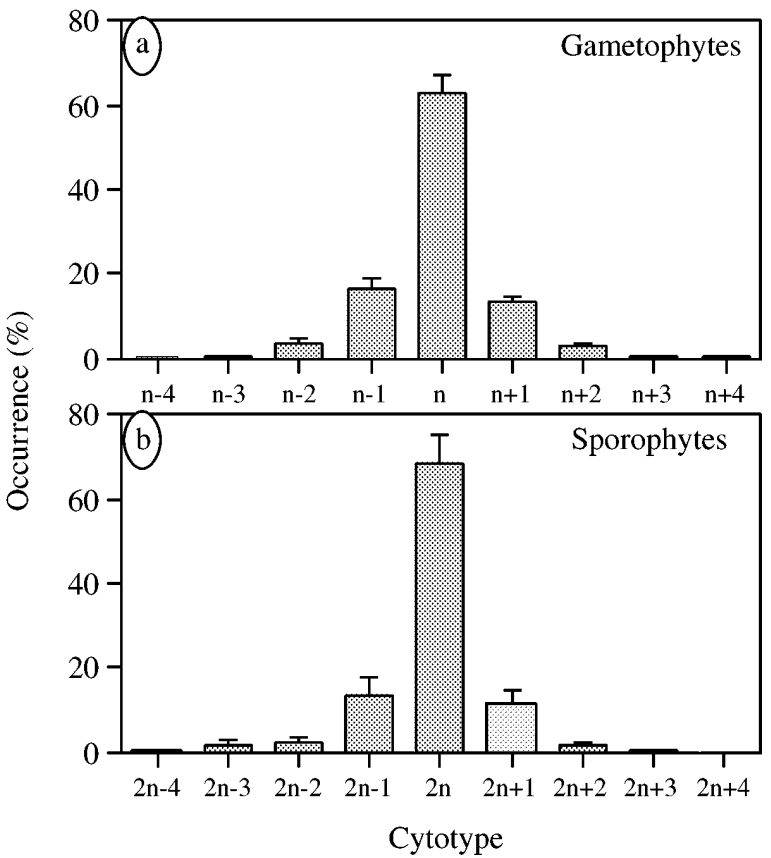

Figure 4 Mean percent occurrence (± 2 SE) of aneuploidy in gametophytes (N = 26) and sporophytes (N = 33) of neopolyploids (auto- and allopolyploids pooled). (*a*) Frequency distribution of pollen cytotypes produced by neopolyploids, as determined from pollen mitoses as well as anaphase I or metaphase II stages in pollen mother cells. (*b*) Frequency distribution of chromosome numbers in the progeny of neopolyploids. Data from Web Tables 4 and 5.

more chromosomes on average constituted <2% of cytotypes (Figure 4*a*; see Web Table 4). Hypoeuploid pollen cytotypes (i.e., aneuploids with less than the euploid chromosome number *n*) were significantly more common than hypereuploid pollen cytotypes (aneuploids with more than the euploid chromosome number *n*) (means 20.8 versus 16.7%; Wilcoxon Signed Rank test, $P = 0.0023$). The likely cause of this phenomenon is the occurrence of lagging univalents, which often fail to incorporate into either daughter nuclei. In essence, there are two mechanisms that lose chromosomes during meiotic divisions (unbalanced anaphase separations, lagging chromosomes), but only one way to gain chromosomes (unbalanced anaphase separations).

These analyses suggest that aneuploid cytotypes constitute a substantial portion of the gametes produced by neopolyploids. The mean frequency of euploid gametes in autoploids (64.0%, N = 22) closely matches the mean occurrence of bivalents (63.7%, N = 93) (see Web Tables 1, 4; Figures 2, 4*a*). Bivalent pairings involving homologous chromosomes, such as would be observed in parental diploid species and autopolyploids, rarely exhibit irregularities at anaphase. This implicates the remaining configurations (univalents, trivalents and quadrivalents) as important contributors to unbalanced meiotic divisions. In contrast, the mean frequency of euploid gametes in allopolyploids (56.9%, N = 7) is much less than the mean occurrence of bivalents (82.3%, N = 78) (see Web Tables 1, 4; Figure 2, 4*a*). This discrepancy may be a spurious result of the small number of anaphase I and metaphase II chromosome distributions determined in allopolyploids. However, this trend holds in individual allopolyploid studies with estimates of the occurrence of both meiotic configurations and aneuploid gametes (Kostoff 1938, Upcott 1940, Singh & Hymowitz 1985). A likely explanation is that a portion of bivalent configurations observed in allopolyploids in fact involve homeologous chromosomes (i.e., allosyndesis), which may lead to irregular separation at anaphase.

Variability in gamete cytotypes is considerably less in the even-ploidy cytotypes (tetraploids, hexaploids, and octoploids) considered here, than in triploids (Ramsey & Schemske 1998, Figure 1). The difference probably originates from the meiotic configurations that occur in odd and even ploidy cytotypes. In triploids, every chromosome will display either (*a*) two bivalents and one univalent; (*b*) one trivalent, or (*c*) three univalents. In each case, a high degree of irregularity is anticipated during anaphase. In tetraploids, univalents and trivalents may occur, but bivalents and quadrivalents are the most abundant associations (Figure 2).

Polyploids Generate a High Frequency of Aneuploid Progeny

The high frequency of aneuploidy in the gametes of neopolyploids has two possible outcomes. First, aneuploidy may be lethal at the gamete or embryo development stages. In this scenario the progeny of neopolyploids are euploid, but of limited number. Second, aneuploid gametes may function similarly to euploid gametes, and generate viable gametes. In this case, polyploid progeny will be more numerous but include a high percentage of aneuploid individuals. Here we summarize the frequency of aneuploids in the progeny of neopolyploids.

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Occurrences of aneuploid progeny from auto- and allopolyploids were not significantly different (mean 29.0 versus 28.3%, Mann Whitney U test, $P = 0.3339$; see Web Table 5), so we consider the two polyploid types together in estimates of cytotype occurrences. Euploid ($2n$) sporophytes were most frequent (mean 68.6%, range 20 to 96.9, N = 33 studies), followed by $2n - 1$ and $2n + 1$ cytotypes (mean 13.4 and 11.5%, respectively) (Figure 4*b*; see Web Table 5). Sporophytes lacking or gaining three or more chromosomes on average constituted <3% of progeny cytotypes (Figure 4*b*; see Web Table 5). Mean occurrences of hypo- and hyper-euploid progeny were not significantly different (means 17.6 and 13.5; Wilcoxon Signed Rank test, $P = 0.6402$). Asymmetries were observed in some individual species (see Web Table 5), but there was no consistent trend for a higher frequency of hypoeuploids in sporophyte cytotypes as observed in pollen cytotypes.

The most striking feature of this analysis is the close correspondence between cytotype distributions of the pollen and progeny of neopolyploids (Figure 4*a*,*b*). Euploids are somewhat more common among sporophytes than gametes, and the difference is marginally significant (68.6 versus 62.5%; Mann Whitney U test, $P = 0.0859$). The lack of cytological observations of megasporogenesis complicates comparisons of gametes and sporophytes. If chromosome separations during megasporogenesis are more balanced than those during microsporogenesis, little selection may be operating on gamete and sporophyte cytotypes in polyploids. Cytologists generally assume that chromosome behavior during micro- and megasporogenesis of polyploids is similar, although some studies of aneuploid chromosome transmission rates (see Riley & Kimber 1961) and analyses of reciprocal crosses involving triploids (Ramsey & Schemske 1998) suggest that there is stronger selection for euploid pollen than ovule cytotypes. Assuming that frequencies of pollen and ovule cytotypes are approximately equal, the observed frequency of euploid sporophytes (mean 62.6%) is significantly different than expected (43.6%) (One-Sample Sign test, $P < 0.0001$).

There is less selection to remove aneuploids from the progeny of even-ploidy cytotypes than from the progeny of odd-ploidy cytotypes. For example, cytotype distributions of the gametes and progeny of triploids are nearly inverted (Ramsey & Schemske 1998, Figures 1, 2, 3), whereas the distributions for even-ploidy cytotypes differ significantly, but are similar in overall shape. There are several explanations for the difference in selection. First, the gametes of triploids have a wider distribution of aneuploid types compared to the gametes of tetraploids, hexaploids, and octoploids. Selection may act strongly on more numerically deviating aneuploid cytotypes, skewing the distribution of sporophyte cytotypes away from that of the gamete cytotypes. Second, the gametes and progeny of triploids on average have a lower total chromosome number compared to the gametes and progeny of tetraploids, hexaploids, and octoploids.

In general, studies indicate that aneuploid cytotypes occur more often, exhibit less deviant phenotypes, and have higher reproductive fitness in polyploid than diploid populations (Khush 1973). For example, the mean occurrence of aneuploids

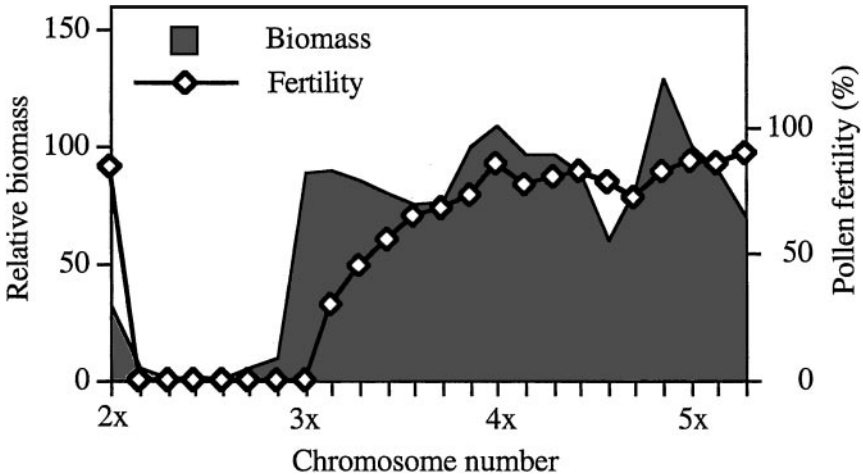

Figure 5 Biomass and fertility of euploid and aneuploid cytotypes of *Dactylis glomerata*, generated by crosses between diploid, triploid, tetraploid and pentaploid cytotypes. Data from Müntzing (1937).

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in surveyed diploid systems is 1% (see Web Table 5), thirtyfold less than the mean occurrence in polyploid systems (37.4%). The difference is attributable not only to the complex meiosis of polyploids, but also to the low viability of aneuploids at the diploid level. In diploids, aneuploids are readily identifiable by their aberrant phenotypes and sterility (Avery et al. 1959, Ellis & Janick 1960, Khush & Rick 1966). For example, many of the *Oenothera* "species" and "mutants" described by Hugo de Vries were trisomics (Emerson 1935). Aneuploid-polyploids often appear somewhat distinctive, but as a rule survive and compete successfully with euploids (Kostoff 1938; O'Mara 1943; Clausen et al. 1945; Einset 1947; Bernstrom 1954; Rommel 1961; Bingham 1968; Ahloowalia 1971; McNaughton 1973; Simonsen 1973, 1975). Müntzing (1937) generated sporophytes with all chromosome numbers between $2n = 2x = 14$ and $2n = 5x = 35$ by crossing $2x$, $3x$, $4x$, and $5x$ cytotypes of established *Dactylis glomerata* (Figure 5). Biomass of aneuploid sporophytes was greatly reduced for $2n = 14$ to 21, but for higher chromosome numbers there was little difference between euploids and aneuploids. Pollen fertility of aneuploid cytotypes showed a similar pattern, but high fertility was regained at $2n = 4x = 28$ rather than $2n = 3x = 21$ (Figure 5). Similar, though less comprehensive, results are reported in neopolyploid *Beta*, *Lactuca*, *Lamium*, *Medicago*, *Nicotiana*, and *Raphanus-Brassica*. As concluded by Clausen et al. (1945) from studies of the spontaneous allohexaploid *Madia sativa* × *citriodora*, the balance of chromosomes and genes in polyploids is relatively flexible, "permitting survival of plants that deviate slightly from the hexaploid level."

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To evaluate the dynamics of aneuploid formation in polyploid populations one must consider the formation of aneuploids both by euploids and by existing aneuploids. A survey of chromosome transmission rates suggests that aneuploid-polyploids tend to generate progeny with cytotypes somewhat closer to the euploid chromosome number than the parent's cytotype (Web Table 6). For example, in a survey of 26 aneuploid cytotypes in 7 species, 19 of the aneuploids generated progeny with a modal chromosome number one or several steps closer to euploid than the parent's chromosome number (Web Table 6). In spite of the tendency to revert to euploid chromosome numbers, aneuploids still generate large numbers of new aneuploids. In neopolyploid *Coix lacryma-jobi*, 70%–80% of the selfed progeny of $2n = 4x - 1$ and $2n = 4x + 1$ plants are euploid (Rao 1976). Euploids are the modal progeny of selfed aneuploid cytotypes ($2n = 4x - 2$ to $2n = 4x + 6$) in neotetraploid *Lamium amplexicaule*, representing on average 39% of offspring (Bernstrom 1954). An exception to this reversion-to-euploid trend relates to those plants that become di-, tetra- or hexasomic for specific homologues or homeologues via aneuploidy and/or chromosome substitution (Riley & Kimber 1961). Such plants are chromosomally balanced and will replicate themselves via selfing.

The frequency of aneuploidy in the gametes and sporophytes of neopolyploids (Figure 4*a*,*b*) and aneuploid-polyploids (Web Table 6) suggests that a component of polyploid populations are "continuously moving through aneuploid conditions" (Riley & Kimber 1961). A schematic of this process is illustrated for maize (Figure 6) (Randolph 1935, Shaver 1962). Newly formed autotetraploid *Zea perennis* is characterized by frequent (41.2%) multivalent associations at metaphase I. Subsequent anaphase divisions are often unequal, and 45% of maturing pollen grains are aneuploid, mostly $2x - 1$ and $2x + 1$ (Figure 6*a*). Progeny of $4x \times 4x$ crosses are only 50% euploid (Figure 6*b*), suggesting that aneuploid gametes function and generate viable aneuploid offspring. The aneuploid progeny of euploid crosses are semifertile, with ovules showing more inviability than pollen (Figure 6*c*). This difference in male and female fertility, which is typical of most polyploid systems (see below), is probably an artifact of measuring pollen fertility early in development (e.g., stainability at anthesis) but ovule fertility late (e.g., percent of ovules producing viable seed). Euploids constitute a large fraction of the progeny of aneuploids (Figure 6*d*, *f*), though a somewhat wider range of aneuploid cytotypes is also recovered. A numerical simulation of this system, including ovule fertility and progeny cytotype parameters and assuming self-fertilization, suggests that an entirely euploid population rapidly accrues aneuploid cytotypes until reaching an equilibrium value of 46% euploid cytotypes in 8–10 generations (data not shown).

The occurrence of aneuploidy in neopolyploid populations has several implications. First, aneuploids represent a form of genetic load (Doyle 1986). Although most polyploids accommodate the loss or gain of individual chromosomes, aneuploid crosses will generate increasingly deviant cytotypes as well as multiple deficiencies for a single chromosome. Second, considerable phenotypic variability can be introduced into a neopolyploid accession via aneuploidy (Kostoff

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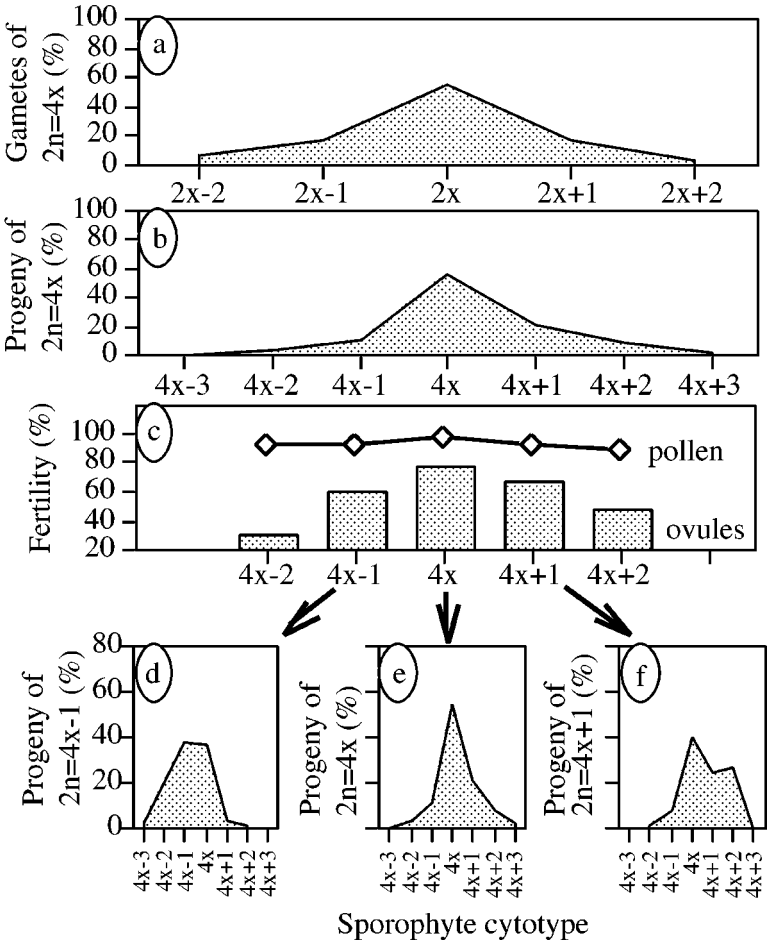

Figure 6 Production and maintenance of aneuploid variation in neoautotetraploid *Zea perennis*. (*a*) Distribution of pollen cytotypes produced by $2n = 4x$ individuals, based on chromosome counts in maturing pollen grains. (*b*) Chromosome numbers of progeny generated by euploid $4x \times 4x$ crosses. (*c*) Pollen and ovule fertility of euploid and commonly occurring aneuploid cytotypes. (*d,e,f*) Chromosome numbers of progeny of euploid and aneuploid individuals, generated by $4x \times 4x$, $4x-1 \times 4x-1$, and $4x + 1 \times 4x + 1$ crosses. Data from Randolph (1935) and Shaver (1962).

1938, Clausen et al. 1945), because of the chromosomal heterogeneity of individual aneuploid cytotypes. For an autotetraploid with $x = 7$, there will be 7 types of the hypereuploid $2n = 4x + 1$, and 28 types of $2n = 4x + 2$. In allopolyploids, the loss or gain of homeologs provides an additional mechanism of phenotypic alteration. Advantageous chromosome combinations in both auto- and alloploids can

be stabilized by hexasomy and disomy. For example, in an autotetraploid, the loss of two copies of a certain chromosome would lead to stable chromosome transmission of the two remaining homologues. Resulting progeny would be disomic for loci on the affected chromosome.

Chromosome Substitution

In polyploids, some gametes with the euploid chromosome number are generated by unequal but numerically compensating divisions during meiosis, which in turn generates chromosomally unbalanced sporophytes. For example, in a tetraploid species, the four homologues (or homeologues) of a chromosome may split 3–1 during anaphase I in a micro- or megaspore mother cell, whereas the homologues (homeologues) of another chromosome may split 1–3 (i.e., double-opposed nondisjunction). If other chromosomes separate equally, the resulting gametes (s), while all $n = 2x$, will be monosomic for one chromosome and trisomic for another.

"Pseudoeuploid" sporophytes are often reported in the progeny of polyploids, but estimating their frequency is problematic because of the difficulty of morphologically distinguishing chromosomes. Simonsen (1973) was able to determine exact chromosome constitutions in one half of 62 "euploid" progeny of neotetraploid *Lolium perenne*, and identified 2 (6.5%) pseudoeuploids. Seven percent of the aneuploid and euploid progeny of neotetraploid *Cyrtanthus parviflorus* × *mackenii* were similarly numerically-compensating (Ising 1966). A general estimate of pseudoeuploid frequencies can be made under the assumptions that (*a*) most pseudoeuploids arise via double nondisjunction (quadruple and sextuple nondisjunctions are rare; see Web Table 4); and (*b*) chromosome nondisjunctions are randomly oriented (Belling & Blakeslee 1924, Beasley 1942). In this scenario, gametes with $n = 2x \pm 2$ (or $n = 3x \pm 2$, $n = 4x \pm 2$, etc.) should occur at the same frequency as unbalanced $N = 2x$ gametes. The mean frequency of $n = 2x - 2$ and $n = 2x + 2$ gametes in our survey is 3.1% (range 0 to 10, $N = 27$; see Web Table 4), suggesting an average occurrence of pseudoeuploids in polyploid sporophytes similar to those reported in *Lolium* and *Cyrtanthus* ($2 \times 3.1 = 6.2\%$). The actual mean frequency may be somewhat higher because pseudoaneuploids may be formed by other means (e.g., quadruple opposed nondisjunction) or, alternatively, lower, because selection favors balanced euploid gametes and sporophytes. In the latter case, chromosome substitution contributes to the reduced fertility of polyploids (see below).

Chromosome substitution in allopolyploids can occur via nonhomologous/nonhomeologous substitution, as well as through homeologous substitution, i.e., replacing a chromosome from one progenitor diploid species with a homeologue from another progenitor. Homeologue substitution can occur via compensating but unequal divisions of univalents and multivalents, but also via bivalent pairing of homeologues. Poole (1932) screened the progeny of a spontaneous *Crepis rubra* × *foetida* for homeologous substitution of a single chromosome that was differentiated by a morphological marker. Thirty-nine percent of the "euploid"

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(4*x*) progeny were unbalanced for these homeologs. If rates of chromosome substitution are comparable across the genome, only 5.8% of the progeny of this allotetraploid would be numerically and genically balanced.

FERTILITY OF NEOPOLYPLOIDS

Reduced fertility is commonly thought to constrain the demographic success of newly formed polyploids, especially autopolyploids (Stebbins 1950, 1971; Darlington 1963; Sybenga 1969; Briggs & Walters 1997). For example, Stebbins (1950) refers to a sterility "bottleneck" in the demographic establishment of polyploids, and Darlington (1963) muses that "in light of the reduced fertility of autotetraploids it is surprising that autotetraploid races and species are by no means uncommon in nature." To assess the fertility of neopolyploids and its evolutionary significance, we surveyed the literature for information regarding the pollen and seed fertility of newly formed autopolyploids and allopolyploids, and of progenitor diploid species and interspecific hybrids (see Web Table 7). In all studies, pollen fertility is expressed as percent pollen viability, measured by standard assays like stainability in aniline blue or acetocarmine. In contrast, measures of seed fertility varied considerably between studies, and included such indices as number of seeds per fruit, number of seeds per inflorescence, seed mass, and proportion of ovules producing seeds (see Web Table 7). To produce a relative index of seed fertility, we include two types of data. First, for studies that measure seed production of neopolyploids and progenitor diploids, we report percent fertility (ratio of neopolyploid to progenitor fertilities). Second, where only neopolyploids are measured, we include an inherently relative measure of fertility such as the proportion of ovules or florets producing viable seeds, when it is implicit that diploid parentals would be fully fertile.

The fertilities of surveyed auto- and allopolyploids varied enormously, ranging from zero to nearly 100% (Figure 7). The mean pollen viability of new auto- and allopolyploids was not significantly different (mean 70.9 versus 72.2%, $N = 176$, Mann Whitney U test, $P = 0.5524$) (Figure 7). Similarly, mean seed fertilities did not differ significantly between polyploid types (mean 39.4 versus 46.6%, $N = 113$, Mann Whitney U test, $P = 0.1929$) (Figure 7). Overall, there are no clear differences in fertilities of newly formed auto- and allopolyploids.

In polyploids, measurements of percent pollen fertility are often much higher than percent seed fertility (see Web Table 7; Figure 7) (Eskilsson 1963). Several factors probably contribute to this trend. First, measures of pollen fertility are made early during development (e.g., stainability at anthesis), whereas seed fertility is measured late (e.g., production of viable seeds). Studies have found that pollen viability is substantially higher than pollen germinability, suggesting that early measures of pollen viability tend to overestimate pollen fertility (e.g., Tanaka 1940). Second, the reduced pollen fertilities of neopolyploids may lead to pollen limitation, because there is not enough functional pollen to fertilize all fertile ovules. Finally, reduced seed fertility may reflect differences in development and

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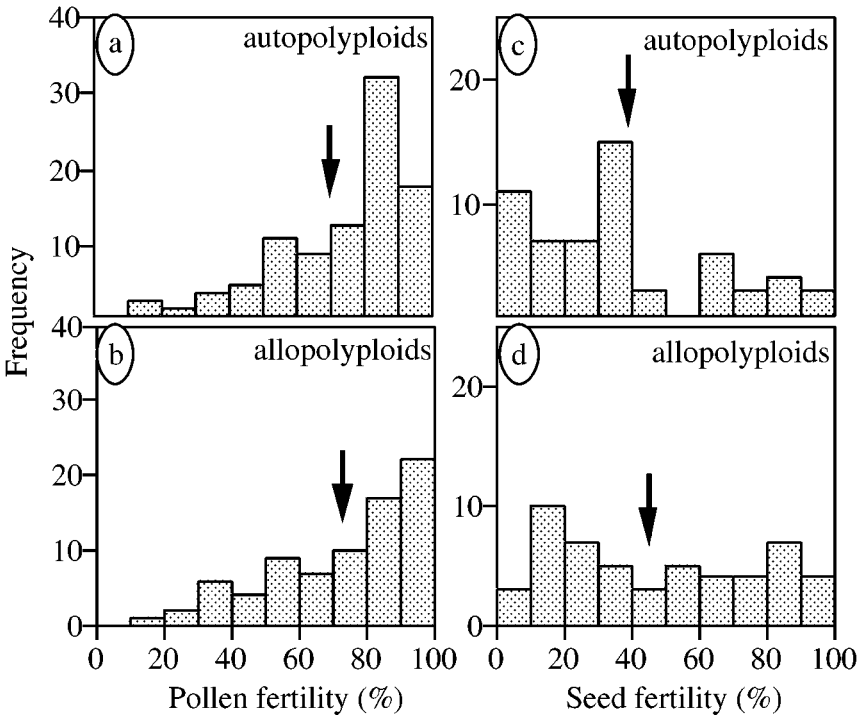

Figure 7 Distributions of percent pollen (*a, b*) and seed (*c, d*) fertility of newly formed autopolyploids and allopolyploids. Arrows show mean values. Data from Web Table 7.

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allocation of neopolyploids. For example, neopolyploids often have larger floral organs made up of fewer constituent parts, and commonly generate fewer, but bigger, seeds (e.g., Howard 1939, Bretagnolle & Lumaret 1995).

Pollen and seed fertilities of neopolyploids are significantly reduced compared to progenitor diploid parentals (pollen mean 71.5 versus 91.4%, N = 94, Wilcoxon Signed Rank test, $P < 0.0001$; seed index mean 27.0 versus 68.1, N = 69, Wilcoxon Signed Rank test, $P < 0.0001$). Pollen fertility of new allopolyploids is significantly greater than their progenitor diploid interspecific F1 hybrids (pollen mean 70.5 versus 16.8, N = 34, Wilcoxon Signed Rank test, $P < 0.0001$). There are too few measures of F1 seed fertilities to allow statistical comparisons.

The results of this survey both support and challenge conventional wisdom regarding the fertility of polyploids. First, it is often assumed that autopolyploids have much lower fertility than allopolyploids, primarily due to the higher expected frequency of univalents and multivalents in autopolyploids (Stebbins 1950, 1971; Briggs & Walters 1997). Our analyses suggest that fertilities of early generation autopolyploids and allopolyploids are enormously variable and not significantly

different. Reduced fertility appears to be a general characteristic of polyploids irrespective of origin, a conclusion also reached by Gottschalk (1978). Second, the reduced fertility of neopolyploids is commonly regarded as a major constraint on polyploid establishment and persistence (Stebbins 1950, Darlington 1963). These analyses do suggest a large reduction in neopolyploid fertility relative to progenitor diploids, with an average 20% reduction of pollen fertility, and a twofold difference in seed fertility. However, the reduction in some systems is modest (see Web Table 7), and even strong reductions could be compensated by increased survivorship and growth. Additional empirical and theoretical studies are needed to evaluate the impact of neopolyploid fertility on demographic establishment.

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The Fertility of Polyploids Can Evolve

The meiotic behavior of plants is known to be under genic control and influenced by chromosome structure (Sybenga 1975, Jackson 1976). To determine if the fertility of polyploids may be improved by natural selection, we reviewed the literature on fertility in neopolyploid populations. Most studies were conducted in agricultural settings, where induced autotetraploids were evaluated for agronomic potential, though the fertility of natural allopolyploid lines has also been studied (see Web Table 8). Populations were selected for 2 to 19 generations, in all cases for seed fertility.

Of 12 studies that quantified pre- and postselection fertility, 11 reported increases. Fertility improvements were generally large, both in terms of rate of increase per generation and in total gains (see Web Table 8). For example, seed fertility of neopolyploid *Brassica campestris* increased from 1.5 to 16.8 over nineteen generations of selection, an average increase of 53.7% per generation (Swaminathan & Sulbha 1959). In four generations of selection, tetraploid *Nicotiana glauca* × *langsdorfii* increased pollen fertility from 59% to 99% (17.1% increase per generation), and seed fertility from 48 to 150 seeds per fruit (53.1% per generation) (Kostoff 1938). Overall, mean increases per generation in our survey were 14.0% for pollen viability (range −0.1 to 36.0%), and 39.7% for seed fertility (range −0.8 to 104.1%) (see Web Table 8). These results suggest that the infertility of polyploids may be a transient phenomenon.

With clear evidence that the fertility of neopolyploids can be increased rapidly by natural selection, we next ask if polyploidy sets an upper limit to fertility. To evaluate this question we surveyed the pollen viability of established, naturally occurring even-ploidy cytotypes and their diploid relatives (see Web Table 9). We sampled taxonomic species consisting of multiple cytotypes, as well as related congeners that differ in ploidy. Average fertilities of diploid, tetraploid, and hexaploid cytotypes were similar (diploid mean 89.1%, N = 33, range 64.9 to 100; tetraploid mean 86.4, N = 34, range 65.7 to 99.8; hexaploid mean 89.9%, N = 17, range 46.0 to 99.0) (see Web Table 9). To evaluate these data statistically, we computed mean values for each cytotype in genera where two or more ploidy levels were sampled. Comparisons of low versus high ploidy values are significantly different (mean

89.2 versus 83.5%; N = 14, Wilcoxon Signed Rank test, $P = 0.0238$). These results suggest that the fertility of polyploids ultimately reaches a level slightly lower than that of their progenitors.

CAUSES OF INFERTILITY IN POLYPLOIDS

Explanations of polyploid infertility are complex and fraught with controversy (Müntzing 1936; Howard 1938; Myers & Hill 1940; Randolph 1941; Sparrow et al. 1942; Stebbins 1950; Doggett 1964; Sybenga 1969, 1973a; Gottschalk 1978). Neopolyploids have simultaneous alterations of chromosome number, gene dosage, allele number, DNA content, cell size, growth and development, so it is difficult to distinguish contributions of each potential factor. Broadly, three causes of sterility have been identified. First, fertility may be reduced by meiotic abnormalities. In particular, univalent, multivalent, and homeologous bivalent pairings can lead to the production of inviable aneuploid gametes and sporophytes. Second, fertility may be reduced by genetic causes that are independent of obvious meiotic aberrations. The nature of these so-called genotypic effects are obscure, but a number of studies point to their importance. Finally, infertility may be related to incidental phenotypic effects of polyploidy. For example, the increased gene dosage, DNA content or cell size of polyploids may affect the development, growth, or physiology of sporophytes or gametophytes in such a way as to reduce the number or viability of gametes produced. Here we review each of the proposed mechanisms.

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Meiotic Aberrations

Meiotic aberrations probably represent the most general factor affecting polyploid fertility. As described previously, polyploids exhibit frequent univalents, trivalents, and quadrivalents during metaphase (Figure 2) that lead to the production of chromosomally and genically unbalanced gametes (Figure 4*a*). Homeologue bivalent pairing in allopolyploids probably generates aneuploid gametes as well. The frequency distribution of sporophyte cytotypes contains significantly more euploids than would be expected on the basis of gamete cytotypes (Figure 4*b*). Moreover, aneuploid sporophytes are typically less fertile than euploid sporophytes (Figures 5, 6). Together, these observations indicate that the production of unbalanced gametes leads to aborted ovules, inviable seeds, and semisterile adults. Strain differences in the fertility of polyploid crops have been correlated with occurrences of aneuploidy (Aastveit 1968, Weimarck 1973). Moreover, established polyploid crops generate substantially fewer aneuploid progeny than neopolyploid cultivars (Riley & Kimber 1961, Bingham 1968, see Web Table 5).

In allopolyploids, multivalents and homeologue bivalent pairing will generate unbalanced gametes that are numerically euploid (Howard 1938). In the allotetraploid, $A_1A_1A_2A_2$, homeologue bivalents (A_1A_1) will separate A_1A_1/A_2A_2 one half the time, generating gametes that contain only one homeologue. Also, A_1A_2/A_1A_2

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separations will sometimes contain recombined segments, which in turn generate unbalanced gametes. First generation allopolyploids derived from unreduced gametes may inherit unbalanced, recombined genomes from homeologous bivalent pairing in the progenitor F1 hybrid (Howard 1938). In a diploid F1, one half of the unreduced gametes produced by homeologous pairing and subsequent formation of a restitution nucleus will be unbalanced for chromosomal segments. Only one quarter of the neopolyploids generated by the unreduced gametes would be a balanced euploid. Hence, infertility caused by homeologous pairing would result both from the production of unbalanced, inviable gametes by balanced sporophytes, and the presence of semisterile unbalanced sporophytes in populations. Some early-generation allopolyploids exhibit surprising variability in fertility that is consistent with a homeologue pairing model of polyploid infertility (Clausen et al. 1945, Stebbins 1949, Gajewski 1953, Stebbins & Vaarama 1954).

Cytological observations of fertility-selected neopolyploid populations generally suggest that improvements to seed set occur concomitant to changes in meiotic pairing behavior. In 10 of the 12 surveyed studies examining meiotic behavior of pre- and postselected plants, an increase in bivalent and a decrease in quadrivalent pairing was documented (see Web Table 8). For example, the mean frequency of bivalents in *Pennisetum typhoides* increased from 5.8 to 10.2 per pollen mother cell during six generations of fertility selection (Jauhar 1970). Overall, the percent increase of bivalent configurations in our survey averaged 4.1% per generation (range 1.6 to 12.6%) in those studies observing increased bivalent pairing (see Web Table 8). These data demonstrate that increased fertility of auto- and allopolyploids is often accomplished by increased bivalent associations.

Other results suggest that increases of quadrivalent pairing may, in some autopolyploids, also improve fertility. In autotetraploid *Lolium perenne*, six generations of fertility selection led to a 30% increase in the frequency of quadrivalent configurations (Crowley & Rees 1968). Hazarika & Rees (1967) induced autotetraploids in inbred lines of *Secale cereale*. Polyploid seed fertility varied substantially among lines and was positively correlated with the occurrence of chiasmata and quadrivalents. The differential effects of quadrivalents on seed and pollen fertility (see Web Table 1) probably reflect variation in quadrivalent orientations. As described earlier, alternate (zigzag) orientations are thought to split evenly, whereas adjacent orientations often have unbalanced separations. Autopolyploids with primarily alternate orientations of quadrivalents may increase quadrivalent frequencies in response to fertility selection, perhaps by increasing the frequency of chiasma (Sybenga 1969, 1975).

Correlation analyses of meiotic configurations versus pollen fertility from surveyed neopolyploids (see Web Tables 1, 7) implicate univalent and trivalent configurations as substantial contributors to reduced fertility. The sum occurrence of odd-numbered configurations is termed the chromosome disjunction index (Hazarika & Rees 1967). In our dataset, the disjunction index of neopolyploids is negatively correlated with pollen fertility (Spearman Rank Correlation, $N = 115$, $r_s = -0.470$, $P < 0.0001$). In contrast, quadrivalent configurations are uncorrelated with pollen

viability ($r_s = -0.073$, $P = 0.4296$), and bivalent pairing only weakly correlated ($r_s = +0.346$, $P = 0.0002$). Due to variability in the quadrivalent orientation among taxa (McCollum 1958), quadrivalents may be negatively correlated with fertility in some systems, but not in others. In contrast, univalent and trivalent configurations always lead to the formation of aneuploid or pseudoeuploid gametes. Although the correlation between the disjunction index and pollen fertility is highly significant, the magnitude of the correlation is less than 1.0. There are several possible explanations. First, the true fertility of polyploids is typically lower than measures of pollen viability indicate (Tanaka 1940, Eskilsson 1963), so the actual correlation between fertility and meiotic configurations may be greater than what is reported here. Second, fertility may be influenced by subtle meiotic features, such as orientation, which are not commonly reported. Finally, as outlined below, polyploid fertility may be affected by factors besides meiotic aberrations.

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Genic Factors

Meiotic aberrations play a clear role in neopolyploid fertility. There is, however, evidence that genic factors with no obvious meiotic effects may also influence fertility. For example, neopolyploid fertility varies substantially between lines and varieties within some species (see Web Table 7). Doggett (1964) induced polyploids in nine varieties of *Sorghum*, and found that percent seed set ranged from 40% to 77%; varietal differences were statistically significant, and highly heritable. Also, substantial increases in seed set of autopolyploids have been obtained by crosses between induced or spontaneous polyploids derived from different lines, strains, and varieties (Randolph 1941; Müntzing 1948b, 1951; Bingham 1980). For example, Doggett (1964) induced autotetraploids in two lines of *Sorghum* and found each had 31% seed set. F1 crosses averaged 68% fertility, and the F2 averaged 74%. In *Antirrhinum majus*, tetraploids induced in intervarietal hybrids averaged 86% pollen fertility, while intravarietal tetraploids averaged 55.3% (Sparrow et al. 1942). Autotetraploids derived from inbred lines of maize set few seeds, while outcrossed plants and interline hybrids exhibit high seed set (Randolph 1941). In *Sorghum*, *Antirrhinum*, and *Zea*, the increased fertilities of hybrids were not associated with obvious changes in chromosome pairing. For example, the mean frequency of multivalents in sterile and fertile lines of autotetraploid maize is fairly constant, between 7.5 and 8 (Randolph 1941), whereas fertility-selected lines exhibited equivalent meiotic pairings to controls (Mastenbroek et al. 1982). The nature of so-called genic fertility effects are obscure, but may relate to the effects of allelic heterozygosity on overall plant fitness (see below).

In some allopolyploids, genic sterility factors impede the development of pollen, ovules, embryos or endosperm but not meiosis per se. In these cases, polyploids of hybrid origin may be partially or completely sterile, but exhibit few or no meiotic abnormalities. Allotetraploid *Nicotiana sylvestris* × *tomentosa* and *N. sylvestris* × *tomentosiformis* exhibited bivalent pairing and >90% pollen viability, but was

completely female sterile due to abortion of developing embryos 1–3 days after pollination (Greenleaf 1941). Backcrosses to the related tetraploid *N. tabacum* (tobacco) generated semi-fertile progeny, while F2 progeny of *N. tobacco* × *N. sylvestris-tomentosiformis* included a few fully sterile individuals. The sterility of the primary allotetraploids were hypothesized to result from complementary sterility genes, possibly few in number, which in certain allelic combinations inhibited ovule development (Greenleaf 1941). Genic and chromosomal sterility is well described in hybrids of diploid species. Allopolyploids generated by semisterile diploid hybrids are generally much more fertile than their progenitors (Web Table 7). Much hybrid sterility in plants may thus be hypothesized to result from unpaired or mispaired homeologous chromosomes and subsequent production of unbalanced gametes (Stebbins 1950), a difficulty corrected in polyploids via the duplication of all chromosomes. However, the fertility discrepancy between parental diploids and new allopolyploids (see Web Table 7; Figure 7) may in part reflect genic incompatibilities that are independent of meiosis. Because the gametes of polyploids are (at least) diploid, incompatibilities may involve both intra- and interlocus interactions. Further research is needed to investigate the impacts of genic incompatibilities on both the viability and fertility of hybrid polyploids.

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Incidental Phenotypic Effects

In some cases, the infertility of polyploids is attributable to specific changes in the development, growth, or physiology of sporophytes or gametophytes. In the trivial case, polyploids may have altered patterns of allocation that reduce fecundity, which is subsequently misinterpreted as reduced fertility. For example, polyploids often have fewer (but bigger) flowers, fewer (but bigger) pollen and ovules, fewer (but bigger) seeds, and delayed flowering (Müntzing 1951, Jaranowski & Kalasa 1971, Roy & Dutt 1972, see below). Also, when grown in competition with more numerous progenitor diploid cytotypes, polyploids may appear semisterile due to triploid block (Randolph 1935, Olsson 1948, Hagberg & Ellerström 1959). Munzting (1951) found that induced tetraploid *Secale cereale* exhibited uniformly low seed unless grown in isolation plots away from diploid progenitors. Reduced fecundity of neopolyploids is probably often attributed to physiological infertility, though clear developmental sterility has been identified in some systems. In induced autotetraploid *Lactuca sativa*, ∼20% of developing ovules abort during megasporogenesis (Einset 1944). Moreover, most pollen grains fail to germinate, or burst while growing through the style.

Population Genetics of Fertility Improvement

Fertility selection on neopolyploid populations rapidly increases pollen viability and seed set, often with corresponding increases in bivalent (or quadrivalent) pairing (see Web Table 8). It is difficult to imagine how a small population of polyploids could possess sufficient genetic variation to produce such rapid

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evolutionary change. Several mechanisms have been discussed, mostly focused on meiotic aberrations (Kostoff 1938; Howard 1938; Hazarika & Rees 1967; Sybenga 1969, 1973a). For autopolyploids, perhaps the simplest explanation involves allele substitutions at loci influencing the frequency and distribution of chiasma. Chromosome synapsis appears to be a polygenic trait (Sybenga 1975, Singh 1993). For example, numerous mutations are known to affect chiasma frequency or distribution in diploid rye, and polygenic inheritance of chiasmata has been shown in crosses of inbred lines (Prakken 1943; Rees 1955, 1961; Koduru & Rao 1981). Bivalent pairing in diploids is somewhat robust to chiasma formation, so chiasma factors may be neutral or under balancing selection and hence segregating in diploid populations. In neopolyploid populations, such alleles may quickly reach fixation due to strong effects on the type and orientation of configurations during meiotic metaphase. For example, increases in occurrences of chiasma in neopolyploids would limit unpaired chromosomes and laggards, commonly associated with polyploid sterility (Web Tables 1, 7, 8). Localization of chiasmata to specific chromosome regions may limit multivalent associations and cause a breakdown of prophase multivalents into metaphase bivalents (Levan 1940, Shaver 1962). Chiasma frequency and distribution also probably affect orientation, for example alternate versus adjacent configurations (Sybenga 1975). Hazarika & Rees (1967) identified variation for the occurrence of chiasma in inbred lines of diploid rye. The frequency of chiasma in induced autotetraploids was correlated with the frequencies in progenitor diploids, and also with the occurrence of quadrivalent configurations and seed fertility.

Genetic control of the frequency and distribution of chiasma may also underlie fertility improvement in new allopolyploids. Alternatively, genic factors could enforce homologous pairing by either altering the premeiotic alignment of chromosomes such that pairing of homeologous chromosomes does not occur, or increasing the stringency of crossover such that recombination only occurs between homologous chromosomes (Luo et al. 1996, Vega & Feldman 1998). Genic control of homologue pairing is known from several established allopolyploid crop species (e.g., Riley & Chapman 1958, Jauhar 1975, Evans & Aung 1985). In allohexaploid wheat, bivalent pairing is controlled in large part by a single gene, *Ph1*, located on chromosome 5B (Sears 1976). The origins of genic factors which influence meiotic pairing in allopolyploid crops and their role in the initial establishment and domestication of cultivars are generally unknown. Recent research in *Triticum* suggests that allelic variation in *Ph1* may exist in wild polyploid species, including wild tetraploid relatives of cultivated bread wheat (Hakan & Feldman 2001, Martinez et al. 2001). Thus hexaploid wheat may have inherited one or more homeologue pairing suppressor alleles directly from their polyploid progenitors at the time of formation, rather than evolving de novo genic control of homologous pairing in the face of strong fertility selection. This scenario may be common for hexaploids, octoploids and other higher-ploidy cytotypes that are derived from long-established polyploids, but presumably cannot explain rapid evolution of meiotic behavior in neopolyploids derived from diploids.

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Changes in chromosome structure could also alter chiasma formation among homologous or homeologous chromosomes in neopolyploids, leading to preferential pairing and "diploidization" (Sybenga 1969, Feldman et al. 1997). Introduction of a reciprocal inversion in autotetraploid maize significantly reduced quadrivalent pairing and segregation of recessive alleles (Doyle 1963), but reciprocal translocations had no effect in autotetraploid rye (Sybenga 1973b). Somewhat increased bivalent pairing of newly formed autopolyploids has sometimes been achieved by inducing chromosomal rearrangements with radiation and mutagens (Srinivasachar & Singh 1967, Gottschalk 1978). Beneficial chromosomal rearrangements are most likely to evolve in selfing species, because identical rearrangements would rarely come together as pairs in an outcrossing population. The accumulation of chromosomal differences probably contributes in part to the evolution of meiotic regularity in selfing autopolyploids (Sybenga 1969), but in isolation are probably inadequate to explain rapid transitions of pairing behavior and fertility. In contrast, chromosomal rearrangements can have a strong effect on chromosome pairing in allopolyploids (Shaver 1963, Sybenga 1973a). For example, inversions greatly reduced allosyndesis in allotetraploid *Zea mays* × *Euchlaena* perennis, but caused only slight preferential pairing in autotetraploid maize. Elimination of DNA sequences may similarly differentiate homeologous chromosomes and thus enforce homologous pairing in allopolyploids (Feldman et al. 1997, Liu et al. 1998a). Hence, the evolution of chromosome structure may strongly limit pairing of homeologues that already differ in the number and position of chiasma initiation points, or the timing of chromosomal processes (e.g., long distance attraction and condensation) (Sybenga 1969).

DEFINITIONS OF AUTO- AND ALLOPOLYPLOIDY

Definitions of auto- and allopolyploidy either emphasize mode of origin (hereafter, MO) or cytological criteria (hereafter, CC) as primary criteria. MO autopolyploids arise within single populations or between ecotypes of a single species, whereas allopolyploids are derived from interspecific hybrids (Müntzing 1936, Darlington 1937, Burnham 1962, Gottschalk 1978). This is the definition used in this chapter. CC allopolyploids are expected to display bivalent pairing, lack of allosyndesis and disomic inheritance, while CC autopolyploids will exhibit multivalent configurations, nonpreferential pairing at metaphase, and multisomic inheritance (Stebbins 1980, Jackson 1982, Jackson & Jackson 1996).

Our review of newly formed auto- and allopolyploids indicates that cytological behavior at the time of origin is more similar than might be expected. For example, 80% of newly formed MO allopolyploids displayed multivalent pairing (Figure 2; see Web Table 1) and are expected to undergo some degree of homeologous pairing. Intergenomic segregation in the progeny of MO allopolyploids was postulated to occur in approximately two thirds of surveyed studies (see Web Table 3). Hence, strict CC allopolyploid definitions would exclude many known

MO neopolyploids, including the famous "*Primula kewensis*" (Upcott 1940), "*Galeopsis tetrahit*" (Müntzing 1932), and possibly "*Raphanobrassica*" (Richharia 1937, Howard 1938). For their part, early generation MO autopolyploids correspond to most definitions of CC autopolyploids, because there is no evidence of preferential pairing or disomic inheritance (see Web Tables 1, 2). However, multivalent configurations can be much less common than is sometimes expected (Figure 2). In later generations, accumulation of chromosomal rearrangements, evolution of genic factors controlling meiotic pairings or hybridization may lead to diploidized MO autopolyploids that cytologically behave like CC allopolyploids.

In short, students of polyploidy are faced with a choice: either (*a*) recognize intuitive, mode of origin polyploid categories, but expect heterogeneity in the genetic characteristics of autopolyploids and allopolyploids; or (*b*) recognize categories that rely on posthoc cytological analyses of polyploids, but maintain homogeneity in the characteristics of polyploid types. The terms genomic and segmental allopolyploids were proposed to distinguish MO allopolyploids with strict versus weak preferential pairing of homologues (Stebbins 1947, 1950) but are now also used to distinguish degrees of CC allopolyploidy (Jackson & Jackson 1996). For the purposes of studies of ecology and systematics, we advocate the use of mode-of-origins definitions of polyploidy. Irrespective of cytological characteristics, the biology of polyploids derived from interspecific hybrids is quite different than the biology of intraspecific polyploids. MO allopolyploids are formed by the breakdown of reproductive isolation between species, followed by polyploidization in a meiotically or mitotically unstable, semifertile hybrids (Ramsey & Schemske 1998). In contast, MO autopolyploids form by the production of occasional meiotic or mitotic aberrations in single species populations. Although derivatives of multisomic allopolyploids will be more polymorphic than the progeny of fixed disomic allopolyploids, all allopolyploids retain a degree of hybrid character unlike anything found in an autopolyploid. Conversely, the evolution of preferential pairing in MO autopolyploids via chromosome rearrangements or genic control of pairing would not lead immediately to the hybridity of allopolyploids.

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IS POLYPLOIDY REVERSIBLE?

Conventional wisdom holds that chromosome evolution via polyploidy is a one-directional process: In a given lineage, ploidy level either increases through time, or remains constant. The production of occasional haploid progeny by otherwise polyploid species challenges this assertion (Randolph & Fischer 1939, Raven & Thompson 1964). These so-called polyhaploids halve the chromosome number of their progenitors, but in the case of tetraploids or octoploids will have a balanced diploid or tetraploid chromosome number. Establishment of polyhaploid mutants in a polyploid lineage may lead to the evolution of diploidy (Raven & Thompson 1964).

Here we examine the mechanistic potential of ploidy reversal by reviewing the occurrence, cytological origins and characteristics of polyhaploids in

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established and neopolyploid systems. Out of 55 reviewed studies, 6 (10.9%) reported the occurrence of polyhaploids (see Web Table 10). In comparison, 52 studies (94.5%) reported aneuploids, while 5 studies (9.1%) found higher polyploids (e.g., neohexaploids in the progeny of tetraploids) (see Web Table 10). In the 6 investigations reporting spontaneous polyhaploidy, frequencies of polyhaploids were generally low (see Web Table 11). For example, Randolph & Fischer (1939) found 23 parthenogenetically produced diploids among 17,165 progeny of neotetraploid maize. Higher frequencies of polyhaploids have been observed in several colchicine-induced neopolyploids (Pundir et al. 1983, Singh 1986). In such circumstances, polyhaploids are often suspected to have originated via ploidy chimaerism (a common artifact of colchicine treatment) coupled with selfing. Excluding these cases, polyhaploids were usually attributed to apomixis (see Web Table 11). Apomictic polyhaploidy was observed to occur spontaneously in seven systems, while in three systems it was induced via interspecific pollinations (see Web Table 11). Polyembryony (twinning) is also associated with a high incidence of haploid progeny in plants, probably via reduced parthenogenesis (Webber 1940, Müntzing 1948a, Dewey 1961). However, the overall frequency of polyembryonic seeds in populations is low.

In evaluating the characteristics of polyhaploids, we pooled induced and spontaneous occurrences. In most systems, polyhaploids were found to have reduced viability, pollen viability, and seed fertility. Eight of ten studies described the polyhaploids as having reduced growth, survivorship and/or reproduction. The polyhaploids were often characterized as being small and slender in appearance (e.g., Lesins 1957, Dewey 1961), opposite the gigas characteristics of polyploids. Mean pollen viability was 6.5% ($N = 10$), as compared to 87.9% ($N = 4$) in diploid or polyploid controls. Mean seed fertility of polyhaploids was 9.4% ($N = 8$). Qualitative assessments of fertility generally paralleled these quantitative data (see Web Table 11). In several studies, diploid polyhaploids were selfed or crossed to related diploids and tetraploids. Tetraploids were the most common progeny reported, followed by triploids, diploids, and aneuploids (Müntzing 1948a, Gerstel & Mishanec 1950, Lesins 1957), suggesting polyhaploids are characterized by frequent asynapsis. Several factors may contribute to the overall reduced fitness of polyhaploids. Polyhaploids derived from allopolyploids (or hybridized autopolyploids) will harbor homeologous chromosomes of different progenitor species, and are expected to be somewhat asynaptic and sterile. In the case of autopolyploids, the presence of multiple chromosome sets may allow the maintenance of deleterious alleles and chromosomal deficiencies that are expressed more in polyhaploids than progenitor tetraploids (Müntzing 1948a, Dewey 1961).

This survey suggests that ploidy reduction via polyhaploidy is, on average, an unlikely event. Excluding studies of suspected chimeric colchiploids, we estimate the occurrence of polyhaploids to be 0.19% (6 of 55 studies reporting polyhaploids, times average frequency of 1.8% in those studies finding polyhaploids). Polyhaploids were reported to have low viability and fertility (average 7% fertility of related diploid and polyploids) and do not perpetuate themselves efficiently. The conditions for establishment of neopolyploids are generally regarded as restrictive

(Felber 1991, Rodríguez 1996). Polyhaploid mutations face the same frequency-dependent selection that limits polyploid establishment, and are characterized by lower average viability, fertility and cytological stability (see Web Table 11 versus Web Tables 4, 5, 6, 7). Our survey supports the view of Stebbins (1980) that polyhaploidy is unlikely to contribute to reversions to diploidy in most established polyploid species.

ARE ALLOPOLYPLOIDS "CONSTANT SPECIES HYBRIDS?"

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In an influential paper, Winge (1932) summarized early investigations of experimental allopolyploids, and hypothesized that hybrid polyploids represent constant species hybrids with "the quality of a pure species." This description was intended to contrast with the character of interspecific diploid hybrids, which segregate extensively in F2 and backcross generations due to allosyndesis and subsequent random segregation of homeologs during meiosis. Ecologists and systematists took their cue from Winge's characterization, and naturally occurring established allopolyploids were expected to be fixed heterozygotes that are phenotypically and ecologically intermediate to their related diploid species (e.g., Clausen et al. 1945, Lewis & Lewis 1955). The primary criteria for identifying allopolyploidy include fixed intermediacy of morphology and genetic markers, bivalent configurations during meiotic metaphase, and disomic inheritance (Stebbins 1950, 1971; Soltis & Soltis 1993).

At a broad stroke, Winge's characterization is certainly correct. Because of preferential pairing of duplicate chromosomes, allopolyploids are more stable than diploid hybrids. However, cytogeneticists often concluded that newly formed allopolyploids were considerably less stable than Winge's initial description would indicate (e.g., Poole 1932, Lindstrom & Humphrey 1933, Richharia 1937, Howard 1938, Kostoff 1938, Davis 1943, Gajewski 1953, Grant 1954, Gerstel & Phillips 1958, Phillips 1964, Day 1965). First, neoallopolyploids display occasional to frequent allosyndesis and multivalent pairing during meiosis (Figure 2; see Web Table 1). Second, allopolyploids sometimes have multisomic rather than disomic inheritance (Figure 3; see Web Table 2) and segregate for parental characteristics in subsequent generations (see Web Table 3). Third, allopolyploids generate large numbers of aneuploid gametes and progeny (Figure 4*a*,*b*; see Web Tables 4, 5). Finally, fertility is observed to be low in first-generation allopolyploids (Figure 7; see Web Table 7), but improves over time (see Web Tables 8, 9).

Kostoff (1938) analyzed the origin, meiotic behavior, chromosome balance, fertility and phenotypic characteristics of early-generation allopolyploid *Nicotiana glauca* × *langsdorfii*. The diploid parental species, *N. langsdorfii* ($x = 9$) and *N. glauca* ($x = 12$), are phenotypically differentiated for a number of growth, leaf and floral characters, and can be crossed (with difficulty) to form a highly sterile F1 hybrid. An allopolyploid ($2n = 4x = 42$) F2 had the intermediate morphological character of the diploid F1, but had gigas characters, including larger and coarser leaves, stems and flowers. The F2 was semifertile (51% and 19% pollen

and seed fertilities), exhibited some multivalent and homeologous bivalent pairing, and frequent unequal chromosome separations at anaphase I (see Web Tables 1, 4). With four generations of fertility selection, Kostoff (1938) substantially increased frequencies of bivalents, euploid gametes, euploid sporophytes, pollen and seed fertility (Figure 8*a,b,c,d,e*). Concomitantly, segregation of the morphological differences of the progenitor diploids was found. For example, the mean corolla length of allotetraploid families differed substantially and was more variable than that observed in parental species or F1 hybrids (Figure 8*f,g,h,i,j*). Kostoff

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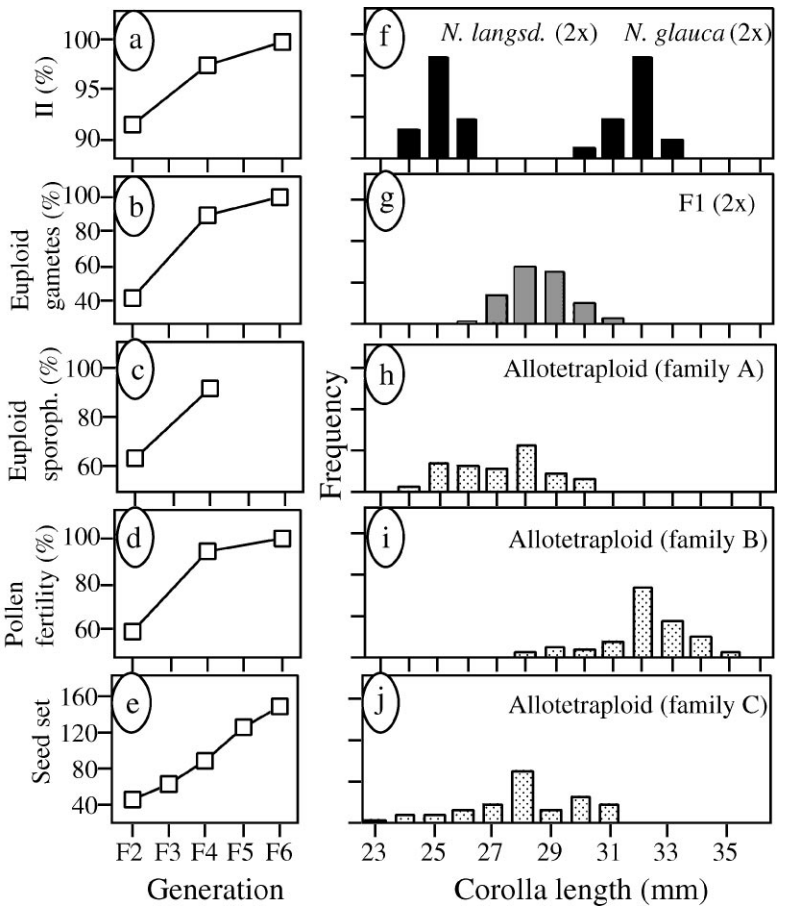

Figure 8 Rapid evolution of meiotic behavior, fertility, and phenotypic traits in neotetraploid *Nicotiana langsdorfii* × *glauca*. Mean percent bivalent pairing (*a*), aneuploid gametes (*b*), aneuploid sporophytes (*c*), pollen and seed fertility (*d*, *e*) of four fertility-selected generations derived by selfing a single spontaneous F2 allopolyploid. Corolla lengths of diploid *N. langsdorfii* and *N. glauca* (*f*), their diploid F1 hybrid (*g*), and three allotetraploid F4 families (*h*, *i*, *j*). Data from Kostoff (1938).

(1938) concluded that the combination of aneuploidy and recombination of genes on homeologous chromosomes of the allotetraploid created phenotypically heterogeneous progenies segregating for parental characteristics. The evolution of preferential pairing decreased the occurrence of aneuploids and homeologous recombination, so that by the F5 generation little intrafamily variation was observed. By the F6 generation there were some plants more or less reconstituting the phenotypes of the parental species, and many varying intermediates (Kostoff 1938).

Allopolyploids may sometimes give rise to polymorphic species consisting of varying amounts of the chromosomes of each parental species (Kostoff 1938; Sybenga 1969, 1996). Kostoff (1938) speculates "it seems that the constancy of the amphidiploids is very questionable . . . the process of meiosis in the majority of the amphidiploids recorded by various authors suggests that they should not be constant, and most of them actually producing inconstant progeny." After similar experiences with allotetraploid *Oenothera*, Davis (1943) concludes "accounts of amphidiploids have frequently assumed that these plants even from hybrids would breed true . . . but as more examples have been investigated it has become evident that irregularities of chromosome distribution at meiosis are common and that the pairing of sister chromosomes may not take place as often as might be expected."

The occurrence of unstable neopolyploids presents a challenge to systematists seeking to evaluate the phylogenetic origins of natural polyploids, and ecologists examining the adaptive significance of ploidy variation in species populations. Many criteria for distinguishing natural auto- and allopolyploids may be reliable for distinguishing only recently derived autopolyploids and genomic allopolyploids (Goodspeed & Bradley 1942, Grant 1975, Sybenga 1996), especially given the possibilities of the extinction of progenitors and interspecific crosses at the polyploid level. Moreover, it may be difficult to evaluate the ecological significance of some established allopolyploids when cytotype differences are created by a combination of polyploidy per se, homeologous recombination and segregation, and genic evolution.

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POLYPLOIDY AND PHENOTYPIC EVOLUTION

Polyploids initially attracted attention because of their unique cytogenetics and their reproductive isolation from diploids (Blakeslee 1921, Jørgensen 1928). It was soon recognized that polyploids also exhibited distinctive phenotypic traits (Müntzing 1936, Randolph 1941). Comprehensive summaries of the characteristics of polyploids have been published previously (e.g., Tal 1980; Levin 1983, 2002; Lumaret 1988), but have not always differentiated between early generation spontaneous or induced polyploids and naturally occurring, established polyploids.

Neopolyploids are commonly differentiated from progenitor diploids by a combination of morphological, reproductive, phenological, life-history, and physiological traits (Table 1). For example, new polyploids commonly exhibit gigas

characteristics, including sturdier foliage, thicker stems, and enlarged reproductive structures that are typically less numerous than in progenitor diploids. In comparison to the progenitor F1 hybrid, spontaneous allotetraploid *Gossypium davidsonii* × *anomalum* exhibit thickened leaves and enlarged flowers and seeds (Brown 1951). Growth and development is often slowed in neopolyploids, leading to a delayed and prolonged flowering phenology. For example, the flowering of induced autotetraploids of several *Medicago* and *Melilotus* spp. was extended weeks or months beyond diploid progenitors, due to a combination of lush growth and reduced fertility (Jaranowski & Kalasa 1971). The life-history of new polyploids is often distinctive. For example, induced autotetraploids of *Agropryon*, *Lamium*, *Pennisetum*, and *Secale* produced substantially fewer tillers than progenitor diploids (Table 1). Water relations, photosynthetic rates, and other physiological traits are known to differ between neopolyploids and progenitors. Induced tetraploid barley exhibited reduced respiration and transpiration rates compared to progenitor diploids (Chen & Tang 1945). Although there are no data on the ecological interactions of neopolyploids, they are likely to differ from those of diploids. For example, delayed phenology may alter associations with pollinators (Segraves & Thompson 1999), whereas changes in secondary chemistry (Kostoff 1938, Sullivan & Myers 1939) could influence plant-herbivore interactions. Most observations of neopolyploids are based in autopolyploid systems. First generation allopolyploids typically exhibit a phenotype intermediate to their diploid parents, though they differ from progenitor interspecific F1 hybrids in a manner similar to the difference between autopolyploids and progenitor diploid parents (e.g., Buxton & Darlington 1931, Davis 1943, Clausen et al. 1945, Gajewski 1953). Later generation allopolyploids may or may not segregate for parental characteristics (see Web Table 3).

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Causes of Phenotypic Alterations

To develop a conceptual framework for evaluating the contributions of polyploidy to phenotypic evolution, we briefly summarize the mechanistic bases of phenotypic alteration.

INCREASED DNA CONTENT Transitions to polyploidy are accompanied by physical alterations in the size and geometry of cells, which in turn may affect biochemistry, development, anatomy, and ultimately whole-plant morphology, growth, and physiology. Many of the gigas traits of neopolyploids, such as increased cell size, enlarged floral structures, sturdier foliage, and robust stems, may be a direct consequence of increased DNA content (Randolph 1941). Also, the characteristic slowed growth, altered phenology, and prolonged flowering of polyploids may, in part, result from slowed mitotic divisions and cell divisions of larger cells with more chromosomes (Noggle 1946, Stebbins 1971). The contributions of DNA content are perhaps the most consistent effects of polyploidy and may characterize both neo- and established polyploids.

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TABLE 1 Common phenotypic characteristics of newly-formed auto- and allopolyploids

Trait type	Characteristic	Genus (reference)
Morphology	Leaves coarser, thicker, larger	*Amaranthus* (Pal & Khoshoo 1977), *Manihot* (Hahn et al. 1990), *Medicago* (Bingham & Binek 1969), *Solanum* (Jørgensen 1928)
Reproductive character	Flowers larger	*Allium* (Levan 1941), *Digitalis* (Buxton & Darlington 1931), *Gossypium* (Beasley 1940; Brown 1951), *Zea mays* (Randolph 1935)
	Seeds larger, but fewer	*Brassica* (Howard 1939), *Dactylis* (Bretagnolle & Lumaret 1995), *Triticum* (Kuspira et al. 1985), *Vicia* (Nordenskiöld 1953)
Phenology	Flowering initiated later	*Artemisia* (Clausen et al. 1940), *Crepis* (Navashin 1925), *Cucumis* (Shifriss 1942)
	Flowering duration longer	*Capsicum* (Raghuvanshi & Joshi 1964), *Luffa* (Roy & Dutt 1972), *Melilotus* (Jaranowski & Kalasa 1971), *Ocimum* (Bose & Choudhury 1962)
Life-history	Reduced tillering	Ag*ropyron* (Tai & Dewey 1966), *Lamium* (Bernstrom 1954), *Pennisetum* (Jauhar 1970), *Secale* (Münzting 1951)
Physiology	Altered water relations	*Hordeum* (Chen & Tong 1945), *Solanum* (Tal & Gardi 1976)
	Altered photosynthesis	*Mimulus* (Hiesey et al. 1971), *Thalictrum* (Mooney & Johnson 1965)

ANEUPLOIDY, CHROMOSOME SUBSTITUTION, AND RECOMBINATION OF HOMEOLOGOUS CHROMOSOMES As described earlier, the cytological instability of neopolyploids generates substantial chromosomal and genic variation. On average, nearly 40% of the progeny of neopolyploids are expected to be aneuploid or pseudoeuploid (see Web Tables 4, 5). Poly-aneuploids are typically fertile and exhibit distinctive phenotypes that contribute to phenotypic variability of populations (Müntzing 1937, Bernstrom 1954). For example, Kostoff (1938) concludes that "aneuploidy augments the numbers of new forms in the progenies of the amphidiploid *Nicotiana glauca* × *langsdorffii* and leads to more striking divergence in the new forms." In allopolyploids, segregation of parental traits is another factor contributing to phenotypic variation (see Web Tables 2, 3). Derivatives of allopolyploids may thus be polymorphic, and include a variety of combinations of parental genomes (Kostoff 1938, Sybenga 1969). Molecular data may corroborate these hypotheses (Soltis & Soltis 1999). Song et al. (1993, 1995) created synthetic allopolyploids from diploid *Brassica* species and compared nuclear RFLP genotypes of parents and polyploid lines derived by selfing a single, homozygous progenitor. Genomic changes were frequent, with evidence for the gain and loss of parental alleles, as well as the appearance of unique DNA fragments. The degree of

genetic change was high, with genetic distances between S6 plants and their parents ranging from 2.1% to 9.6%. Moreover, polyploid lines displayed substantial heritable variation for phenotypic traits (Schranz & Osbourne 2000). For example, days to flowering of S6 progeny varied from 39–75 days, with parent-offspring regression indicating high heritability of this trait. Hence, "de novo" genetic and phenotypic variation may be induced by allopolyploidy in *Brassica* (Schranz & Osbourne 2000). Intergenomic recombination was proposed to be the major cause of the observed genome changes (Song et al. 1995), but other factors could also be involved (see below).

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GENE DOSAGE EFFECTS Polyploidy causes an immediate increase in gene dosage throughout the genome. With more gene copies, polyploids may have increased (or altered) gene expression, which would potentially affect many phenotypic traits. Guo et al. (1996) compared gene expression in leaves of 1*x*, 2*x*, 3*x*, and 4*x* maize, and found that most studied loci were expressed in proportion to dosage. In contrast, experiments using aneuploid dosage series revealed extensive alterations in expression (Guo & Bircher 1994). Guo et al. (1996) proposed that chromosomal imbalance in aneuploids would change the stoichiometry, resulting in altered gene expression, whereas in euploid series, dosage is changed proportionally. These results may explain the common observation that aneuploids, especially at the diploid level, exhibit more deviant phenotypes than polyploids (Khush 1973). Further research is needed to link dosage effects with specific phenotypic characters of polyploids and aneuploids.

A particular type of dosage effect relates to the loss of self-incompatibility (SI) in polyploids (Stout & Chandler 1941, Pandey 1968). Crossing experiments between self-compatible polyploids and self-incompatible diploids indicate that the breakdown in the SI reaction occurs in pollen. Hence, it is generally believed that interactions between incompatibility alleles in diploid pollen grains will induce self compatibility in systems where the SI reaction is determined by the genotype of pollen (i.e., gametophytic SI) (Lewis 1947). We surveyed the literature to determine the frequency of SI breakdown in neopolyploids (see Web Table 12). In sporophytic systems in which the SI reaction is determined by the sporophyte genotype rather than the pollen genotype, no breakdown was observed (N = 6 studies; see Web Table 12). Moreover, no loss of SI was observed in monocot species with either 1- or 2-locus gametophytic SI (N = 3 studies; Web Table 12). Among dicot taxa with 1-locus gametophytic SI, the induction of polyploidy generated self-compatible plants in 8 of 10 systems (Web Table 12).

In systems exhibiting a loss of SI, self-pollination generally resulted in variable seed set, which, on average, was considerably less than that observed from outcrossing. For example, mean seed set from self pollinations on neotetraploid *Trifolium hybridum* was 8% of that generated from outcrossed pollinations (Armstrong & Robertson 1956). In neopolyploid pear, seed set from self pollinations was about 60% that of outcross pollinations (Crane & Lewis 1942). Limited seed set observed from selfing self-compatible neopolyploids is probably

explained by varying degrees of competition between alleles in heterozygotes, though inbreeding depression may also be a factor.

INFERTILITY Neopolyploids generally exhibit reduced fertility compared to their diploid progenitors (see Web Table 7). Abortion of developing pollen grains and ovules, coupled with reduced seed development, alters growth and allocation late in the life cycle. The common observation that neopolyploids have prolonged flowering and luxurious growth late in the season (Table 1) may be a simple result of infertility.

ALLELIC DIVERSITY For a given locus, diploids will possess a maximum of two alleles. Increased gene dosage allows polyploids to harbor three or more alleles per locus, and hence exhibit greater overdominance than a diploid (Bingham 1980, Bever & Felber 1992). The proposed advantage is that multi-allelic, overdominant loci will allow polyploid individuals to achieve higher fitness in a wider diversity of environments than diploids. There is strong evidence that the growth, fertility, and yield of polyploid crops is correlated with heterozygosity, as illustrated by the performance of intervarietal autopolyploid hybrids as well as neopolyploids derived from highly heterozygous unreduced gametes versus somatic doubling (Bingham 1980, Stebbins 1980, Werner & Peloquin 1991).

In spite of the clear importance of allelic heterozygosity in plant breeding, there are reasons to doubt the impact of allelic diversity in early-generation neopolyploids in natural populations. First, it is unlikely that a few individual diploid progenitors of first-generation polyploids will possess the required allelic diversity, i.e., three or more alleles per locus (e.g., Bretagnolle & Lumaret 1995). Moreover, it is improbable that an entire diploid progenitor population would possess three or more overdominant alleles at a single locus. As Futuyma (1998, p. 385) concludes, "only under exceptional circumstances can heterozygous advantage maintain three or more alleles as a stable polymorphism." Second, only strong overdominance will maintain substantial heterozygosity in self-fertilizing populations thus neopolyploids derived from self-fertilizing progenitors are unlikely to possess overdominant alleles. Finally, as noted by Bever & Felber (1992), allelic overdominance in diploids is rare.

GENETIC LOAD With the potential for harboring three or more alleles per locus, neopolyploids may express deleterious codominant and recessive alleles less often than their progenitor diploids. Because the genetic load of early generation polyploids is the same as that of diploids, and the probability of producing a recessive homozygote is low, the mean fitness of neopolyploids may be consistently higher than that of diploids. Recent simulations show that new autopolyploids will, in fact, possess lower genetic load than diploids, but the advantage declines through time as a function of the genetic basis of inbreeding depression (Otto & Whitton 2000). The expected magnitude of inbreeding depression in polyploids has been estimated

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at mutation–selection equilibrium. Assuming that inbreeding depression is due to recessive deleterious alleles, Lande & Schemske (1985) proposed that autopolyploids possess half the inbreeding depression of diploids. In contrast, Ronfort (1999) concluded that under the model of complete recessivity, diploids and autopolyploids should have equivalent inbreeding depression. Estimating the expected inbreeding depression in the more plausible case where deleterious alleles are partially dominant is complicated by the fact that polyploids produce several heterozygous genotypes. Such an analysis revealed that inbreeding depression at equilibrium can decrease or increase with changes in the selfing rate (Ronfort 1999).

There are few studies comparing inbreeding depression of polyploids and related diploids. Results are mixed for populations of established cytotypes (Kalton et al. 1952, Dewey 1966, Johnston & Schoen 1996, Husband & Schemske 1997). The few studies of early generation polyploids indicate lower inbreeding depression in neopolyploids than diploids. Dewey (1969) found a 17% reduction in forage yield in selfed neotetraploids of *Agropyron cristatum* as compared to a 55% reduction for their selfed diploid progenitors. These results are consistent with observations of neopolyploids in *Lolium multiflorum*, maize, and clover (Dewey 1969). There are no empirical data examining inbreeding depression in newly formed allopolyploids, or theoretical models that evaluate the evolution of genetic load in allopolyploid populations. The genetic system of allopolyploids limits allosyndetic pairing that would lead to the production of homozygous genotypes, so inbreeding depression in new allopolyploids is expected to be very low (Sybenga 1969). The fixed heterozygosity of allopolyploids may be an important cause of their evolutionary success.

GENOMIC EVOLUTION In addition to homeologous recombination (discussed above), genome evolution in polyploids may involve gene silencing, divergence of gene function, and other processes (Wendel 2000). Many aspects of genome evolution occur over long timescales, but some mechanisms could cause substantial genomic evolution in early-generation polyploids. Feldman et al. (1997) and Liu et al. (1998a) found that nonrandom elimination of noncoding DNA sequences in allotetrapoid and allohexaploid wheat contributes to molecular diploidization and the diploid-like meiotic behavior of early generation polyploids. A parallel study of coding sequences identified loss of parental fragments and the appearance of novel fragments, but no elimination of parental sequences (Liu et al. 1998b). These changes may cause gene inactivation, reduced expression, and functional diversification. Liu et al. (1998b) conclude that the changes in coding regions are a result of methylation, not intergenomic recombination.

Although gene silencing via mutation is thought to be a slow process, epigenetic control of gene expression can be immediate (Wendel 2000). The instability and infertility of early generation allopolyploids may reflect intergenomic incompatibilities, which can be resolved by gene silencing (Comai 2000). Comai et al. (2000)

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produced synthetic allopolyploids of *Arabidopsis thaliana* × *Cardaminopsis suecica* and estimated that 0.4% of genes are silenced, some by epigenetic regulation. Epigenetic gene silencing is also observed in nonhybrid systems. Scheid et al. (1996) observed epigenetic regulation of a transgene in *Arabidopsis thaliana*, with reduced expression in triploids as compared to diploids. They suggest that epigenetic silencing in plants is a direct response to changes in chromosome number or nuclear DNA content that could have substantial effects on gene regulation.

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POPULATION GENETICS Autopolyploids exhibit multisomic inheritance that alters basic population genetic processes. It might be asked whether neopolyploids can respond more rapidly to selection and thus be more "adaptable" than progenitor diploids. Single-locus theory shows that polyploids may evolve faster or slower than diploids, depending on the dominance coefficients of advantageous alleles. For an additive, completely dominant allele, Hill (1971) found that the response to selection was always greater in diploid than in autotetraploid populations. Otto & Whitton (2000) showed that tetraploids with tetrasomic inheritance will evolve faster than diploids when $h_1 > h/2$, where h_1 and h are the dominance coefficients for the advantageous mutant allele in tetraploids (*AAAa*) and diploids (*Aa*), respectively. In tetraploids with disomic inheritance, an advantageous mutant allele will become fixed in only one of the two gene copies. In this case, tetraploids will evolve faster than diploids if $h_1 h_2 > h/2$, where h_2 is the dominance coefficient of the mutant allele in tetraploid genotype *AAaa* (Otto & Whitton 2000). See Bever & Felber (1992) for a comprehensive review of the population genetic consequences of polyploidy.

Ignoring epigenetic sources of genetic variation and that due to aneuploidy, chromosomal rearrangements, and homeologous recombination, neopolyploids depend on the genetic variation present in the founding population. In most systems, the effective population size of early generation neopolyploids will be exceedingly small, even in cases of multiple formation. This genetic bottleneck will reduce the genetic variation available to a new polyploid population, and the small population size will limit input of new variation by mutation. Adaptive evolution by the fixation of individual alleles may be relatively unimportant during the early phases of polyploid establishment.

FITNESS AND ADAPTATION

Polyploidy may contribute to local adaptation in several distinct ways. First, neopolyploid populations may exhibit increased phenotypic variability due to the combined effects of aneuploidy, chromosome substitution, homeologous recombination, and epigenetic changes. Although auto- and allopolyploids both tend to display more variability than progenitor diploids, allopolyploids probably vary more due to the greater phenotypic consequences of numerical representation and recombination of homeologous than homologous chromosomes. According

to this model, polyploidy contributes to adaptation by making populations adaptable to a wider range of environmental conditions. Second, polyploidy may induce immediate phenotypic changes that incidentally preadapt plants to a new ecological niche. For example, increased DNA content, gene dosage effects, and masked genetic load could alter the traits of a species in such a way as to increase its survival and reproduction in a novel environment. According to this hypothesis, the important phenotypic effects of polyploidy are imbued immediately and are in some ways predictable.

Although polyploidy is widely believed to be a mechanism of local adaptation (Clausen et al. 1945, Levin 1983), little is known about the fitness of neopolyploids (or, in fact, established polyploids) in different environments. The seed yield of early-generation polyploid crops is generally reduced compared to progenitor diploids (e.g., Hagberg & Ellerström 1959, Tai & Dewey 1966, Jaranowski & Kalasa 1971). In experimental plantings of rye, induced autotetraploids exhibited fewer flowering tillers, fewer flowers per spike, and lower seed set than diploids (Müntzing 1951). However, tetraploid seeds were 50% larger than diploid seeds and germinated better. In general, yield differences are attributed to the reduced fertility of neopolyploids and do not reflect possible differences in survival and growth in natural field conditions involving environmental stress and competition. There is a general need for investigations of the fitness of neopolyploids in natural plant species, especially when grown in the field. Stebbins (1949, 1985) induced autotetraploids in the exotic annual grass *Ehrharta erecta* and planted seeds and seedlings in 22 environmentally contrasting sites in central California. Diploid plants were demographically successful in most sites, but tetraploids survived in only two. In these two transplant sites, tetraploids were less numerous than diploids and occurred in a narrower range of environmental conditions. Bretagnolle & Lumaret (1995) examined the phenotypic characteristics and reproductive fitness of several neotetraploid clones of *Dactylis glomerata* generated by unreduced gametes. Diploids and tetraploids were grown in a common garden with four environmental treatments. In all environments, tetraploids had lower seed set and similar total biomass compared to diploids.

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CONCLUSIONS AND FUTURE DIRECTIONS

We find that early-generation autopolyploids are characterized by random associations of homologous chromosomes, variable degrees of multivalent pairing, multisomic inheritance, and frequent production of aneuploid and pseudoeuploid gametes and progeny. Although some newly formed allopoyploids exhibited characteristics of true genomic allopolyploids, most exhibited occasional allosyndesis and multivalent configurations, inheritance intermediate to disomic and multisomic models, and frequent production of aneuploid gametes and offspring. Hence, the cytogenetic character of newly formed auto- and allopolyploids differ statistically, but are not as distinct as might be expected. In particular, allopolyploids may

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not always represent constant species hybrids due to allosyndetic pairing and homeologous recombination.

Although aneuploids and pseudoeuploids are commonly observed in the progeny of neopolyploids, their evolutionary significance is poorly understood. Aneuploidy may contribute to phenotypic variability, and hence adaptability, of neopolyploid populations, but also represents a form of genetic load. In the case of allopolyploids, homeologous recombination may also contribute to genetic and phenotypic variation in populations. A critical evaluation of the evolutionary significance of aneuploidy and homeologous recombination will be difficult, requiring measurements of the occurrence, phenotypes, progeny, and fitness of aneuploid and segregant genotypes in different environments.

Autopolyploids are traditionally thought to be less fertile than allopolyploids, and hence less likely to establish and maintain viable populations. Although we find that neopolyploids exhibit significantly reduced pollen and seed fertility compared to their diploid progenitors, there are no differences between the fertilities of newly formed auto- and allopolyploids. The fertility of neopolyploids may thus be a general barrier to establishment of both polyploid types. Rapid evolution of pollen and seed fertility is often observed in fertility-selected neopolyploid populations, suggesting infertility of neopolyploids may be somewhat transient. However, comparisons of naturally established low and high ploidy cytotypes indicate that polyploidy may set an upper limit to the fertility of a cytotype. Additional studies are needed to evaluate the demographic consequences of fertility because neopolyploids may compensate for reduced fertility by their increased survival and growth.

The causes of polyploid infertility are complex and include meiotic aberrations, physiological effects of polyploidy, and genic factors. Meiotic aberrations related to univalent and multivalent pairings probably represent the primary cause of sterility in most polyploids. Fertility selected neopolyploids nearly always show an increase in bivalent pairing, or else quadrivalent pairing. In our datasets, pollen fertility is significantly correlated with the occurrence of univalents and trivalents, but not with quadrivalent configurations. Increased fertility of autopolyploids is hypothesized to occur primarily by the fixation of alleles controlling the frequency and distribution of chiasma. In contrast, fertility improvement of allopolyploids probably involves suppression of homeologue pairing via genic control of pre-meiotic chromosome alignment or the stringency of crossover. Evolution of chromosome structure (e.g., chromosomal rearrangements or sequence elimination) may also be an important factor in allopolyploids. Further cytological studies, perhaps in combination with linkage mapping approaches, will be necessary to unambiguously identify the genetic architecture of fertility improvement in neopolyploids.

Neopolyploids often differ from their diploid progenitors by a combination of morphological, reproductive, phenological, and life-history traits. The distinctive characteristics of neopolyploids are probably caused by a variety of factors, including increased DNA content and cell size, gene dosage effects, aneuploidy, homeologous recombination, masked genetic load, and epigenetic changes.

The combined dataset regarding the cytogenetics and phenotypes of neopolyploids is deep, and historical investigations of cultivars and model systems have elucidated many of the characteristics of newly formed auto- and allopolyploids. However, to evaluate questions related to the establishment of polyploid populations and the nature of polyploidy as an evolutionary mechanism, it will be necessary to link classical cytogenetic approaches with investigations of neopolyploid formation in natural populations. In spite of the widespread belief that polyploidy is an agent of adaptation and speciation, there are no studies of neopolyploid fitness and reproductive isolation in the field, much less the impacts of specific chromosomal and genic factors on the evolution of neopolyploid populations. Moreover, investigations of the dynamics of polyploid formation and establishment remain theoretical, even though published evaluations of neopolyploid crops demonstrate the feasibility of an empirical approach.

Hence, there is a need for experimental studies that compare the genetic and phenotypic characteristics of neopolyploids and early-generation polyploids with those of established polyploid and progenitor populations. Critical questions include: What fraction of the total fitness differential between established polyploids and their progenitors is obtained in neopolyploids? Which characters of established polyploids are the products of genic evolution, and which are due to polyploidy per se? What are the genetic, developmental, and ecological attributes of neopolyploids, and how do these contribute to polyploid establishment?

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