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VIEWPOINT

The timetable for allopolyploidy in flowering plants

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• *Background* Our understanding of the processes and dynamics of allopolyploid speciation, the long-term consequences of ploidal change, and the genetic and chromosomal changes in new emerged allopolyploids has substantially increased during the past few decades. Yet we remain uncertain about the time since lineage divergence when two taxa are capable of spawning such entities. Indeed, the matter has seemed intractable. Knowledge of the window of opportunity for allopolyploid production is very important because it provides temporal insight into a key evolutionary process, and a temporal reference against which other modes of speciation may be measured.
• *Scope* This Viewpoint paper reviews and integrates published information on the crossability of herbaceous species and the fertility of their hybrids in relation to species' divergence times. Despite limitations in methodology and sampling, the estimated times to hybrid sterility are somewhat congruent across disparate lineages. Whereas the waiting time for hybrid sterility is roughly 4–5 million years, the waiting time for cross-incompatibility is roughly 8–10 million years, sometimes considerably more. Strict allopolyploids may be formed in the intervening time window. The progenitors of several allopolyploids diverged between 4 and 6 million years before allopolyploid synthesis, as expected. This is the first study to propose a general temporal framework for strict allopolyploidy. This Viewpoint paper hopefully will stimulate interest in studying the tempo of speciation and the tempo of reproductive isolation in general.

Key words: Allopolyploidy, cross-incompatibility, divergence time, hybrid sterility, life history, reproductive isolation, S-locus, speciation.

INTRODUCTION

During the past decades, novel genetic and genomic approaches have substantially advanced our understanding of the processes and dynamics of polyploid speciation and of the long-term consequences of ploidal change (Otto, 2007; Soltis, 2010; Soltis and Soltis, 2012; Abbott *et al.*, 2013). New approaches also have fuelled our understanding of the genetic, epigenetic and chromosomal alterations that polyploid species experience very early in their histories (Xu *et al.*, 2009; Flagel and Wendel, 2010; Petit *et al.*, 2010; Ng *et al.*, 2012; Buggs *et al.*, 2012; Shi *et al.*, 2012); and new quantitative applications have shed light on diversification rates in diploids and polyploids (Mayrose *et al.*, 2010, 2011; Arrigo and Barker, 2012).

In contrast to our broad understanding of population and phylogenetic dynamics, and of the lability of neopolyploid genomes, we do not know when diploid taxa are sufficiently different to spawn allopolyploids with two very distinctive genomes (strict allopolyploids), i.e. when their diploid interspecific hybrids would be sterile or nearly so. What is the waiting time for strict allopolyploidy within a phylad? Are we talking about a few thousand years after divergence from a common ancestor or a few million years, or more? Even the most recent and very comprehensive treatment of hybridization and speciation does not address this question (Abbott *et al.*, 2013). Knowledge of the window of opportunity for allopolyploid production is very important because it provides temporal insight into a key evolutionary process, and a temporal reference against which other modes of speciation may be measured. It also informs us of when ancient species contacts could have spawned strict allopolyploids and when they could not.

The level of divergence in the genomes of allopolyploids falls along a continuum. Whereas strict allotetraploids are characterized by disomic inheritance and bivalent formation, some allopolyploids may have a mixture of the former, and tetrasomic inheritance and quadrivalent formation. These have been referred to as segmental allopolyploids (Stebbins, 1947). Segmental allotetraploids are derived from diploid hybrids that are partially fertile and whose chromosomes are partially homologous (Ramsey and Schemske, 2002). These hybrids would form unreduced gametes at a higher rate than diploid members of a species, but at a lower rate than hybrids with quite divergent genomes. This paper focuses on strict allopolyploids.

The duration over which strict allopolyploids may be generated is based in part on the time it takes for diploid species to become so divergent that anomalous chromosomal pairing in their F_1 hybrids yields an elevated level of unreduced gametes. In some species combinations, unreduced gamete production approaches 30 % vs. the average of 0·5 % for non-hybrids (Ramsey and Schemske, 1998). However, the rate in hybrids may be considerably lower, as in *Gilia* (Grant, 2002), *Alstromeria* (Ramanna *et al.*, 2003) and *Solanum* (Bani-Aameur *et al.*, 1992), where values typically are <10 %. Different parentages of a given interspecific hybrid may yield substantially different unreduced gamete productions. Meiotic errors that produce $2n$ gametes may occur at the first meiotic division, resulting in first division restitution or in second division restitution (Ramsey and Schemske, 1998).

Once hybrids produce only univalents or nearly so, the window of opportunity for strict allopolyploid production will remain open until lineages are no longer cross-compatible or until pre-pollination barriers preclude hybridization. The waiting time for hybrid sterility recently has been addressed in flowering plants, as estimated from data on hybrid fertility in relation to taxon divergence times (Levin, 2012). Based on an array of herbaceous lineages, it appears that roughly 4–5 million years (My) passes before first-generation hybrids become sterile or nearly so. The bases for sterility, chromosomal pairing anomalies or genetic incompatibility seem not to have a different temporal signal.

Given that it takes roughly 4–5 My of divergence for hybrid sterility to arise in herbaceous genera, we may ask about the time necessary for the cross-compatibility of lineages to be seriously compromised. The greater the time between the loss of fertility and the loss of cross-compatibility, the broader will be the window for the genesis of strict allopolyploids. During that period, local or regional environmental change and/or long-distance dispersal may allow once isolated species to hybridize and spawn polyploids. The difference between the onset of substantive hybrid sterility and the onset of cross-incompatibility represents the maximum window of opportunity for strict allopolyploidy.

Based on a comprehensive literature review, I will show here that pollen–pistil incompatibility is likely to take much longer to evolve than hybrid sterility, and that the opportunity for the production of strict allopolyploids may extend for millions of years. Indeed if hybrid sterility was longer in the making than cross-incompatibility, allopolyploids would not be formed. I will obtain estimates of the time to cross-incompatibility from approximate divergence times of taxa in relation to their ability to interbreed. When divergence times in the literature are presented between two values, I will use the mid-point of the range. Cross-compatibility refers to the production of hybrid seeds. Taxa are considered to be cross-compatible even if crosses are productive in one direction, but not in the other. The waiting time for hybrid sterility has been estimated previously from approximate divergence times of taxa in relation to their hybrid's fertility (Levin, 2012). Only species with the same ploidal level are included in the study.

The genesis and union of unreduced gametes in F_1 hybrids is the most prominent avenue to allopolyploidy (Ramsey and Schemske, 1998; Levin, 2002), and the only one considered herein. In addition to the abundance of data on hybrid sterility and unreduced gamete production in both natural and artificial hybrids, and the association of sterile hybrids with allopolyploids in nature, we know that the production of unreduced gametes from sterile hybrids depends on the genotype of the diploid parents, and that allopolyploid production from sterile hybrids varies with parentage within a taxon combination and from one taxon combination to another, even in the same genus (Ramsey and Schemske, 1998). Studies on *Gilia* (Grant, 1965, 2002), *Solanum* (Bani-Aameur *et al.*, 1992) and *Alstromeria* (Ramanna *et al.*, 2003) are notable in these respects.

Another avenue to allopolyploid (in this case allotetraploid) formation involves allotriploids (AAB). The products of unreduced gamete formation in a diploid and interspecific hybridization, these entities in turn must cross (using an unreduced gamete) with a member of species B. This process rarely appears in the recent literature and ostensibly is infrequent in nature (Ramsey and Schemske, 1998). Finally, an allotetraploid could be produced through the fusion of unreduced gametes from two diploid species, thereby by-passing the need to produce diploid interspecific hybrids. This 'bilateral sexual polyploidization' is rarely mentioned in the recent literature beyond manipulations with cultivars (e.g. *Lilium*; Khan *et al.*, 2010).

THE PERSISTENCE OF CROSS-INCOMPATIBILITY

The long persistence of cross-compatibility is most evident in the numerous, successful crosses between genera. In the grass family, crosses are possible between *Hordeum* and *Triticum* (Fedak, 1980), which diverged roughly 13 million years ago (Mya; Gaut, 2002), and between *Hordeum* and *Secale* (Forster and Dale 1983), which split roughly 25 Mya (Gaut, 2002). Crosses between *Sorghum* and *Saccharum*, which shared a common ancestor about 20 Mya (Zeng *et al.*, 2012), also have been successful (Hodnett *et al.*, 2010). Hybrids may be obtained from *Festuca* and *Lolium* (Whittington and Hill, 1961), whose lineages split about 13 Mya (Zeng *et al.*, 2012). In contrast to the aforementioned generic pairs, *Zea* and *Sorghum* are cross-incompatible, although they diverged only approx. 9 Mya (Gaut, 2002). In many crossing combinations between widely divergent parents, seed set is low and/or embryos need special treatment in order to develop normally.

The ability of some older lineages to cross is no guarantee that younger ones will be able to do the same. Having just referred to *Zea*, consider the genus *Silene*. Crosses between *Lychnis* and four *Silene* species are successful (Kruckeberg, 1962; Crang and Dean, 1971), even though the genera diverged roughly 10–15 Mya (Frajman *et al.*, 2009; Sloan *et al.*, 2009). Hybrids are also obtained between *S. douglasii* and *S. hookeri* (Kruckeberg, 1961), and between *S. virginica* and the latter (Kruckeberg, 1955), which split approx. 10–16 Mya (Sloan *et al.*, 2009). Conversely, crosses between *S. noctiflora* and other members of the section Elisanthe fail (Prentice, 1978). Divergence time between this species and other members of the section is roughly 7 Mya (Frajman *et al.*, 2009). Species with more recent divergence times (3–4 Mya) readily interbreed (e.g. *S. douglasii* and *S. virginica*, and *S. douglasii* and *S. latifolia*; Kruckeberg, 1963; Frajman *et al.*, 2009; Sloan *et al.*, 2009).

When do lineages lose the ability to interbreed? The data on mustards and grasses presented earlier suggest that it may be well over 10 My. However, it need not be that long. *Collinsia* species may become cross-incompatible 5–7 My after divergence (Garber, 1975; Baldwin *et al.*, 2011). In *Silene*, cross-incompatibility may arise in <7 My (Prentice, 1978; Frajman *et al.*, 2009). In *Lupinus*, crossing barriers may arise within 6–10 My of lineage splitting (Williams *et al.*, 1980; Drummond, 2008). There is no reason why different genera or different lineages within genera should be synchronous in this respect.

All species pairs with estimated divergence times of 4·5–6 Mya that I could find are cross-compatible. These pairs include *Aquilegia flabellata* and *Aquilegia viridiflora*, and *Aquilegia ecalcarata* and *Aquilegia sibirica* (Taylor, 1967; Bastida *et al.*, 2010), *Circaea lutetiana* and *Circaea alpina*, and *Circaea*

cordata and *Circaea erubescens* (Boufford, 1990; Xie *et al.*, 2009), and *Arabidopsis thaliana* and diploid *Arabidopsis arenosa* (Koch *et al.*, 2000; Bomblies and Weigel, 2010), and the former and *Arabidopsis lyrata* (Nasrallah *et al.*, 2000; Kuittinen and Aguade, 2000).

THE BASIS FOR CROSS-INCOMPATIBILITY

In some lineages, the self-incompatibility (or S-) locus and modifiers of S-gene activity are prime players in cross-incompatibility, and divergence at these loci contributes to incompatibility. The role of the S-locus in cross-incompatibility is very well documented in the Solanaceae (Bernacchi and Tanksley, 1997; McClure *et al.*, 2000; Li and Chetelat, 2010; Bedinger *et al.*, 2011). The S-locus also has been implicated in cross-incompatibility within *Prunus* (Šurbanovski *et al.*, 2007), *Brassica* (Hiscock and Dickinson, 1993), *Papaver* (Paape *et al.*, 2011) and in several other genera.

It is also important to recognize that other loci may also reduce the crossability of species (Liedl *et al.*, 1996; McClure *et al.*, 2000; Hancock *et al.*, 2003). For example, the *Tcb1* gene and the genetically linked *Ga-1* gene confer the pollen–pistil barrier between maize and teosinte (Kermicle and Evans, 2005; Kermicle, 2006). These genes are also involved in the inability of flint and dent strain pollen to fertilize popcorn strains, although reciprocal crosses are effective (Kernicle and Evans, 2005; Dresselhaus *et al.*, 2011). In *Leptosiphon*, variation in the rejection of heterospecific pollen is unrelated to the S-genotype (Goodwillie and Ness, 2013).

Where the S-locus is important in cross-incompatibility, the slow rate of barrier building may be a consequence of the slow rate of S-gene divergence. Substantial sequence divergence is required for the genesis of new S-allele specificity. In other words, mutation rates are low. Castric *et al.* (2008) have shown that sequence divergence among S-alleles tends to be very high, while that within S-alleles is generally low. S-alleles differ in as many as 40 % of the amino acid sites (Schierup *et al.*, 2001). Identical or nearly identical S-gene sequences are shared among congeneric species, as in *Physalis* (Lu, 2001), *Prunus* (Šurbanovski *et al.*, 2007; Sutherland *et al.* 2008) and *Lycium* (Savage and Miller 2006). Even different genera may share S-alleles (e.g. *Brassica* and *Arabidopsis*; Edh *et al.*, 2009).

Thus far, cross-incompatibility has been considered in terms of pollen–pistil incompatibility. However, seed abortion may also contribute to reduced seed production in some species combinations. Abortion may result from abnormal development of either the embryo or the endosperm. Both are sensitive to genetic incompatibilities (Levin, 2000, 2003*a*; Tiffin *et al.*, 2001). Hybrid incompatibility in seeds is especially well understood from physiological/developmental and genetic perspectives in *Solanum* (Lester and Kang, 1998; Moyle and Graham, 2005; Moyle and Nakazato, 2010), where both pollen–style incompatibility and seed abortion contribute to the reproductive isolation of species (Bedinger *et al.*, 2011). Multiple quantitative trait loci (QTLs) contribute to hybrid seed lethality in *Solanum* and in *Arabidopsis* (Burkart-Waco *et al.*, 2012). Three QTLs contribute to seed inviability in crosses between *Brassica* and *Raphanus* (Tonosaki *et al.*, 2013). A recent survey of reproductive isolation in angiosperms showed that reduced production of hybrid seeds was a much stronger barrier than the failure of hybrid seeds to germinate (Lowry *et al.*, 2008).

THE ALLOPOLYPLOID WINDOW

Given that that roughly 4–5 My passes before first-generation hybrids become sterile or nearly so (Levin, 2012), the information presented above indicates that crossability is apt to decline much later than hybrid fertility, which leaves a window for strict allopolyploid formation. This window extends from a few to several million years. The most compelling argument for a million year plus window is obtained within genera. For example, in *Collinsia*, hybrid sterility arose about 4 My after lineage splitting compared with 5–7 My for cross-incompatibility (Garber, 1975; Baldwin *et al.*, 2011). In *Silene*, hybrid sterility emerged 3–7 Mya compared with 7–12 Mya for cross-incompatibility (Kruckeberg, 1962, 1963; Frajman *et al.*, 2009). The conclusion that sterility emerges before cross-incompatibility differs from that of Moyle *et al.* (2004), who found no difference in the evolutionary rates of these barriers in *Silene*, when using genetic distance as a surrogate for time.

The notion that strict allopolyploid production occurs within a window of a few to several million years also is supported by the interval between species divergence and the genesis of their allopolyploids. For example, the progenitors of the tetraploid *Nicotiana tabacum* diverged about 4·5 Mya, whereas the latter evolved only 0·2 Mya (Clarkson *et al.*, 2005). The antecedents of the tetraploid *Viola guadalupensis* evolved about 13 Mya, while the diploids arose roughly 8 Mya. The lineages of *Brassica oleracea* and *B. rapa* diverged roughly 3·7 Mya, whereas their allotetraploid derivative, *B. napus*, arose $<10\,000$ years ago (Cheung *et al.*, 2009). *Arabidopsis thaliana* and *A. arenosa* diverged about 6 Mya (Koch *et al.*, 2000), while their allotetraploid, *A. suecica*, evolved $<300\,000$ years ago (Jakobsson *et al.*, 2006). The B and C genomes of the *Oryza officinalis* complex split about 4 Mya, but BC tetraploids formed only between 0·3 and 0·6 Mya (Wang *et al.*, 2009). The carriers of the A and D genomes in *Gossypium* diverged about 6·7 Mya, whereas allopolyploid cotton formed roughly 1·5 Mya (Senchina *et al.*, 2003).

The level of genetic divergence typically is greater for progenitors of strict allopolyploids than for progenitors of diploid hybrid species (Buggs *et al.*, 2009; Paun *et al.*, 2009). Accordingly, we would expect parental divergence times to be shorter in the latter. The products of diploid hybrid speciation in *Helianthus* provide support for this notion. The parental *Helianthus annuus* and *H. petiolaris* diverged roughly 1·6 Mya (Timme *et al.*, 2007; Strasburg and Rieseberg, 2008); and their hybrid derivatives (*Helianthus anomalus*, *H. deserticola* and *H. paradoxus*) were formed between 60 000 and 200 000 years ago (Rieseberg *et al.*, 2003). Accordingly, the parental species were about 1·5 My old when the hybrid lineages were formed vs. the 4–6 My spread for the progenitors of the aforementioned allopolyploids.

Recently, there has been a vigorous debate as to whether there is a strong connection between genetic/chromosomal divergence and the occurrence of polyploidy (Buggs *et al.*, 2011). I do not argue that such a connection does or does not exist, but rather that there is probably a relationship between the level of divergence and the type of polyploid that is formed. Very little

divergence would yield an autopolyploid, modest divergence a segmental allopolyploid, and substantial divergence a strict allopolyploid.

Given the presence of a window for allopolyploid formation, we may ask whether such formation is likely to be soon after hybrid sterility 'evolved' or very much later. The former is the logical choice because cross-compatibility would be the highest immediately after the fertility demise, and would subsequently decline due to stochastic changes at the loci affecting crossing relationships. This progression is suggested by the reduction in crossability with increasing species divergence times in *Silene* (Kruckeberg, 1962, 1963; Frajman *et al.*, 2009) and in *Collinsia* (Garber, 1975; Baldwin *et al.*, 2011), and by the inverse relationship between species crossability and genetic distance (e.g. *Nolina*, Jewell *et al.*, 2012; sexually deceptive orchids, Scopece *et al.*, 2007, 2008). Allopolyploids are also more likely to be formed early in the window because hybrids would become less vigorous as their parental taxa aged due to their gradual stochastic accumulation of many Dobzhansky–Muller incompatibilities with small effects (Orr and Turelli, 2001; Coyne and Orr, 2004).

If species were sympatric during the rather wide window for allopolyploid production, the 'same' polyploids could evolve repeatedly at multiple points in time and space, and become extinct many times as well. Neither the A nor the B genome would be constant in time, so each recapitulation of the AABB species may be somewhat different. Indeed, alternative AABB lines may go forward on independent evolutionary trajectories. If synchronous in time, different 'transfigured' allopolyploids may be able to interbreed with each other.

Sympatry does not ensure polyploidy even if chromosomally disparate species are cross-compatible, because pre-pollination barriers (e.g. divergent habitat preference, flowering time, and floral architecture and attractants) typically appear much earlier (after lineage divergence) and develop at a much faster rate than hybrid sterility (Levin, 2012). A considerable time differential between the emergence of pre- and post-pollination barriers is well illustrated in many Hawaiian genera, wherein substantial adaptive radiation during the past 3–4 My has not been accompanied by strong post-pollination barriers (Baldwin and Sanderson, 1998; Price and Wagner, 2004; Keeley and Funk, 2011). Pre-pollination barriers probably are the direct targets of diversifying natural selection (Levin, 2003*b*; Givnish, 2010), whereas post-pollination barriers probably arise very slowly through the gradual stochastic accumulation of genic and chromosomal differences (Levin, 2012). The ecological, temporal and pollination strategies of long separated allopatric taxa may be conserved by habitat selection, pleiotropy and the lack of genetic variation (Wiens, 2004). Accordingly, the level of pre-pollination isolation is not expected to increase progressively over time, because the niches of related lineages do not diverge progressively over time (Prinzing *et al.*, 2001; Wiens and Graham, 2005; Couvreur *et al.*, 2011; Peterson, 2011). Given that other pre-zygotic barriers may evolve before cross-incompatibility, the window of opportunity for strict allopolyploid production between specific taxon pairs may close well before cross-incompatibility emerges. The time required for substantial pre-pollination isolation may be orders of magnitude less than the time required for the emergence of genomic and cross-incompatibility (Schluter, 2000; Seehausen, 2002; Mendelson, 2003; Fitzpatrick, 2004; Malone and Fontenot, 2008).

The reinforcement of pollen–pistil incompatibility by natural selection against hybrid production (or gametic wastage) also would reduce the opportunity for allopolyploid production among sympatric species prior to the time dictated by the stochastic elaboration of cross-incompatibility. Such reinforcement has occurred in natural populations of *Costus* (Kay and Schemske, 2008; Yost and Kay, 2009). The potential for strengthening crossing barriers is evident in the substantial responses to artificial selection for such in *Zea* (Paterniani, 1969) and *Phlox* (Fritz, 1997).

Whereas there is a temporal window during which strict allopolyploids may evolve, no such window exists for autopolyploids. New independent diploid lineages may produce autoploid derivatives from early in their history until they become extinct. This may amount to tens of millions of years, which is much longer than the opportunity window for strict allopolyploidy. Diploids simply need to produce unreduced gametes; time since their inception is not an issue. The production of sterile or semi-sterile hybrids, and the retention of interspecific cross-compatibility are not requirements for autopolyploidy.

Segmental allopolyploids fall between auto- and allopolyploids in their genetic and chromosomal behaviour. These entities contain genomes that are less divergent than those of strict allopolyploids. Since the magnitude of genomic divergence is a function of time (Coyne and Orr, 2004), we may surmise that the progenitors of segmental allopolyploids were younger at the time of hybridization than were the progenitors of strict allopolyploids. The waiting time for segmental allopolyploidy may vary from a few hundred thousand years to a million years or more depending on the rate of genetic and chromosomal change, and thus may differ substantially among lineages. Such polyploids may be formed until their progenitors are so divergent that their derivatives would be deemed strict allopolyploids. Accordingly, the same two lineages which generated strict allopolyploids at one point in time may have generated segmental versions at earlier points in their histories. I do not suggest that one form of allopolyploid is more likely to form and to persist longer than another.

Thus far, the focus has been on an approximate timetable for allopolyploidy in herbs. This timetable may vary in relation to plant habit and life history. In trees, partial fertility and cross-compatibility tend to persist for a much longer time, so the window for allopolyploidy in trees is likely to be much later than that for herbs. It is not clear whether the window will be wider. The North American/Asian *Liriodendron tulipifera* and *L. chinense* are between 10 and 16 My old, and form partially fertile hybrids (Parks and Wendel, 1990). In *Liquidambar*, some species combinations that diverged roughly 10 Mya are quite cross-fertile, but yield sterile hybrids (Hoey and Parks, 1991). The North American/European *Platanus occidentalis* and *P. orientalis* separated about 50 Mya (Feng *et al.*, 2005), yet their hybrid is partially fertile (Panetsos *et al.*, 1994). Fertile hybrids are obtained between the North American disjuncts *Acer rubrum* and *Acer saccharinum*, which separated about 4 Mya (Santamour, 1965; Renner *et al.*, 2008).

The longer waiting time for sterility and cross-incompatibility in trees is expected, because the generation time in trees is much longer than that in herbs. Notably, the rate of molecular evolution

in herbaceous plants is roughly 2·5 times faster than that in woody plants based on a global phylogenetic analysis of angiosperms (Smith and Donoghue, 2008). Annuals have faster substitution rates than perennials (Yue *et al.*, 2010).

Life history also might be a factor affecting the onset of hybrid sterility and cross-incompatibility. Self-fertilizing colonizing species, especially those with short population lives and very small effective sizes, are more prone to the stochastic genetic and chromosomal changes which promote post-pollination isolation than are outbreeding species that experience fewer bottlenecks per unit time. For example, genetic drift is the likely cause of chromosomally based hybrid sterility among conspecific populations of *Draba nivalis* (Grundt *et al.*, 2006; Skrede *et al.*, 2008). These populations are thought to have arisen within the past 1 million years.

We cannot dismiss the possibility that crossing barriers might have arisen prior to other post-pollination barriers in some incompatible taxon combinations. Partial cross-incompatibility may evolve in a relatively short time when populations are subjected to multiple genetic bottlenecks, substantial inbreeding and repeated episodes of intense directional selection, as occurs during domestication (Gross and Olsen, 2010). Rapid emergence of crossing barriers is manifest during the domestication of annual *Phlox drummondii* during the past 200 years (Levin, 1976). Cultivars most derived from their wild progenitor are the least cross-compatible with the latter. Along somewhat similar lines, crossing barriers have evolved among maize cultivars, and between maize and its progenitor (teosinte), which diverged about 9000 years ago. The growth of maize pollen is restricted on the silks of teosinte owing to the *Tcb-1* locus and the genetically linked *Ga-1* locus (Kermicle, 2006).

Partial incompatibility also may arise coincident with bottlenecking, inbreeding and selection in natural populations. The passage through an extreme bottleneck (perhaps <5 individuals) with a concomitant decline in S-locus diversity and emergence of self-fertility may be responsible for the evolution of partial cross-incompatibility between *Capsella rubella* and *Capsella grandiflora* (Hurka and Neuffer, 1997), which diverged about 30 000–50 000 years ago (Guo *et al.*, 2009). The cross-incompatibility within the Aegean *Nigella arvensis* complex also may emerge from the stochastic processes that ostensibly shaped some phenotypic and genetic variation (Strid, 1970; Comes *et al.*, 2008).

If crossing barriers arose prior to hybrid sterility, then viable, fertile hybrids would lie beyond a crossing barrier. To assess whether fertile hybrids indeed might reside there, we may consider somatic cell (parasexual) hybrids produced from the fusion of the protoplasts of congeneric species or those in different genera. Most fusion products involving rather divergent taxa are weak, and have abnormal development and/or unstable chromosome complements in which the chromosomes of one species or the other are eliminated during development (Sherraf *et al.*, 1994; Begum *et al.*, 1995; Spangenberg *et al.*, 1995; Wang *et al.*, 2003). These plants typically have much reduced fertility or are sterile (e.g. intergeneric somatic cell hybrids in the Brassicaeae; Prakash *et al.*, 2009).

A few caveats about when strict allopolyploids may evolve are in order. The dates used to estimate the demise of hybrid fertility and cross-compatibility are not the product of a precise, uniform methodology; so they must be considered quite approximate. One concern is that the error terms in phylogenetic estimates of divergence times may be considerable (Ho and Phillips, 2009; Schwartz and Mueller, 2010). Secondly, the genes used in estimating divergence time vary across studies, and may deviate from molecular rate constancy across lineages (Gaut *et al.*, 2011). Then there is the matter of sample size. Only a few molecular phylogenies contain species about which the hybrid fertility and/or species crossability are known, so the database is a bit shallow. Finally, the populations used to establish hybrid fertility and taxon crossability may not be representative of the taxa as a whole (Levin, 1978, 2000; Grant, 1981; Scopece *et al*, 2010).

CONCLUSIONS

This is the first study to propose a general temporal framework for strict allopolyploidy. Moreover, it is the first study to assess the approximate times required to reach two major milestones of allopatric speciation. Despite limitations in methodology and sampling, the estimated times to hybrid sterility, and to a lesser extent cross-incompatibility, are somewhat congruent across disparate lineages. This lends credibility to the correlational approach. Moreover, the parental divergence times of several allopolyploids are rather similar across phylads. This level of congruence is somewhat surprising, given that hybrid sterility and cross-incompatibility are products of stochastic processes. It is also surprising because the degree of local sympatry among congeners during the polyploid window must have varied widely among phylads, as must have the degree of pre-pollination isolation.

The temporal difference between the onset of substantive hybrid sterility and the onset of cross-incompatibility represents the maximum potential window of opportunity for strict allopolyploidy. Given the frequent evolution of pre-pollination barriers between lineages, it would not be surprising that strict allopolyploids form well before cross-incompatibility is strongly developed. The genesis of several allopolyploids roughly 4–8 My after the divergence of their antecedents (as noted above) is consistent with this view.

Whereas the approximate time to hybrid sterility and cross-incompatibility for given lineages no doubt will be revised as more data accrue, as will the mean time across lineages, the larger message will endure. There is a window of opportunity for strict allopolyploidy, and it will not be soon after species split from a common ancestor. The waiting time for hybrid sterility is probably millions of years, and the time for cross-incompatibility is likely to be a few to many millions of years longer. If not by cross-incompatibility, the window of opportunity will close with the emergence of pre-pollination barriers. Given that the chromosomal and genic divergences yielding hybrid sterility and cross-incompatibility are products of stochastic processes, there is no reason to assume that the times to hybrid sterility and cross-incompatibility will be very similar across taxon pairs.

This review has addressed crossing and fertility relationships of lineages in time. The bases for fertility decline are somewhat understood, especially where chromosomal change is a prime contributor (Levin, 2012). In contrast, our knowledge of the genetic control of cross-incompatibility is still in its infancy, and many questions remain. To what extent is the S-locus involved in cross-incompatibility, and what changes at this locus confer cross-incompatibility? Are losses of self-incompatibility within

species associated with altered interspecific compatibilities? How do severe population contractions and inbreeding influence cross-compatibility? How does a shift away from a hermaphroditic reproductive system impact species' crossability? Are the genetic changes associated with the reinforcement of cross-incompatibility the same as those associated with a gradual increase in cross-incompatibility? Is there any relationship between the expression of pollen–pistil incompatibility and the genetic mechanism underlying it? Answers to these questions will allow us to make informed predictions about the decline of cross-compatibility over time and in relation to the demographic and mating history of taxa, and thus allow us to appreciate more fully the dynamics of speciation and the timetable for allopolyploidy.

Finally, the window of opportunity for strict allopolyploidy is best understood when information on post-pollination isolation and divergence times is available for the same clusters of congeneric species. There is a substantial literature on species' crossability and the fertility of their hybrids, and an expanding literature on species divergence times, but almost invariably they do not involve the same species. A marriage between traditional biosystematics and molecular phylogenetics will yield insights well beyond those obtainable from phylogenetics alone.

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