Biological relevance of polyploidy: ecology to genomics
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'Why polyploidy is rarer in animals than in plants': myths and mechanisms

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Although polyploidy has been involved in speciation in both animals and plants, the general perception is often that it is too rare to have been a significant factor in animal evolution and its role in plant diversification has been questioned. These views have resulted in a bias towards explanations for what deters polyploidy, rather than the somewhat more interesting question of the mechanisms by which polyploidy arises and becomes established in both plants and animals. The evidence for and against some of the traditional views on polyploidy is reviewed, with an attempt to synthesize factors promoting evolution through genome duplication in both groups. It is predicted that polyploidy should be more common in temperate than in tropical breeders because environmental fluctuations may promote unreduced gamete formation, it should be most common in organisms with sufficient numbers of gametes that random meiotic problems can be overcome, and it should be more frequent when mechanisms to promote assortative mating are a direct byproduct of genome duplication. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **82**, 453–466.

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INTRODUCTION

The study of polyploidy in both plants and animals has been strongly biased by discounting of its potential importance in evolutionary diversification by several highly influential researchers. In 1925, H. J. Muller published a paper entitled 'Why polyploidy is rarer in animals than in plants' (Muller, 1925) that has tended to diminish the value of polyploidy research in animals ever since. Although details of the argument have been revisited on occasion (Orr, 1990), the central dogma that animals should not tolerate polyploidy because of their mode of sexual reproduction has been maintained, despite accumulating evidence that many animals do exist as polyploids (reviewed in Bogart, 1980; Lokki & Saura, 1980; Schultz, 1980; Otto & Whitton, 2000).

Similarly, L. G. Stebbins, in addition to a number of primary papers on the subject, wrote two seminal books that have significantly shaped the focus of polyploid research in plants (Stebbins, 1950, 1971). Although Stebbins devoted large sections of each of these books to polyploidy and recognized its wide prevalence in plants, he clearly viewed it as a 'complicating factor' that 'retards rather than promotes progressive evolution', so that polyploids are effectively evolutionary dead ends. Stebbins' surveys of polyploid distributions and patterns have been highly valuable to plant polyploid research but his emphasis on evolutionary limitations has tended to downplay its potential significance.

By contrast, since the late 1960s, S. Ohno has promoted gene and genome duplication as a significant factor in the evolution of all eukaryotes (predominantly based on allozyme data in fish) (Ohno, Wolf & Atkin, 1968) and predicted that vertebrates have arisen through two rounds of ancient polyploidiza-

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tion events in the evolution of fish through to mammals (Ohno, 1970, 1999). Although details of the number and timing of these duplication events remains controversial (e.g. Meyer & Schartl, 1999; Escriva *et al*., 2002; Page & Cotton, 2003; Furlong & Holland, 2004 – this issue), recent genome analyses have generally supported these early contentions (e.g. Meyer & Schartl, 1999; Nadeau & Sankoff, 1997; Spring, 1997; Pennisi, 2001; Wolfe, 2001; Furlong & Holland, 2004).

Although the question of why polyploidy is less frequent in animals than plants is intriguing in its own right, the question has been concentrated largely on a limited number of taxa where it is particularly rare (predominantly mammals and *Drosophila*) and which are unlikely to reflect the full diversity of animal reproductive strategies. This approach has tended to curtail studies of polyploid evolution in animals, especially in groups like mammals where the first reports of polyploid species have been made only recently (Gallardo *et al*., 1999, 2004 – this issue). A somewhat more fruitful approach for understanding the limits to polyploidization is to ask: 'Why is polyploidy more common in some animal groups than in others?' and 'What features do these taxa share with plants that promote evolution through polyploidization?' Fankhauser (1945) provided a detailed review of the consequences of polyploidy for development in amphibians compared with plants (and insects) but this type of synthetic approach has not been the focus of many recent studies (but see Otto & Whitton, 2000).

The purpose of this paper is to revisit some of the classical views about the evolution of polyploidy in both plants and animals in order to dispel 'myths' that may misdirect research attention and to identify similarities between plant and animal polyploids that could elucidate mechanisms of polyploid origin and establishment in both. In the interests of space conservation, comparisons will be drawn predominantly between plants and amphibians but similar examples could be drawn from fish (e.g. Mable, 2003; Le Comber & Smith, 2004 – this issue) or various invertebrate taxa (e.g. Lokki & Saura, 1980; Adamowicz *et al*., 2002).

TRADITIONAL VIEWS: CHALLENGING THE MYTHS

SEX AND POLYPLOIDY: THE *DROSOPHILA* EYE VIEW

Muller's (1925) argument relied on the assumptions that (1) the system of sex determination displayed by *Drosophila* (i.e. XY male heterogamety, in which gender is determined by the ratio of X chromosomes to autosomes in homogametic females) represented that found in most animals, and that (2) triploids were a necessary intermediate in the formation of even-ploidy individuals. He suggested that imbalances in sex chromosomes in triploids would lead to intersexes and non-viable gametes, making it unlikely that balanced tetraploids could be formed (and if tetraploids were formed they would be at a reproductive disadvantage compared with diploids owing to random segregation of sex chromosomes). He predicted that if this were true, then polyploidy should also be rare in dioecious plants with genetic control of sex determination. This hypothesis was soon falsified by botanists based on the relatively frequent occurrence of polyploidy among dioecious plants (Westergaard, 1940; Stebbins, 1950; including experimental production of polyploid lines in dioecious plants: Westergaard, 1958). In fact, based on a dataset compiled by Bertin (1993) and chromosome numbers based on Darlington & Wylie (1955), 56% of gynodioecious species include polyploids compared with 47% of gynomonoecious species (my unpubl. data). In addition, Muller's hypothesis was subsequently suggested as being too restrictive even by other *Drosophila* geneticists because not many animals show a *Drosophila*-like sex determination system (e.g. Orr, 1990). Nevertheless, a surprisingly large number of papers have continued to cite Muller's thesis to dismiss polyploidy as a significant factor in animal evolution. In 1925, polyploidy had been characterized in relatively few species of plants or animals and very little was known about the genetic control of sex determination in the vast majority of organisms; the *Drosophila* model was thought to represent the majority of animals simply because few other systems had been characterized. Later research showed that the *Drosophila* system was actually the exception, even among dipterans (Sturtevant, 1965), whereas Y dominance was thought to be a more widespread mechanism (Bull, 1983).

Based instead on the assumption that Y (or Z) dominance (involving a genetically degenerate sex chromosome) was the predominant mode of sex determination in animals, Orr (1990) proposed that rarity of polyploidy in animals was due to disruption of the dosage compensation necessary to maintain genetic balance between genders for genes found on the fully functional sex chromosome. He suggested that 'unbalanced genotypes would almost surely be lethal' in such cases. Although the model is elegant and some of Orr's predictions could explain the difficulty of maintaining polyploidy in groups such as mammals, Stebbins' conclusion that Muller's model 'could hardly be expected to be responsible for the scarcity of polyploidy in the animal kingdom as a whole' (Stebbins, 1950: 368) could just as easily be applied to Orr's thesis.

In reality, little is known about the factors that control sex determination in the vast majority of dioecious organisms, but it has not been demonstrated that the

dosage compensation model is widely prevalent outside of mammals and insects (although its apparent absence in birds has been questioned recently: see Ellegren, 2002). Among dioecious plants, heteromorphic sex chromosomes are found in a number of groups (reviewed by Charlesworth, 2002) and there is evidence for early stages of Y degeneration in at least one species (*Silene latifolia*: Guttman & Charlesworth, 1998). In amphibians, where polyploidy is relatively frequent, sex chromosomes for some polyploid species are in an initial state of differentiation (Bogart, 1980; Kobel, 1985) and there appears to be a great deal of flexibility in sex determination that could allow for polyploidy without sex disruption. One fascinating system occurs in the *Rana rugosa* species complex, where variation in sex-determining mechanisms occurs within a single species (Nishioka *et al*., 1994), with some populations showing male heterogamety (XX/XY) and some showing female heterogamety (ZW/ZZ) as well as individuals being capable of switching to environmentally determined sex under some conditions (Fig. 1). It is true that a number of polyploid vertebrates (Dawley & Bogart, 1989) and invertebrates (Muldal, 1951; Suomalainen, 1958) reproduce parthenogenetically (development of unreduced eggs without male input), gynogenetically (development of unreduced eggs with male gamete stimulation but without sperm incorporation) or hybridogenetically (development of unreduced eggs with one parental genome eliminated premeiotically and replaced by fertilization with sperm from a sexual species), but these modes of reproduction are also found among diploids (e.g. Bogart *et al*., 1987) and not all triploids reproduce asexually (Stöck *et al*., 2002). Similarly, in plants, a

strong association has been noted between polyploidy and apomixis (Stebbins, 1950, 1971) but it is not clear whether polyploidy is a cause, a consequence or a tolerated byproduct of the loss of sexual reproduction (see Mable, 2003, for a comparison of unisexual reproductive strategies in plants and animals).

Conclusion. Although the consequences of polyploidy for sex determination is a fascinating area of research and may account at least partially for the apparent rarity in groups such as mammals, disruption of sex-determining mechanisms alone cannot explain limits to patterns of polyploidization across most plant and animal taxa.

PHYSIOLOGICAL/DEVELOPMENTAL CONSTRAINTS

One of the direct consequences of polyploidization is an increase in cell size, which could alter physiological or developmental processes that rely on carefully balanced regulatory systems. A popular view is that animal development is more easily perturbed by changes in genome copy number because their development is more complicated than the relatively 'simple' scheme found in plants (Wettstein, 1927; Stebbins, 1950). Orr (1990) rejected this view on the basis that parthenogenetic and hermaphroditic animals frequently show polyploidy but do not appear to suffer from excessive developmental abnormalities. In addition, it is relatively easy to produce polyploids experimentally in many animal groups (Jackson, 1976), with higher ploidy offspring often appearing more vigorous than their progenitors (e.g. Fankhauser, 1945; Bogart & Wasserman, 1972). The frequency of unreduced gametes in plants also may be higher than previously thought (Maceira *et al*., 1992; Ramsey & Schemske, 1998; Husband & Schemske, 2000). In amphibians, developmental difficulties in hybrids between diploids and polyploids are found more often when the diploid is the female parent and often become apparent at the gastrula stage (when the male genome first becomes involved in gene expression), suggesting that the ratio of nuclear–cytoplasmic factors is critical but can be maintained as long as the polyploid genome contributes the cytoplasmic component (e.g. Bogart, 1980; Mable & Bogart, 1995). In plants, similar reciprocal differences in polyploid hybrid viability are often apparent (Stebbins, 1950, 1971) and imbalances in endosperm development have been implicated in the infertility of triploid individuals (Johnston *et al*., 1980). This added complication in plant development could actually make polyploidy more and not less difficult than in animals.

Plants and animals, in general, may employ different strategies to cope with the increase in cell size accompanying polyploidy. Whereas many plants main-

Rana rugosa

XX x ZZ   ZW x XY

↓   ↓   + TSD

all XZ   ZX   ZY   WX   WY
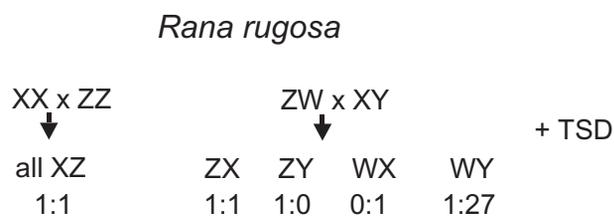1:1   1:1   1:0   0:1   1:27

Figure 1. Flexibility in sex determination systems. Populations of *Rana rugosa* from Japan show either male (XY) or female (ZW) heterogamety (Nishioka & Hanada, 1994). Crosses between individuals from these populations and sex reversal studies indicate that the female-determining genes on the W chromosome are dominant to male-determining genes on the Z and Y but that those on the X are coexpressed with the Z, and that individuals are capable of switching to environmentally determined sex under some conditions (TSO). Segregation of genotypes and ratios of male to female progeny are indicated for crosses between an XX female and a ZZ male, and between a ZW female and an XY male.

tain the same number of cells as diploids and thus develop larger organ and body size (e.g. Stebbins, 1950), many animal polyploids instead reduce the overall number of cells and maintain a similar organ and body size to their diploid progenitors (e.g. Fankhauser, 1945; Bachman & Bogart, 1975). These cellular changes are often achieved without major changes in physiology (e.g. Ralin, 1981; Kamel, Marsden & Pough, 1985). Especially in cases where the number of cells per unit area is not reduced (Petit & Thompson, 1997), certain aspects of plant physiology may be altered by the change in cell size accompanying polyploidy (e.g. polyploids may be more tolerant to water deficit: Li, Berlyn & Ashton, 1996; or may have higher photosynthetic rates: Wullschleger *et al.*, 1996) but this varies considerably across taxa (e.g. Stebbins, 1950).

Although there is probably a lower limit to the number of cells necessary to form tissues and organs, it is possible that the very fact that animals can regulate cell numbers would enable them to deal better with changes in gene dosage and developmental pathways. For example, octoploids in some species of cultivated plants (e.g. wheat) are often not as vigorous as tetraploid or hexaploid individuals (Stebbins, 1950), whereas high polyploid series are found in some animals, such as the frog genus *Xenopus* (Kobel & Du Pasquier, 1986). It is interesting that triploid *Drosophila* apparently do not preserve body size through changes in cell number (Fankhauser, 1945), and polyploidy is rare in this group. In frogs, whereas triploid hybrids between tetraploid *Hyla versicolor* females and diploid *Hyla cinerea* males are very vigorous and show some fertility, a replicable problem in eye development accompanies this cross combination (Mable & Rye, 1992). It has been suggested that cell numbers are not reduced in polyploid neural tissues (Fankhauser, 1945; Jackson, 1976), opening the possibility that regulation of cell numbers may facilitate developmental balance in polyploid animals.

Conclusion. Many animals and plants are capable of accommodating and compensating for developmental and/or regulatory changes in physiological processes associated with polyploidization. Although polyploidy might be rarer in groups that cannot tolerate such changes, these factors are not sufficient to explain distributions of polyploids over all animal groups.

RARITY OF POLYPLOIDY

Another long-held view is that polyploidy should be a rare evolutionary transition within groups and should occur only under specialized conditions, which are more frequent in plants than in animals. Stebbins (1950) suggested that polyploidy should be more com-mon in perennials than in annuals (to allow a longer opportunity for finding a mate of the same cytotype), in species capable of vegetative or apomictic reproduction (to generate more local mating partners of the same cytotype or to make mating unnecessary), and in species capable of self-fertilization (which can bypass problems of mate availability). Many polyploid animals have iteroparous reproduction and many have the capacity for asexual reproduction, suggesting that the same conditions could be satisfied in animals. By contrast, there are few hermaphroditic animals that reproduce through selfing, which could represent a potential advantage in plants. However, it is unclear how strong the association between selfing and polyploidy actually is among angiosperms. Both ploidy and self-compatibility are highly labile traits (Mable, 2004), there are a relatively large number of species that show both polyploidy and strong self-incompatibility (e.g. Stebbins, 1950; Barrett, 1998), and outcrossing rates do not always differ between tetraploids and their diploid progenitors (Soltis & Soltis, 2000). In the arctic, Brochmann *et al.* (2004 – this issue) found that most species (regardless of ploidy) were self-compatible, emphasizing potential confounding factors when generalizing patterns of this type.

Stebbins (1950) suggested that autopolyploids were probably more frequent than often considered because of the 'fallacy' that simple segregation rules (i.e. autopolyploids showing multivalent associations and allopolyploids showing bivalent associations) can be used to distinguish modes of origin. However, he also concluded that autopolyploids usually experienced reduced fertility associated with chromosome imbalances (although this was not found by Ramsey & Schemske, 2002) and showed a reduced capacity for generating novel adaptive gene complexes due to the buffering effects of having extra gene copies (Stebbins, 1971). This has promoted the view that allopolyploids should be more successful because they effectively stabilize new gene combinations brought together through hybridization (Clausen, Keck & Hiesey, 1945; Stebbins, 1950, 1971) and that polyploidy should be rare in animals because hybridization is rare (Stebbins, 1950; Swanson, 1958; Dufresne & Hebert, 1994). However, hybridization in mammals occurs frequently enough that it poses a conservation threat to a number of mammalian species (e.g. red deer: Goodman *et al.*, 1999; wolves: Wilson *et al.*, 2000), and it is even more widely prevalent in other animal groups (reviewed by Bogart, 1980; Dowling & Secor, 1997). In addition, tetrasomic inheritance may mean that autopolyploids are not as genetically depauperate as often assumed, explaining why autotetraploids often show higher levels of enzyme heterozygosity than their diploid progenitors (reviewed in Soltis & Soltis, 1993; Petit, Thompson & Bretagnolle, 1996).

In the plant literature there has been a complete shift from the view that most polyploids should result from a single origin to a generalized rule that multiple origins are most common for both allo- and autopolyploids (Soltis & Soltis, 1993, 1999; Leitch & Bennett, 1997; Ramsey & Schemske, 1998 and Abbott & Lowe, 2004; Ainouche, Baumel & Salmon, 2004; Doyle *et al.*, 2004; Soltis *et al.*, 2004 – all this issue). This is also true in many animal groups. For example, both the grey treefrogs (genus *Hyla*) of North America (with polyploidy arising relatively recently) and burrowing frogs (genus *Neobatrachus*) of Australia (an older group with multiple recognized polyploid species) show clear evidence that polyploidy has arisen on multiple occasions (Ptacek, Gerhardt & Sage, 1994; Mable & Roberts, 1997). In amphibians, allopolyploidy has only been demonstrated conclusively for a few groups (Kobel & Du Pasquier, 1986; Channing & Bogart, 1996) but this may be due to the often cryptic nature of diploid–polyploid species complexes (e.g. Fig. 2).

Conclusion. Polyploidy does not appear to be as difficult an evolutionary transition as is often proposed, with multiple origins of both allo- and autopolyploids frequent in both plants and animals. Differences in reproductive strategies may influence the likelihood of polyploid establishment but do not appear to explain differential patterns in plants and animals.

POLYPLOIDY AS AN EVOLUTIONARY DEAD END

The view of polyploids as evolutionary dead ends is obviously contradicted by many of the papers in this volume and needs little justification here. Evidence of ancient polyploidy in organisms now considered to be diploid suggests that polyploidy is a dynamic process that has contributed to evolutionary diversification in plants and animals through successive rounds of polyploidization and rediploidization (Haufler & Soltis, 1986; Werth & Windham, 1991; Larhammar & Risinger, 1994; Spring, 1997; Wolfe, 2001; Blanc, Hokamp & Wolfe, 2003; Bowers *et al.*, 2003; Furlong & Holland, 2004). Mainly based on allozyme data in fish, neutral models in the 1970s predicted that duplicate genes should lose function through time via random genetic drift (Ohno, 1970; Allendorf, 1978) but rates of loss have been far below expectations. For example, catostomid and salmonid fish retain approximately 50% duplicate gene expression, despite at least 40 million years of divergence as polyploids (Bailey, Poulter & Stockwell, 1978) and many genes are retained in duplicate in polyploid series of *Xenopus* frogs (Hughes & Hughes, 1993). In relatively young lineages of polyploid frogs (Danzmann & Bogart, 1983) and fish (Danzmann & Down, 1982) inheritance may vary between tetrasomy, disomy and mixed models by enzyme locus,
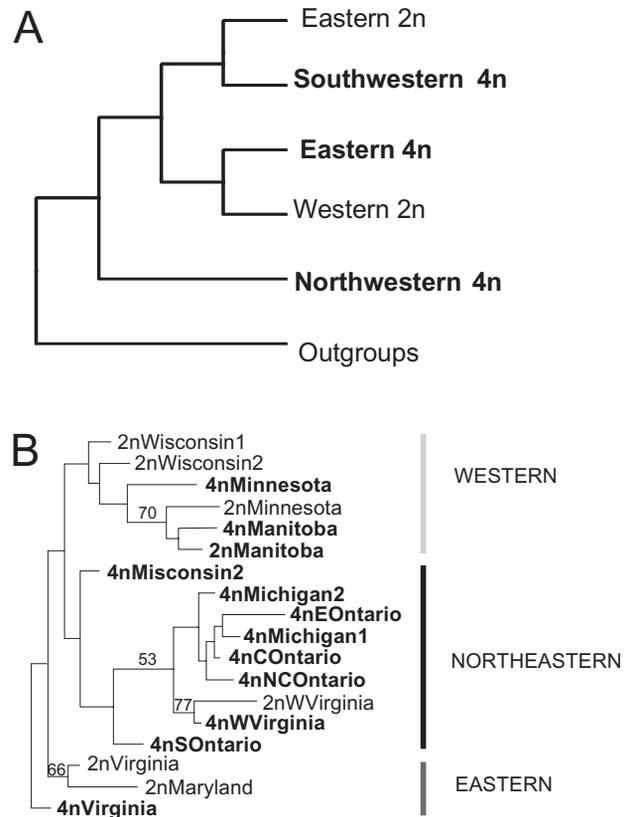

Figure 2. The difficulty of establishing modes of origin from comparisons based on uniparentally inherited and biparentally inherited genes. For the North American grey treefrog complex (*Hyla versicolor*, $4x = 48$, and *Hyla chrysoscelis*, $2x = 24$) (A) mtDNA sequences (cytochrome *b*, based on Ptacek *et al.*, 1994) indicate that tetraploid lineages (in bold) are most closely related to non-sympatric diploids, whereas (B) allozyme data (based on Mable, 1996) suggest that tetraploid lineages (in bold) are most closely related to their sympatric diploids. This could indicate hybrid origins but the completely cryptic nature of speciation in this group (i.e. no morphological differences between tetraploids or diploids from different parts of the range) cannot rule out parallel selection on allozymes in similar habitats.

tissue type or individual. It is clear that duplicate genes may also develop novel functions (e.g. Ferris & Whitt, 1977; Walsh, 1995; Nadeau & Sankoff, 1997) or divide functions between different tissue types or stages of development (e.g. Ferris & Whitt, 1977; Lynch, 2001, 2002; Adams *et al.*, 2003). This emphasizes the dynamic and unpredictable nature of processes resulting in gene silencing and functional divergence that could vastly expand genetic diversity among polyploid lineages. Polyploids from multiple origins are not always genetically or ecologically

equivalent (e.g. Segraves & Thompson, 1999; Soltis & Soltis, 2000; Soltis *et al*., 2004) and polyploid groups may speciate further either through 'normal' allopatric channels to produce additional species at the same ploidy level or through successive increases in ploidy level (Kobel & Du Pasquier, 1986; Mable & Roberts, 1997; Soltis & Soltis, 1999). With some exceptions (e.g. Cronn, Small & Wendel, 1999; Frieman *et al*., 1999; Axelsson *et al*., 2000), polyploidy has been shown to result in rapid and dramatic rearrangements in genome structure in a number of plants (e.g. Song *et al*., 1995; Leitch & Bennett, 1997; Schranz & Osborn, 2000; Ozkan, Levy & Feldman, 2001; Shaked *et al*., 2001; Osborn *et al*., 2003; Levy & Feldman, 2004 – this issue).

Conclusion. Rather than representing an evolutionary dead end, polyploidization has the potential to be an important source of evolutionary novelty that has contributed to the diversification of both plants and animals (*sensu* Levin, 1983).

MODERN APPROACHES: MECHANISMS

It is clear that polyploid lineages have evolved frequently, via a variety of pathways, and continue to contribute to evolutionary diversification. However, relatively little is known about the mechanisms by which they arise and become established in competition with their diploid counterparts (Bogart, 1980; deWet, 1980; Lumaret, 1988; Felber, 1991; Thompson & Lumaret, 1992; Ramsey & Schemske, 1998; Soltis & Soltis, 2000). Theory suggests that the likelihood of polyploid formation is limited by the rate at which unreduced gametes are produced and the patterns of mating that unite these gametes, whereas the likelihood of the establishment of independently evolving polyploid lineages will be limited by the difficulty of encountering a mate of the same ploidy level and by hybrid inviability (Levin, 1975; Fowler & Levin, 1984; Felber, 1991; Thompson & Lumaret, 1992; Bever & Felber, 1998; Ramsey & Schemske, 1998). These elements are currently receiving more research attention in plants (Husband, 2004 – this issue) but have been described more mechanistically in animals in the past. The following section outlines some similarities between plants and animals that suggest alternative models that could explain how perceived barriers to polyploid establishment are overcome.

ENVIRONMENTAL INFLUENCES

It has often been noted that there is a higher frequency of polyploid plants and animals at higher latitudes and higher altitudes, with particularly high proportions of polyploid taxa in arctic populations (e.g.
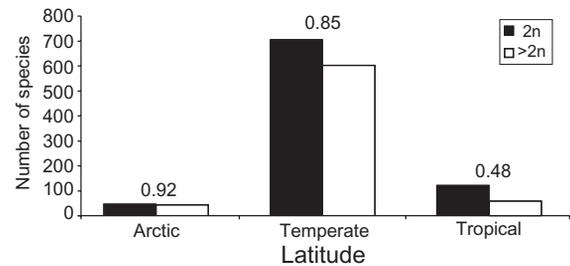
Figure 3. Distributions of diploid and polyploid plant species in arctic, temperate and tropical regions. Proportions of polyploid species in each region are indicated above the nodes. Although the proportion of species suggests an increasing frequency of polyploids with increasing latitude, the overall number of species indicates more diploids in all regions and more species overall in temperate zones. This reflects a bias in research effort on temperate plants.

Stebbins, 1950; Muldal, 1951; Johnson & Packer, 1965; Jackson, 1976; Lokki & Saura, 1980; Beaton & Hebert, 1988; Soltis & Soltis, 1999; Brochmann *et al*., 2004). The most common explanation has been that polyploids are capable of tolerating and invading harsher environments than their diploid counterparts due to changes in physiology resulting from increased cell size (e.g. Löve & Löve, 1943; Stebbins, 1950; Ehrendorfer, 1980; Salemma, 1984) and/or increased genetic buffering provided by having 'extra' genome copies (e.g. Swanson, 1958; Johnson & Packer, 1965; Roose & Gottlieb, 1976; Tal, 1980; Levin, 1983; Soltis & Soltis, 1993). However, these patterns are not universal and it remains unclear what mechanisms best explain current polyploid distributions. For example, in fireweed (*Chamerion angustifolium*) diploids are distributed further north and at higher elevations than their autotetraploid derivatives (Husband & Schemske, 1997; Husband, 2004). In addition, there are more herbaceous plants (Stebbins, 1950), more self-compatible plants (Brochmann *et al*., 2004), and more asexually reproducing plants (Stebbins, 1950, 1971) and animals (Muldal, 1951; Suomalainen, 1958; Cole, 1980; Beaton & Hebert, 1988) at higher altitudes and latitudes, making it difficult to dissociate polyploidy *per se* from factors that may favour its occurrence. Whereas the proportions of polyploids in arctic, temperate and tropical regions successively decrease, absolute numbers indicate more diploids in temperate and tropical regions and more species overall in temperate zones (Fig. 3). This emphasizes the sensitivity of trends of this type to sampling: work on tropical plants has been much more limited than in other regions (Stebbins, 1971; Jackson, 1976), potentially distorting the pattern. Although greater ecological amplitude has been demonstrated in some polyploids compared with their diploid progenitors (Jackson,

1976; Felber-Girard, Felber & Buttler, 1996; Petit *et al*., 1996; Soltis & Soltis, 2000), this trend varies widely when multiple diploid–polyploid pairs are compared, with some diploids showing broader ranges than their tetraploid derivative (e.g. Stebbins, 1950). Tolerance of extreme conditions such as cold does not necessarily accompany polyploidization; in fact, some polyploids have been demonstrated to show lower cold tolerance than their diploid counterparts due to changes in osmotic pressure resulting from altered surface area to volume ratios (Stebbins, 1971; Sugiyama, 1998).

An alternative explanation for the relative frequency of polyploids at higher latitudes and altitudes could be proposed based on the likelihood of producing unreduced gametes. Although it was previously thought that somatic doubling was the predominant mode of polyploidization in plants, more recent literature suggests that formation of diploid gametes through meiotic non-disjunction is the more likely route (Jackson, 1976; deWet, 1980; Felber, 1991; Watanabe, Peloquin & Endo, 1991; Rabe & Haufler, 1992; Ramsey & Schemske, 1998) as has long been assumed for animals (e.g. Fankhauser, 1945; Bogart & Wasserman, 1972). In plants, unreduced gametes (pollen and oocytes) may be generated experimentally through colchicine treatment (e.g. Eigsti, 1957; Pandey, 1968) but may also be produced by exposure to fluctuating environmental conditions (deWet, 1980; reviewed in Felber, 1991; Rabe & Haufler, 1992). Recent studies have suggested that unreduced gametes are also produced at non-trivial rates in field populations or laboratory crosses (de Haan *et al*., 1992; Maceira *et al*., 1992; Rabe & Haufler, 1992; Ramsey & Schemske, 1998; Burton & Husband, 2000; Husband & Schemske, 2000; Husband, 2004). In amphibians, unreduced oocytes have been induced at high frequency using cold, heat or pressure shock in many species and commonly occur in untreated laboratory-raised females (e.g. Fankhauser, 1945; Bogart & Wasserman, 1972; Bogart, 1980) or in natural populations (Lowcock & Licht, 1990). If the production of unreduced gametes is increased during times of environmental instability in natural populations, it is possible that there are more polyploids in temperate and arctic regions (and at higher altitudes) because there is a higher chance that individuals will experience cold or heat shock during their breeding season. This was originally suggested in principle for plants (Hagerup, 1932) and later for animals (Mable, 1996) but has not received much further attention. In addition, potential problems with finding a mate of the same ploidy level (i.e. minority cytotype exclusion: Levin, 1975) could be reduced if large numbers of unreduced gametes from the same individual are produced (for species capable of selfing) or if sufficient numbers of individuals in a population produce unreduced gametes in a localized area.

Prediction. Polyploidy should be more prevalent in organisms likely to be exposed to environmental instability during their breeding season, which could promote higher frequencies of meiotic non-disjunction, and increase the potential numbers of polyploid individuals in local mating pools. Thus, polyploids might be expected to be more frequent in temperate than in tropical regions, and at higher altitudes simply because there is a higher probability of their initial formation.

GAMETE INTERACTIONS

Formation of polyploid individuals is only the first step in the problem of establishing polyploid lineages. Especially if there are differences in the rate of production of unreduced male and female gametes, it is likely that triploid individuals will be produced most often (at least initially). Although triploids are effectively inviable in some groups (humans, for example, may produce a relatively large proportion of diploid sperm but triploid individuals generally do not survive to adulthood: Carothers & Beatty, 1975), reducing the likelihood of establishment of polyploid lines, in many plants and animals triploids are vigorous and healthy but largely infertile (e.g. Fankhauser, 1945; Stebbins, 1950; Bogart & Wasserman, 1972; Levin, 1975; Felber, 1991). This has been seen as a major stumbling block in the generation of even-ploidy lineages. However, in plants, triploids may show at least low frequencies of viable gametes (Felber, 1991; Bretagnolle & Thompson, 1995; Ramsey & Schemske, 1998; Burton & Husband, 2000; Husband & Schemske, 2000; Ramsey & Schemske, 2002) and not all triploid animals are sterile (e.g. Stöck *et al*., 2002; Bogart, 2003). Apomictic, automictic or unisexual polyploids have often been viewed as a separate class from sexually reproducing species but it is possible that they could form a critical intermediate step in the formation of even-ploid sexual lineages. In animals, triploid amphibians are often capable of gynogenetic reproduction to produce unreduced triploid eggs that subsequently could be fertilized by diploid males (e.g. Bogart, 1980; Bogart, Elinson & Licht, 1989; Elinson *et al*., 1992). For example, all-female gynogenetic salamanders in the genus *Ambystoma* form an ancient polyploid complex of unisexual lineages with a complex history of genetic interactions with sympatric sexual species that have resulted in continual changes in ploidy level and nuclear genome composition (Bogart, 2003). In plants, although many apomictic species display at least low levels of sexual reproduction (e.g. Kollmann, Steinger & Ba, 2000; van Baarlen *et al*., 2000; Nakayama, Seno

& Matsuda, 2002), this has not been suggested as a major route to tetraploid formation. The 'alternative' reproductive strategies employed by both plants and animals could be key to formation of bisexual lineages rather than merely sexual anomalies.

It has also been suggested that fertility of polyploid hybrids may be increased with genetic divergence of the parental genomes in both plants (Stebbins, 1950, 1971) and amphibians (Blair, 1972; Bogart, 1980; Mable & Bogart, 1995). This may be due to mechanisms for recognition and preferential pairing of homeologous chromosome sets such as occurs during hybridogenetic reproduction, where one parental genome is eliminated premeiotically (e.g. Vinogradov *et al*., 1990). For example, hybrids between female tetraploid grey treefrogs (*Hyla versicolor*) and diploid males in the same genus indicated that, whereas triploid hybrids with the putative diploid progenitor (*Hyla chrysoscelis*) were vigorous but reproductively sterile (Bogart & Wasserman, 1972; Bogart, 1980), those with more distantly related males (*Hyla arborea*, *Hyla cinerea*) had at least low levels of fertility (Mable & Bogart, 1995). Surviving backcrosses between triploid males and tetraploid females lacked both distinctive allozyme and chromosomal markers from the diploid grandfather. Although chromosome morphology is highly conserved among hylids and preferential gene silencing could explain the results, it is possible that only gametes with balanced chromosome sets from the tetraploid female parent were viable. Chromosomes from the diploid progenitor may be too similar to recognize, reducing the probability of preferential sorting of chromosomes from each parent. Such preferential pairing of homeologous chromosomes has also been found in rainbow trout hybrids (Diter, Guyomard & Chourrout, 1988). In crop plants, wheat pairing genes (*Ph*) have long been known to influence homeologous pairing (Waines, 1976) and more recent work has elucidated mechanisms whereby such systems could operate to sort chromosomes premeiotically in polyploid hybrids (e.g. Jackson & Casey, 1980; Martinez-Perez, Shaw & Moore, 2001).

If triploids produce even a small proportion of gametes with balanced chromosomes, it is possible that the number of gametes is a critical factor in determining which taxa are capable of producing polyploid lineages. This would be enhanced if mechanisms exist for recognition and preferential sorting of chromosomes from each contributing parental genome. Although this would be facilitated in allopolyploids, Stebbins (1980) suggested that chromosome recognition mechanisms might also operate in autopolyploids resulting from crosses between genetically divergent populations of the same species. Most animal polyploids produce large numbers of both male and female gametes and most sexually reproducing polyploid lineages have external fertilization, where random mixing of gametes would be facilitated. Even though most plants do not produce large numbers of female gametes, most produce large numbers of pollen. Especially if pollen with unbalanced chromosome sets do not produce pollen tubes, sorting of 'undesirable' pollen could be facilitated at the surface of the stigma so that only those with balanced chromosome complements would reach the ovaries.

Prediction. Even with limited triploid fertility, polyploidy should be favoured in organisms producing multiple male (and female) gametes to allow differential survival and selection of zygotes (or gametes) containing balanced chromosome sets. External gamete sorting (mixing and filtering of gametes based on self, species or cytotype compatibility) could facilitate this process, as could mechanisms allowing preferential pairing of particular combinations of chromosomes at meiosis.

ASSORTATIVE MATING

Reliance on predominantly random associations would still make the probability of establishment of even-ploid lineages low, even if selection were only strong for survival of individuals derived from balanced gametes. However, this process would be facilitated if gametes of the same ploidy level were effectively prefiltered to achieve a higher probability of assortative mating by cytotype. This would be particularly effective if such mechanisms operated prezygotically, to reduce wasted reproductive effort. Polyploidy is often accepted as the only unambiguous mechanism for sympatric speciation because of the 'automatic' postzygotic isolation that can result from triploid hybrid sterility. Under this view, prezygotic isolation mechanisms are expected to evolve secondarily with genetic divergence. However, polyploidization may also have immediate effects on prezygotic isolating mechanisms. Because cell size normally increases with increases in genome size (e.g. Cavalier-Smith, 1978; Bogart, 1980; Masterson, 1994; Kondorosi, Roudier & Gendreau, 2000), characters that are directly influenced by cell size, shape or number may change as a byproduct of changes in DNA content. For example, for several diploid–polyploid pairs of frogs, tetraploids produce mating calls (the major feature used by females to select mates) that have a slower pulse repetition rate than their diploid progenitors (Bogart, 1980; Castellano *et al*., 1998). Bogart & Wasserman (1972) noted that the ratio of pulse rates in diploids compared with tetraploids was almost exactly the inverse of the ratio of cell sizes. Observations that tetraploid calls remain the same despite multiple origins (Bogart, 1980) and that artificially

produced autotriploids show intermediate calls to diploids and tetraploids (Keller & Gerhardt, 2001) reinforce this conclusion. Bogart (1980) suggested that organisms like salamanders may only be able to reproduce unisexually as polyploids because females do not have as reliable cues to choose mates of the appropriate ploidy level. In plants, despite recognition that features such as flower size, number, nectar quantity, pollen tube size and flowering time often differ between diploids and their tetraploid derivatives (Fankhauser, 1945; Stebbins, 1950; Lewis & Suda, 1976; Lumaret, 1988; Davis *et al.*, 1996), few studies have so far examined the relative importance of prezygotic isolating mechanisms to polyploid origins and establishment. However, this is an area of growing interest (Thompson & Lumaret, 1992; Bretagnolle & Thompson, 1995; Petit *et al.*, 1997). Husband (2004) and coworkers have shown that pollinators preferentially visit flowers of particular cytotypes (Husband & Schemske, 1998, 2000; Husband *et al.*, 2002), and that separation in flowering time, variation in cytotype distributions and differential growth rates of diploid and tetraploid pollen tubes may facilitate reproductive isolation between cytotypes. Thompson, Nuismer & Merg (2004 – this issue) and coworkers (Thompson *et al.*, 1997; Segraves & Thompson, 1999; Nuismer & Thompson, 2001; Husband, 2004) have shown that predatory insects may show differential preferences for diploid and tetraploid plants, but it is not clear which cues are used. It is very difficult to distinguish changes occurring at the time of polyploidization from characters selected after establishment but flowering time has been shown to be altered in neopolyploids compared with their diploid progenitors, at least in some cases (Lewis & Suda, 1976; Schranz & Osborn, 2000), although Ramsey & Schemske (2002) found few generalized trends in neopolyploids.

Prediction. Polyploidy should be most prevalent in organisms that have the potential to achieve reproductive isolation automatically from their diploid progenitors through prezygotic mechanisms related to changes in cell size accompanying polyploidization.

CONCLUSIONS

Classical views on the evolution of polyploidy in plants and animals were often generated prior to the availability of detailed studies on the distribution, prevalence and genetic characterization of polyploid taxa. Although these early views provided excellent insights and have formed the basis for large numbers of studies on polyploidy, many of their basic assumptions have not held up to scrutiny with more extensive and modern data. Many early studies drew conclusions based on painstaking chromosome counts and allozyme data. We now have more modern tools such as flow cytometry to enable us to screen genome sizes rapidly within and between populations, and comparative mapping and gene expression studies should allow us to broaden our perspectives far beyond the limitations of this early work. It is much harder to find things when you are not looking for them and the long-promoted views that polyploidy is a rare and difficult evolutionary transition may have inhibited discovery of the true extent of polyploidy, especially in animals. Fankhauser (1945) suggested that study of polyploidy was not as common in animals because, unlike crop plants, there were few obvious benefits to animal breeding. Recent findings of multiple polyploidization events in mammals (Gallardo *et al.*, 1999, 2004) emphasize the need to screen for polyploidy in both plants and animals before conclusions can be drawn definitively on its putative rarity. The fact is that chromosome counts in multiple individuals per population have not been as frequent in animals, which could explain why so many fewer examples of polyploids are known.

The main purpose of this paper was to survey plant and animal taxa that do exist as polyploids, and to identify common mechanisms favouring the origin and establishment of polyploid lineages. The model proposed suggests that polyploidy should be most common in: (i) populations exposed to environmental fluctuations during their breeding season that may induce higher frequencies of unreduced gametes; (ii) organisms producing sufficient numbers of gametes that random meiotic problems can be filtered; and (iii) in organisms for which mechanisms to promote assortative mating have the capacity to change as a direct consequence of polyploidization. These predictions could be evaluated by addressing the following questions, preferably using closely related species pairs:

1. Are polyploids in arctic and temperate regions more exposed to environmental fluctuations during their breeding season than those from tropical regions?
2. What proportion of gametes or individuals experience meiotic non-disjunction with environmental change?
3. Is there geological evidence that polyploid species arose most frequently during times of severe climatic change?
4. Is there a threshold gamete number that allows polyploidy?
5. Are mechanisms that allow preferential chromosome pairing sufficient to result in balanced chromosome sets beyond random associations?
6. When polyploid fertility is limited, how often is gamete mortality related to unbalanced chromosome sets?

7. Is polyploidy more common in organisms with external fertilization or gamete sorting?

8. Are there more polyploids in organisms with mate choice mechanisms that operate before zygote formation?

9. How commonly do isolating mechanisms change automatically with cell size change in neopolyploids?

We are still in the early stages of understanding the factors contributing to the origin and establishment of polyploidy lineages, but the diversity of papers in this symposium related to these questions (Abbott & Lowe, 2004; Ainouche *et al*., 2004; Brochmann *et al*., 2004; Gallardo *et al*., 2004; Husband, 2004; Soltis *et al*., 2004) demonstrates great promise for future advances in this area.

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