Breaking down taxonomic barriers in polyploidy research

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Polyploidy is important in the evolutionary history of plants, and it has played a crucial role in shaping the genome structures of all eukaryotes. New and rapidly improving techniques in genomics, cytogenetics and molecular ecology have resulted in a dramatic increase in publications about duplicate genes, genome rearrangements and detection of ancient duplication events. Similarly, research associated with the origins of polyploidy, its persistence in natural populations and the resulting ecological consequences is receiving more attention. Although polyploidy research has been conducted using both animal and plant systems, inferences based on cross-disciplinary comparisons have been rare. Here, I review recent developments in the field in both plants and animals, emphasizing the benefits of communication between the two groups.

POLYPLOIDY (see Glossary) has long been recognized to be an important process in the evolutionary history of plants, but many questions remain about how it arises and persists in populations, and about its ecological and genetic consequences. Increasing technological advances in the analysis of genome structure and function have enabled researchers to study the genetic consequences of genome duplication at an unprecedented level. This has resulted in a dramatic increase in interest in polyploidy (Figure 1), particularly in relation to the fate of duplicate genes, the detection of ancient genome duplication events and genomic rearrangements or changes in gene expression following polyploidization [1–6]. In addition, new technologies in cytogenetics and molecular ecology have resulted in a resurgence of interest in the modes of origin and establishment of polyploid lineages in the midst of their diploid progenitors [7–11]. Together, these data have generated a greater appreciation for the wide distribution of genome duplication across all eukaryotes [12–16]. These approaches underscore the potential for building a unified framework for polyploidy that includes both plant and animal biology. However, research findings in animal biology are rarely considered by plant biologists. This is at least partly because there are more highly accessible reviews on polyploidy in plants but there has been much less focus on polyploidy in animals in recent years (but see Ref. [9]).

The purpose of this article is to compare recent developments in the study of polyploidy in plants and animals by setting the smaller body of animal research into the larger context of the plant research, and to suggest areas that could benefit by more mutual consideration of results. A review of this length cannot begin to be comprehensive and thus I focus predominantly on vertebrates and on TRIPLOIDS and TETRAPLOIDS rather than higher ploidy states, and restrict the discussion to research conducted within the past few years; these papers should be consulted for references to earlier work in these fields.

Perspectives on plant and animal research

The long-held view that polyploidy is rare in animals [17] has tended to restrict study to a handful of taxa and has dissuaded plant biologists from considering animal-based results. In reality, polyploidy occurs in a wide range of animal groups, including insects, molluscs, crustaceans, amphibians, reptiles, fish and mammals [9]. There has been a long history of study of the modes of origin and

Glossary

Allopatric: two species or populations living in geographically separated localities.
Allopolyploids: polyploids in which the chromosome sets are derived from more than one species through hybridization.
Assortative mating: the tendency of like to mate with like.
Concerted evolution: the generation and maintenance of homogeneity among members of a family of DNA repeats or among gene copies in a gene family within a species or population.
Cytonuclear: referring to cytoplasmic and nuclear attributes.
Cytotype: individual with a particular ploidy level.
Gametes: haploid reproductive cells formed through meiosis that fuse to form zygotes.
Gene family: set of related genes arising from a common ancestral sequence through gene duplication.
Homologous: chromosomes or genes derived from a common ancestor.
Homeologous: in allopolyploids, chromosomes or gene copies derived from the same parental origin.
Hybridization: integration of genomes from two different species or genetically divergent populations.
Neopolyploids: newly generated polyploid individuals, often induced through artificial means.
Phenological: having to do with visible life cycle events.
Phytophagous: plant eating.
Polyploidy: possessing more than two sets of chromosomes.
Postzygotic isolation: reproductive isolation in which a zygote is successfully formed but then either fails to develop or develops into a sterile adult.
Prezygotic isolation: reproductive isolation occurring before zygote formation.
Tetraploids: individuals with four sets of chromosomes.
Triploids: individuals with three sets of chromosomes.
Quantitative trait loci: genetic loci showing continuous variation in populations that are mapped to particular traits.
Reproductive isolation: inability of two individuals to produce fertile offspring.
Sympatric: two species or populations living in the same geographic locality so that there is the opportunity to interbreed.
Zygote: cell formed by union of male and female gametes.

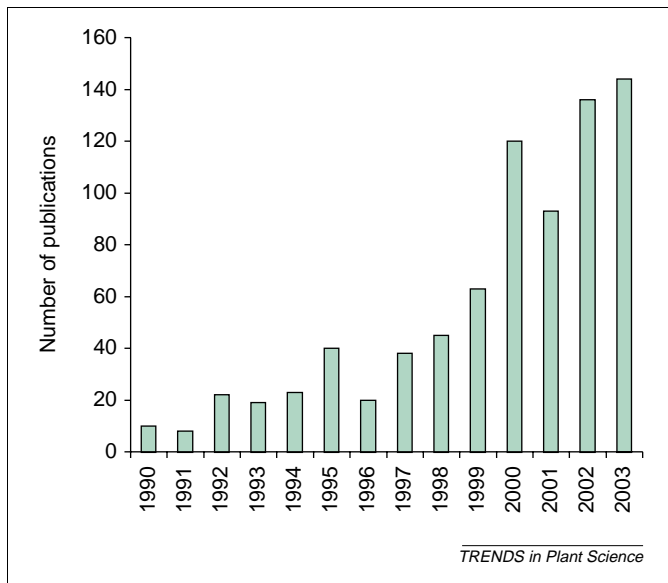*Corresponding author:* Barbara K. Mable (bmable@uoguelph.ca).

Figure 1. Number of publications associated with polyploidy during the past few years. The bars indicate the number of PUBMED hits for the key words 'triploid', 'tetraploid' or 'polyploid' since 1990, excluding publications concerned with aneuploidy or polyploidy in individual cell lines (which have had more of a steady rate of publication). These values have not been corrected for overall increases in the number of publications and the values for 2003 are extrapolated based on the number published in the first six months of 2003.

genetic consequences of genome duplication, particularly in amphibians and fish [12,18,19]. Historically, although plant and animal biologists often ask remarkably similar evolutionary questions, there has not been an emphasis on joint evaluation of results. Polyploidy research has been so dominated by plant studies that there has been much less perceived need for plant biologists to consult animal-based results than vice versa. Nevertheless, plant and animal biologists often take different approaches to similar problems and insights could be gained by considering these different perspectives. For example, in the 1970s and 1980s, polyploidy research in animals tended to focus on functional genetics of polyploidy and used allozymes to study phenomena such as rates of gene silencing and tissue- or development-specific expression of duplicate genes [e.g. 20,21]. At the same time, plant researchers focused more on the taxonomic implications of polyploidy and used allozymes to identify polyploids and to characterize their ecological attributes and heterozygosity levels relative to diploids [e.g. 22].

There are also unique attributes of plants and animals that could offer opportunities to explore the same questions in different ways. For example, external reproduction in some amphibians and fish allows researchers to assess genetic incompatibilities easily in artificial crosses because developmental stages (from cleavage to larval development) can be monitored visually and provide easy access to large numbers of eggs (which is not often possible in plants). In addition, because animals are mobile and exhibit many easily observed behaviours that are often used in mate selection, they can be useful for examining the effects of genome duplication on behaviour as well as physiology, life history and morphology. Plants, however, are more easily manipulated genetically using techniques such as transformation, and there are far more genomic

tools currently available than for animals with much larger genomes. They also stand still and thus can be transplanted and grown more readily in common garden experiments to determine the relative fitness of diploid and tetraploid CYTOTYPES in different habitats.

Finally, there are interesting differences between the attainment of polyploidy in plants and animals that warrant further study, although there are exceptions in both systems. For example, many polyploid animals tend to preserve the same body size as diploids in spite of an increase in cell size by reducing the overall number of cells, and are often morphologically indistinguishable from their diploid progenitors [18]. By contrast, polyploid plants more often have larger bodies and thus could be ecologically or reproductively altered compared with diploids [9,23]. The causes or consequences of such developmental differences for the adaptive potential of polyploids in new environments have yet to be explored.

Recent progress in polyploid research
Modes of origin of polyploid individuals
In the formation of polyploid lineages, the first step is the production of GAMETES (or other cell lines) with duplicated DNA contents. In plants, in spite of a suggestion by Öjvind Winge in 1917 [24] that production of unreduced gametes was the primary mechanism for polyploidization, somatic doubling has long been considered to be the predominant mode. Recent work quantifying the frequency of unreduced gametes leading to the production of higher-ploidy offspring [11,25] questions this view and suggests that meiotic nondisjunction (or meiotic restitution; Box 1) should not be overlooked as an important route [7]. Understanding the cytological mechanisms [26,27] and number and location of genes involved in the production of diploid gametes [28] is a current goal of plant research.

Animals do not have the capacity for somatic routes to polyploidization, so animal biologists have focused on increases in the frequency of unreduced gametes as the major factor explaining how polyploid individuals arise [18]. There is a great deal of information in the older literature on the frequency of nondisjunction under various conditions. In frogs, for example, colchicine can be used to induce unreduced eggs, but cold shock and pressure shock can produce frequencies of up to 90% [18] and a relatively high frequency of unreduced eggs can occur in natural populations [e.g. 29]. The relative ease of examining segregation of chromosomes in animals such as amphibians, and the ability to examine the ploidy of many progeny from controlled crosses has facilitated such studies. Studies of unreduced gametes in both plants and animals have become easier through the use of rapid screening techniques such as flow cytometry (originally developed for human medical research) rather than painstaking chromosome counts or indirect measures such as blood cell or pollen grain size.

In both plants and animals, although an intermediate triploid stage often has been proposed as the most likely route to tetraploid formation, the frequent sterility of triploid hybrids in both has questioned the mechanism by which this might occur [7,11,18]. In plants, recent evidence suggests that low frequencies of viable gametes in triploids

Box 1. Modes of 'asexual' or unisexual reproduction in polyploids

Polyploidy is often accompanied by a loss of normal sexual reproduction in both plants and animals, particularly in odd-ploidy individuals (e.g. triploids). Although unreduced gametes are often involved in asexual reproduction in both groups, the use of different terminology and the larger number of cell types that can be involved in apomixis in plants make it difficult to compare reproductive modes directly in plants and animals. Gynogenesis and hybridogenesis in animals require physical or genetic input from sperm and provide potential for occasional incorporation of male genomes or recombination between male and female genomes [35]. It is not clear whether these modes of reproduction are also found in plants, but facultative apomixis (i.e. occasional sexual reproduction) is widespread in some groups and pseudogamy requires pollination in some plants for proper endosperm development. Complications associated with maintaining endosperm balance [27] are unique to plants and some of the modes related to this have no counterpart in animals. Different terminology used to describe mechanisms for unreduced gamete production also confuses similarities. The list below provides definitions for terms used to describe modes of asexual reproduction in plants [105] and animals [35], with an indication of which modes might be common to both.

Plant modes
First division restitution
Retention of both sets of homologous chromosomes during meiosis I owing to some meiotic aberration; the resulting unreduced egg is homogeneous and genetically similar to the parent (retention of first polar body in animals).

Second division restitution
Retention of both sets of sister chromatids during meiosis II owing to some meiotic aberration; the resulting unreduced egg is heterogeneous and genetically different from the parent (retention of second polar body in animals).

Agamospermy
Production of seeds without sex (fusion of male and female gametes.

Sporophytic apomixis
Embryos originating from sporophytic tissues by adventitious embryony.

Gametophytic apomixis
Embryos originating from unreduced megagametophytes.

Apospory
Unreduced megagametophytes derived from the megasporangium wall.

Diplospory
Unreduced megagametophyes derived from archesporium, arising by restitutional meiosis or mitosis.

Apogamety
Embryo formed from unreduced embryo-sac cell.

Parthenogenesis
Embryo formed from unreduced egg (parthenogenesis in animals).

Automixis
Embryo derived from fusion of two haploid egg cells after normal meiosis.

Pseudogamy
Embyro formation requires pollination and subsequent fusion of polar nuclei by male gamete to generate the endosperm (closest to gynogenesis in animals).

Animal modes
Apomixis
Production of unreduced gametes without meiotic reduction.

Automixis
Production of unreduced gametes via premeiotic endoreduplication (i.e. doubling of chromosomes before meiosis) followed by meiotic reduction.

Parthenogenesis
Embryo produced from an unreduced egg without male involvement (agamospermy or parthenogenesis in plants).

Gynogenesis
Physical stimulation by sperm required to initiate cleavage of unreduced eggs but male genome is not normally incorporated (closest to pseudogamy in plants).

Hybridogenesis
Male parental genome is expressed in triploid hybrids but is discarded during oogenesis so that diploid eggs contain only maternal nuclear genes; triploidy is restored by incorporation of sperm from excluded parental type. (Also referred to as hemiclonal reproduction [60]).

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might help to overcome this barrier [11,25,30] but it is unclear how high this rate would have to be for triploids to form a tenable bridge to tetraploid formation. Intriguingly, although most triploid animals reproduce asexually, sexually reproducing populations of triploid toads (*Bufo viridis*) have been found [31], emphasizing that polyploid reproductive systems might not be as constrained as is often assumed [17] and that perceived barriers to triploid fertility deserve closer examination. Also in animals, research on the role of unreduced gametes in complex reproductive systems such as gynogenesis and hybridogenesis (Box 1) [e.g. 32] and in mechanistic explanations for the production of unreduced gametes [33,34] could provide insights into how tetraploid lineages could be formed via unreduced gametes, a mechanism that has not been as explicitly considered in plants.

Apomictic, automictic or unisexual polyploids (Box 1) have often been viewed as a separate class from sexually reproducing species, but they could form a crucial intermediate step in the formation of even-ploidy sexual lineages. For example, all-female gynogenetic salamanders (Box 1) in the genus *Ambystoma* form an ancient polyploid complex of unisexual lineages with a complex history of genetic interactions with SYMPATRIC sexual species. This has resulted in the maintenance of an ancient maternal cytoplasm (suggested by extremely low levels of variation in maternally inherited mitochondrial DNA) with nuclear genomic information incorporated from sexual males (suggested by allozyme and nuclear microsatellite DNA variation) throughout their history [35]. Similarly, in cyprinid fishes, cyclical loss, gain or replacement of parental genomes has occurred frequently throughout

the evolutionary history of the complex, and diploid hybrid males might be important mediators to the formation of tetraploids [36]. In plants, although many apomictic species display at least low levels of sexual reproduction [e.g. 37–39], this has not been suggested as a major route to tetraploid formation. The 'alternative' reproductive strategies used by both plants and animals (Box 1) could be the key to the formation of bisexual lineages, rather than being merely sexual anomalies.

Nondisjunction is thought to be particularly common in hybrids but might be induced by environmental factors such as cold shock, heat shock or environmental fluctuations [9]. If such environmental variation can produce large numbers of unreduced gametes in a localized area, opportunities for production of higher ploidy levels could be more frequent than often assumed, helping to explain the multiple origins of both auto- and allopolyploidy now thought to be the rule in both plants and animals [7,40]. The frequency with which tetraploids are produced from the union of two unreduced gametes remains unclear, but rapidly developing cytological and molecular tools (such as flow cytometry, chromosome painting and genomic techniques) should allow this question to be addressed more fully in both plants and animals.

Establishment of polyploid lineages

Relatively little is known in plants or animals about the mechanisms by which polyploids spread or are maintained in populations once they have been formed [7,8]. The establishment of independently evolving polyploid lineages is limited by the difficulty of encountering a mate of the same ploidy level, by hybrid inviability, by the viability and fertility of polyploids relative to diploids, and by the potential for genetic swamping by the more frequent cytotype (i.e. the minority cytotype exclusion principle) [7,41–43]. Plants capable of self-fertilization and individuals with multiple lifetime opportunities for reproduction have been thought to overcome problems associated with intercytotype mating most readily [e.g. 41,44] but strong ASSORTATIVE MATING could achieve a similar effect, particularly in the presence of local adaptation of cytotypes to different environments [41]. Assortative mating would be a particularly strong force if prezygotic isolating mechanisms were involved that changed in direct association with polyploidization rather than gradual accumulation of changes through time. Although little information is available on this topic in plants, pollinators have been shown to prefer flowers of particular cytotypes, and separation in flowering time, variation in cytotype distributions and different growth rates of diploid and tetraploid pollen tubes could facilitate REPRODUCTIVE ISOLATION between cytotypes [25,45,46]. Whether these patterns arise concomitantly with cell size changes or whether they are a byproduct of subsequent genetic divergence has not been established.

Emphasis on the role of prezygotic reproductive isolating mechanisms in polyploid formation has been much more prevalent in work on animals, probably because behavioural mechanisms used to choose mates are much easier to quantify and test experimentally than comparable isolating factors in plants. In addition, animals play a

more active role in selecting their mating partners and the relative frequency of different cytotypes has not been suggested to be as important as mechanisms to ensure assortative mating. In amphibians, previous suggestions that mating calls might change automatically with cell size and thus immediately allow assortative mating by cytotype [18,47] have recently been supported experimentally [48]. In addition, the discovery that animals might choose mates that are genetically dissimilar at loci involved in immune responses (e.g. the major histocompatibility locus) based on olfactory cues [49] provides another route to PREZYGOTIC ISOLATION that could be tested in polyploids. Differential silencing of genes at this locus, such as occurs in polyploid pipid frogs [50], could result in differential recognition of surface proteins in diploids and tetraploids. This possibility has not been investigated. The intriguing similarity of these cell–cell recognition systems to self-incompatibility systems in plants has not gone unnoticed [e.g. 51] and the effects of polyploidy on such systems have been investigated [52]; however, possible parallels related to pathogen response have not received much attention.

The role of POSTZYGOTIC ISOLATION between cytotypes (i.e. sterility of triploid hybrids) is complicated because it could reduce the probability of initial establishment of tetraploid lineages formed through an intermediate triploid stage but could also reinforce prezygotic mechanisms (thus promoting positive assortative mating by cytotype) and would enhance tetraploid establishment in the long term through genetic separation of cytotypes. It has been suggested that the fertility of polyploid hybrids could be increased with genetic divergence of the parental genomes [18,53–55], which might aid the establishment of ALLOPOLYPLOIDS, but it is unclear to what extent the pattern can be generalized [56]. CYTONUCLEAR interactions, including maintaining balances in endosperm ratios [27], have been implicated in the genesis of postzygotic isolation in plants [57] but it is unclear what involvement this has had in the establishment of polyploid lineages. In amphibians, developmental difficulties in hybrids between diploids and polyploids are found more often when the diploid is the female parent, and they often become apparent at the gastrula stage (when the male genome is first expressed), suggesting that maternal effects or the ratio of nuclear to cytoplasmic factors require that the higher-ploidy genome contributes the cytoplasmic component [18]. In the grey treefrog complex, for example, whereas triploids produced from crosses involving tetraploid females and males from their diploid progenitor species are completely sterile, increased fertility is seen in crosses involving distantly related males [58]. This might be due to mechanisms for the recognition and preferential pairing of HOMEOLOGOUS chromosome sets such as occurs during hybridogenetic reproduction, where one parental genome is eliminated premeiotically [59,60]. In polyploid hybrid crop plants, a single gene (*Ph1*) has been implicated in premeiotic sorting of chromosomes by centromere associations during anther development [61]. This allows effective separation of parental genomes in allopolyploids, which could reduce problems with infertility. Many advances in cytogenetic techniques such as chromosome painting, chromosome sorting, high resolution banding,

microdissection and *in situ* HYBRIDIZATION are now being extensively applied to both plants and animals [62–66], and should allow more precise dissection of factors that control HOMOLOGOUS and homeologous pairing during meiosis in polyploids, which could also be used to examine factors controlling the fertility of triploids.

Problems associated with hybrid inviability could be reduced with ecological or PHENOLOGICAL separation of cytotypes, minimizing potential for accidental mismatings. Although few general trends are apparent in NEO-POLYPLOIDS [11], experimental evidence is accumulating to support this notion. For example, PHYTOPHAGOUS insects show different preferences for diploid and tetraploid plants [67], and flowering time is altered in some neopolyploids compared with their diploid progenitors [68]. Polyploids have been thought to persist only when they can exploit new habitats (to avoid competition with their diploid progenitors) but previous data have been largely correlational. This is an area that is receiving renewed attention using molecular ecological techniques in plants [7,8] but has not been studied as extensively in animals.

In both plants and animals, investigation of isolating mechanisms and factors contributing to hybrid fertility in neopolyploids (produced through meiotic nondisjunction rather than colchicine treatment of somatic cells) is the key to determining which factors regulate polyploid establishment. In addition, neopolyploids are ideal candidates for molecular approaches to determining the genetic basis of reproductive isolation. Although assessing the consequences of polyploidy in neopolyploids is an area of growing interest in plants [11], creating such lines through environmental variation is not trivial because of the difficulty of assessing the DNA content of individual pollen cells (particularly considering the multinucleate nature of pollen in many species) and of accessing eggs nondestructively for ploidy testing. In animals such as amphibians, which have large, accessible female gametes and haploid sperm, chromosome counts or flow cytometric determination of DNA can be performed using actively growing tail tips in larvae to assess rapidly whether a given cross has produced higher-ploidy offspring [18] and it should be possible to use flow cytometry to sort sperm (and possibly eggs) by their DNA content before using them for crosses to generate even-ploidy lines. At least until improved techniques for inducing polyploidy in plants without colchicine treatment are established, valuable insights could be gained by examining changes occurring in environmentally induced animal neopolyploids.

Ecological consequences of polyploidy

The ecological consequences of polyploidy could be different in plants and animals, where differences in strategies for dealing with increases in cell size with increases in DNA content exist. In plants for which changes in body size accompany polyploidization, there are often distinctive morphological differences that could result in differential adaptations of cytotypes [69]. Similarly, certain aspects of plant physiology are sometimes altered by changes in cell size accompanying polyploidy (e.g. polyploids might be more tolerant to water deficit [70] or have higher photosynthetic rates [71]). By contrast, retention of

the same body size by reducing the number of cells in some animals means that tetraploids are often completely morphologically indistinguishable from their diploid progenitors [9]. In such cases, cellular changes with polyploidization could be achieved without major alterations in physiology [18,72], although changes in muscle development [73] and fin regeneration [74] have been found in induced triploid salmonid fish that could affect the relative performance of the different ploidy levels. Although some plants also do not experience a change in body size with polyploidization, the implications for regulation of cell size and number for ecological adaptation have not been extensively explored in either group.

It is often assumed that polyploids spread because they can tolerate and invade harsher environments than their diploid counterparts owing to increased hardiness and/or increased genetic buffering provided by having 'extra' genome copies [9]. However, it remains unclear how general this pattern is. Greater ecological amplitude has been demonstrated in some polyploid plants compared with their diploid progenitors, but this trend varies widely when multiple diploid–polyploid pairs are compared, with some diploids showing broader ranges than their tetraploid derivatives [8,9,75,76]. Several new polyploid taxa arising from hybridization between introduced and native plant species [8,77,78] have been shown to be insidious invaders and could pose conservation threats to natural populations, supporting the notion that polyploids excel at exploiting new environments.

This is an area that has received surprisingly little attention in vertebrate animals but could be tested in relation to home range sizes or differences in microhabitat usage, diet choice or breeding site fidelity in diploids and tetraploids that could result in ecological separation. A trend for more polyploids at higher altitudes and latitudes has been proposed for both plants and animals but has exceptions [e.g. 45] and tolerance of extreme conditions such as cold does not necessarily accompany polyploidization (e.g. some polyploid plants have been demonstrated to show lower cold tolerance than their diploid counterparts owing to changes in osmotic pressure resulting from altered surface-area:volume ratios [79]). There are particularly high proportions of polyploid taxa in arctic populations [40,80] but there are also more apomictic and selfing plants and asexual animals, so it is difficult to tell whether polyploidy or reproductive mode best explains this pattern.

In plants, ecological adaptations are now being studied at the molecular level by looking at changes in regulatory genes [81] and QUANTITATIVE TRAIT LOCI (QTLs) involved in particular traits [82] that could result in different adaptations by polyploid genomes and their diploid counterparts. In animals, this type of research has been more limited but mapping techniques currently applied to genetic models such as rainbow trout [83,84] and African clawed frogs [85] could be used to address similar questions. Detailed comparisons of diploid–tetraploid pairs are required in both plants and animals before the ecological and physiological consequences of polyploidization are fully understood. However, genetic tools that are currently being implemented promise imminent breakthroughs that

could be evaluated in both types of systems to determine whether often-cited generalized patterns hold up to more intense scrutiny.

Genetic and genomic consequences of polyploidy

Evidence of extensive gene duplication in organisms now considered to be diploid suggests that polyploidy has contributed to evolutionary diversification in plants and animals through successive rounds of polyploidization and rediploidization. Understanding the mechanisms and consequences of such changes is undoubtedly the most topical area of polyploid research in plants and has been thoroughly reviewed elsewhere [e.g. 2,5,15]. The continually increasing number of whole genome sequences, linkage maps and QTL maps currently available for a wide range of plant groups has resulted in a rapid accumulation of information on molecular alterations following polyploidization. Overall, evidence supports the view that duplicate genes have multiple fates (silencing, development of novel functions, subdivision of functions among tissue types or developmental stages), so that the rate and direction of genomic changes following polyploidization are not completely predictable [5,54,55,86]. In addition, recent evidence suggests that changes in genome size might be mediated by transposable elements [87–89], that CONCERTED EVOLUTION in ribosomal DNA (rDNA) genes might proceed in different directions in polyploid hybrids [90,91] and that epigenetic factors can result in differential gene expression in newly created polyploid lineages [5,6]. All of these data emphasize the vast potential for polyploidization to increase genetic diversity in multiple ways. This is further supported by population level studies: polyploids from multiple origins are not always genetically or ecologically equivalent [8,92,93] and polyploid groups might speciate further through 'normal' ALLOPATRIC channels to produce additional species at the same ploidy level or through successive increases in ploidy level [40,94].

In animals, the fate of duplicate genes received a great deal of attention based on allozymes in the 1970s and 1980s [12], and data about individual genes are beginning to accumulate [14,50,95], including suggestions that epigenetic silencing can lead to multiple fates for duplicated copies [96], as has been demonstrated experimentally in plants [6]. The use of more advanced genomics techniques has, in general, lagged behind plant research but progress is being made in a few model species, several of which just happen to be polyploids. For example, linkage mapping and genetic transformation have been applied to model species such as rainbow trout [84,97] and African clawed frogs [85,98]. Genome sequencing projects are currently under way for the ancient (50 million to 60 million years) tetraploids Atlantic salmon (*Salmo salar*) and *Xenopus laevis*, as well as for the diploid amphibians *Silurana tropicalis* (formerly *Xenopus tropicalis*) and *Ambystoma mexicanum* (related to the *Amybstoma* complex of polyploid unisexual salamanders). These data will allow more direct comparisons of genomic changes following polyploidization for a much larger array of genes, which can then be compared with comparable studies in plants to determine whether plants and animals experience similar types of genomic changes following polyploidization. Other model amphibians, such as the hybridogenetic triploid frog complex *Rana 'esculenta'* (used extensively for European biochemical, physiological and genetic studies) and more salmonid fish (such as rainbow trout), would make good candidates for future genome projects to expand this potential. Except for economically important plants such as wheat and rice, plant scientists have tended to bias genomic efforts to the angiosperms [e.g. 99] and are only now concentrating more on 'model' conifers, ferns, brophytes and algae [100] that will allow broader phylogenetic comparisons. Polyploid taxa have only been included for economically important model species such as wheat, but it would be worthwhile to add diploid–polyploid pairs for comparison, as for the polyploid frog complex discussed above.

Even without complete genome information, animal researchers are making progress in understanding genomic changes that occur after polyploidization that can be compared with the more extensive body of literature available for plants. For example, comparative QTL mapping of related polyploid taxa with structurally divergent chromosomes (arctic charr and rainbow trout) suggests that similar types of structural rearrangements to those seen in plants occur following polyploidization [101]. For example, similar to recent studies on tobacco suggesting alterations in rDNA repeat number [90], there is evidence for changes in repeat element number in intergenic rDNA spacers subsequent to polyploidization in tetraploid *Odontophrynus americanus* frogs [102]. Genome size reduction following successive rounds of polyploidization has been suggested in sturgeon based on a microsatellite-based phylogenetic analysis [103] and in hybridogenetic triploid *Rana esculenta* exposed to radioactive contamination around Chernobyl (intriguingly, such effects are not seen in their sympatric diploid parent) [104]. Similar changes in genome size have also been noted in plants [88]. These preliminary data in animals generally support conclusions based on studies of genomic consequences of polyploidy in plants but there could still be important differences to be revealed by more extensive characterization of polyploid animal genomics or insights based on animal research that could suggest new directions for plant research. In both plants and animals, it is becoming clear that genomic efforts should be expanded from model organisms to include a broader phylogenetic context that would allow more detailed comparative studies. Expanding this emphasis to more joint considerations of patterns seen across taxonomic boundaries should soon be an achievable goal.

Conclusions

In this exciting age of technological advancement, genetic tools permit increasing dissection of the structure and function of polyploid genomes in both plants and animals. Many of the early advances in animal research in this area are being 'rediscovered' in plants, and vice versa, but a more efficient approach in the future will be to combine results from both groups to increase our understanding of the factors involved in the origins and establishment of polyploid lineages, as well as the genetic, ecological and

economic consequences of genome duplication. The time is ripe to develop new hypotheses using insights gained across taxonomic groups.

For more extensive discussion of the areas touched on here, readers should consult the proceedings of an international conference on polyploidy held at the Linnean Society and Kew Gardens (London, UK) in April 2003, which should be published in *Biol. J. Linn. Soc.* in 2004.

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