The role of hybrid seed inviability in angiosperm speciation

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Key words: reproductive isolation, endosperm, imprinting, Bateson Dobzhansky Muller Incompatibility, genetic distance, parental conflict, Endosperm Balance Number

Abstract

Understanding which reproductive barriers contribute to speciation is essential to understanding the diversity of life on earth. Several contemporary examples of strong hybrid seed inviability (HSI) between recently diverged species suggest that HSI may play a fundamental role in plant speciation. Yet, a broader synthesis of HSI is needed to clarify its role in diversification. Here, I review the incidence and evolution of HSI. HSI is common and evolves rapidly, suggesting that it may play an important role early in speciation. The developmental mechanisms that underlie HSI involve similar developmental trajectories in endosperm, even between evolutionarily deeply diverged incidents of HSI. HSI is often accompanied by whole-scale gene misexpression in hybrid endosperm, including misexpression of imprinted genes which have a key role in endosperm development. I explore how an evolutionary perspective can clarify the repeated and rapid evolution of HSI. In particular, I evaluate the evidence for conflict between maternal and paternal interests in resource allocation to offspring (i.e. parental conflict). I highlight that parental conflict theory generates explicit predictions regarding the expected hybrid phenotypes and genes responsible for HSI. While much phenotypic evidence supports a role of parental conflict in the evolution of HSI, an understanding of the underlying molecular mechanisms of this barrier is essential to test parental conflict theory. Lastly, I explore what factors may influence the strength of parental conflict in natural plant populations as an explanation for why rates of HSI may differ between plant groups and the consequences of strong HSI in secondary contact.

72 *Introduction*

73 Evaluating which reproductive barriers contribute to the origin and maintenance of species is
74 foundational to speciation research. The exceptional floral diversity and prevalence of local
75 adaptation in angiosperms has inspired plant biologists to argue for a primary role of extrinsic
76 prezygotic barriers such as immigrant inviability or pollinator isolation (Ramsey et al., 2003;
77 Lowry et al., 2008; Kay and Sargent, 2009; Sobel, 2014; Todesco et al., 2020; Wessinger, 2021;
78 Christie et al., 2022). Undoubtedly, these barriers played a crucial role in the diversification of
79 the ~300,000 extant angiosperms (Christenhusz and Byng, 2016). Yet, other angiosperm key
80 innovations likely contributed to their diversity (Sanderson and Donoghue, 1994). Here, I argue
81 that the evolution of the endosperm has contributed to angiosperm diversification via its
82 contribution to a common, rapidly evolving, and strong intrinsic postzygotic reproductive
83 barrier– hybrid seed inviability (HSI).

84 Endosperm is a nutritive tissue essential for embryo development unique to
85 angiosperms (Baroux et al., 2002). Endosperm is initiated after fertilisation of the central cell
86 and usually has a composition of 2:1 maternal:paternal genomes (though see (Williams and
87 Friedman, 2002)). This 2:1 ratio is crucial for endosperm development, as many genes
88 expressed therein are imprinted (i.e. their expression is parent of origin biased). The balance of
89 maternally- and paternally-expressed genes (i.e. MEGs and PEGs) mediates typical endosperm
90 development (Spillane et al., 2000; Köhler et al., 2003a; b, 2005; Tiwari et al., 2010; Batista et
91 al., 2019). In interploidy crosses, an excess of maternal or paternal expression results in
92 canonical parent of origin specific developmental abnormalities (Lin, 1984; Ehlenfeldt and
93 Ortiz, 1995; Scott et al., 1998). Typical development can be restored by modifying imprinted
94 gene expression (Erilova et al., 2009; Jullien and Berger, 2010; Kradolfer et al., 2013; Wolff
95 et al., 2015), highlighting the importance of imprinting in endosperm development.

96 The endosperm's role as a nutritive conduit makes it a prime target for conflict between
97 ovule- and pollen-parents over resource allocation to offspring (Haig and Westoby, 1989;
98 Moore and Haig, 1991). Parental conflict arises in non-monogamous systems because pollen
99 parents are not equally related to all of the offspring produced, thereby favouring the evolution
100 of paternally-derived alleles that preferentially solicit maternal resources (Trivers, 1974;
101 Charnov, 1979; Queller, 1983; Haig and Westoby, 1989). In response, maternally-derived
102 alleles that restrict resource allocation to offspring can evolve, and a co-evolutionary arms race
103 between paternally-excessive and maternally-repressive alleles can ensue. Within populations,
104 ovule- and pollen-parents should be well matched, but populations can differentially
105 experience this arms race (Haig, 1997; Wilkins and Haig, 2001; Van Cleve and Feldman, 2007;
106 Brandvain, 2010; Brandvain and Haig, 2018). Crosses between populations with different
107 histories of conflict can reveal such mismatches, resulting in parent of origin growth effects
108 (Lloyd, 1968; House et al., 2010; Willi, 2013; Cailleau et al., 2018; Raunsgard et al., 2018).
109 Mismatches can also lead to dysfunctional endosperm and inviability. Given this rapid
110 evolution, HSI may play an important role early in speciation (Zeh and Zeh, 2000; Gutierrez-
111 Marcos et al., 2003).
112 Differences in the extent of parental conflict between taxa have been conceptualised
113 with endosperm balance numbers (i.e. effective ploidy; (Johnston and Hanneman, 1980, 1982;
114 Lin, 1984)). Inspired by the observation that interploidy and interspecific HSI exhibit similar
115 phenotypes, endosperm balance number is a relative ranking of taxa based on crossing
116 outcomes when each taxon acts as an ovule- or pollen-parent, where higher effective ploidy
117 taxa mimic higher ploidy taxa (Johnston and Hanneman, 1980, 1982; Lin, 1984; Städler et al.,
118 2021). Despite phenotypic parallels, the underlying genetic basis of inviability likely differs
119 between interploidy and interspecific HSI, as HSI is instantaneous with polyploidization and
120 requires no allelic evolution (Scott et al., 1998). Conversely, interspecific HSI must be caused

121 by divergence of genes with parent of origin effects. Thus, while both types of HSI can
122 elucidate if/how parental conflict manifests in seeds, interspecific HSI can reveal if/how
123 parental conflict shapes allelic evolution. Yet, much less is known about the incidence, pace,
124 and mechanisms underlying interspecific HSI.

125 Here I review HSI among diploid taxa and assess its commonality and evolutionary
126 rate. I synthesise current knowledge of the genetic and developmental bases of interspecific
127 HSI, and discuss whether they support a role of parental conflict. Lastly, I consider why HSI
128 might evolve more readily in some plant groups, and its implications for secondary contact.

129

130 *HSI is a significant reproductive barrier*

131 HSI arises when heterospecific pollen fertilises an ovule of another species, but the hybrid seed
132 does not reach maturation, usually due to defective endosperm. Many incidences of HSI were
133 described in both crops and natural systems in the twentieth century (Table 1). Often,
134 reproductive isolation was complete in at least one cross direction. While these classic studies
135 highlight the commonality of HSI, only more recently have we begun to understand its
136 evolutionary pace.

137 At the most extreme end, incomplete HSI between *Clarkia xantiana* subspecies has
138 evolved in 65KYA (Briscoe Runquist et al., 2014) and strong, asymmetric HSI between selfing
139 and outcrossing populations of *A. lyrata* evolved in 35KYA (İltaş et al., 2021). In many cases,
140 strong HSI evolves in hundreds of thousands of years to ~1-2MYA (Table 1). This is much
141 faster than hybrid inviability in organisms like *Drosophila,* frogs, *Lepidoptera,* birds, and fish
142 which often take >>1MYA (Coyne and Orr, 1997; Sasa et al., 1998; Presgraves, 2002; Price
143 and Bouvier, 2002; Bolnick and Near, 2005). Similarly, in orchids, which lack endosperm, HSI
144 evolves later than hybrid sterility or necrosis (Scopece et al., 2007, 2008). Despite these

145 intriguing patterns, formal comparisons between endosperm-bearing angiosperms and other
146 lineages are needed.

147 Work in *Mimulus, Streptanthus,* and Solanaceae indicate that HSI can evolve rapidly,
148 and in some cases faster than postmating-prezygotic isolation (Fig. 1; (Vickery, 1964; Jewell
149 et al., 2012; Garner et al., 2016; Oneal et al., 2016; Kostyun and Moyle, 2017; Christie and
150 Strauss, 2018; Roth et al., 2018a; Coughlan et al., 2020; Sandstedt et al., 2020)). In *Mimulus*
151 nearly complete HSI has been found between lineages of *M. decorus*, which diverged
152 ~150KYA, and within the *M. tilingii* complex, which diverged ~400KYA (Sandstedt et al.,
153 2020), but, no incidence of complete postmating-prezygotic isolation is reported for this group.
154 In *Streptanthus* and *Jaltomata*, the earliest complete HSI is found at ~2.5MYA and 1.1MYA,
155 respectively (Fig. 1). For *Streptanthus*, the earliest incidence of complete postmating-
156 prezygotic isolation is similar to that of complete HSI, but HSI is generally a stronger barrier
157 (mean fruit set RI=0.43, mean HSI RI=0.81 (Christie and Strauss, 2018)). Within the
158 Solanaceae, seed set evolves more slowly than HSI (*Jaltomata* (Kostyun and Moyle, 2017),
159 *Nolana* (Jewell et al., 2012), and three pairwise crosses within *Solanum* (Roth et al., 2018a)).
160 However, other incidences of strong postmating-prezygotic isolation occur in *Solanum* (Baek
161 et al., 2015, 2016)), and many species pairs within *Jaltomata* and *Nolana* are unable to form
162 fruits due to pollen-pistil incompatibilities (Jewell et al., 2012; Kostyun and Moyle, 2017),
163 suggesting that postmating-prezygotic barriers evolve rapidly in the Solanaceae. In total, HSI
164 is common, evolves rapidly, and can confer significant reproductive isolation. Given that HSI
165 manifests in the first generation of hybridization, it may serve as a formidable reproductive
166 barrier.

167

168 *HSI is borne in the endosperm*

169 Like interploidy crosses, interspecific HSI is conferred by parent of origin specific endosperm
170 defects (Ishikawa et al., 2011; Rebernig et al., 2015; Baek et al., 2016; Oneal et al., 2016;
171 Lafon-Placette et al., 2017; Roth et al., 2018a; Coughlan et al., 2020; İltaş et al., 2021;
172 Sandstedt and Sweigart, 2022). A causal link between inappropriate endosperm development
173 and inviability is evidenced by embryo rescue experiments, where dissected embryos are plated
174 on a nutritive medium akin to a synthetic endosperm. Often, dissected embryos develop into
175 healthy plants, suggesting that incompatibilities in the endosperm, rather than embryo, cause
176 HSI (Sukno et al., 1999; Rodrangboon et al., 2002; Rebernig et al., 2015; Lafon-Placette et al.,
177 2017, 2018; Sandstedt and Sweigart, 2022).

178 Parent of origin specific endosperm defects are remarkably similar across incidences of
179 HSI, even between highly diverged taxa with different endosperm developmental programs. In
180 one direction of the cross seeds are larger, though flat or disc-like. In these crosses, endosperm
181 fails to cellularize in taxa with nuclear-type endosperm (Ishikawa et al., 2011; Rebernig et al.,
182 2015; Lafon-Placette et al., 2017, 2018; İltaş et al., 2021), or cells become overly large and fail
183 to divide in taxa with cellular-type endosperm (Roth et al., 2018a; Coughlan et al., 2020;
184 Sandstedt and Sweigart, 2022). This delayed development results in diffuse endosperm,
185 arrested embryos, and seed collapse, reminiscent of paternal-excess interploidy crosses. The
186 reciprocal cross resembles maternal-excess interploidy crosses; seeds are smaller, narrower
187 and/or shrivelled (Ishikawa et al., 2011; Rebernig et al., 2015; Lafon-Placette et al., 2017, 2018;
188 Roth et al., 2018a; Coughlan et al., 2020; İltaş et al., 2021; Sandstedt and Sweigart, 2022).
189 Endosperm proliferation is precocious; for taxa with nuclear-type endosperm, endosperm
190 cellularizes prematurely (Rebernig et al., 2015; Lafon-Placette et al., 2017). For taxa with
191 cellular-type endosperm, development is accelerated (Roth et al., 2018a; Coughlan et al., 2020;
192 Sandstedt and Sweigart, 2022). The resultant endosperm is smaller, with fewer cells than pure-
193 species crosses in both cases. These parallel developmental phenotypes among divergent

194 incidences of HSI and developmental systems hint at a shared evolutionary explanation, and
195 the parent of origin effects that mimic excess paternal or maternal expression support parental
196 conflict.

197 Finer scale patterns of endosperm dysregulation offer unique insights into the
198 mechanistic causes and evolutionary drivers of HSI. Successful seed development requires
199 coordination of endosperm, embryo, and maternal integuments, facilitated by a dynamic
200 exchange of nutrients, hormones, and other signals (Doll and Ingram, 2022; Povilus and
201 Gehring, 2022). Endosperm itself is a complex tissue, with many specialised components.
202 Under parental conflict, tissues that mediate nutrient exchange should exhibit paternal-excess
203 or maternal-repression phenotypes. In the endosperm, chalazal haustoria directly facilitate
204 nutrient exchange between maternal tissues and embryos (Povilus and Gehring, 2022). The
205 chalazal haustorium is also involved in regulating cellularization in taxa with nuclear-type
206 endosperm via *TERMINAL FLOWER 1* (*TF1*) expression (Zhang et al., 2020). Cellularization
207 signals a transition from a phase of endosperm growth and sucrose deposition by the maternal
208 plant to one of endosperm consumption by the embryo (Doll and Ingram, 2022). Lastly, the
209 chalazal haustorium is a hotspot for imprinted gene expression (Walia et al., 2009; Picard et
210 al., 2021), and genes that are uniquely expressed therein show elevated rates of adaptive
211 evolution (Geist et al., 2019). Together, this makes it an ideal target for parental conflict. In
212 *Mimulus,* chalazal haustoria persist later in development in paternal-excess hybrids than pure
213 species or maternal-excess hybrids (Sandstedt and Sweigart, 2022). Similar abnormalities have
214 been described in other systems (Brink and Cooper, 1947). Although it's well established that
215 HSI is borne in the endosperm, a mechanistic understanding of embryo-endosperm-maternal
216 integument communication during development is required to understand how these
217 relationships fail in HSI.
218

219 *Genetic of HSI*

220 Parental conflict predicts that lineages with different effective ploidies have diverged in
221 imprinted loci involved in resource partitioning and subsequent mismatches of these MEGs
222 and PEGs leads to parent of origin endosperm abnormalities and inviability. It follows that if
223 parental conflict were driving the evolution of HSI 1) taxa with different effective ploidies
224 should exhibit signals of adaptive divergence in imprinting, 2) hybrids should exhibit abnormal
225 expression of loci that are imprinted in at least one parental species, and 3) the loci that cause
226 HSI should correspond to a subset of the loci in 1 and 2. However, many particulars of this
227 model remain unanswered, and an integration of expression surveys, population genetics, and
228 genetic mapping is required.

229 Imprinting can evolve rapidly. Conservation of imprinted loci is generally low,
230 suggesting rapid turnover (Zhang et al., 2011; Waters et al., 2013; Hatorangan et al., 2016;
231 Klosinska et al., 2016; Chen et al., 2018; Flores-Vergara et al., 2020; Picard and Gehring,
232 2020). In *Capsella,* species generally exhibit more PEGs than MEGs, with the number of PEGs
233 and the expression of MEGs scaling with effective ploidy, suggests that compensatory
234 expression of MEGs may effectively balance PEG expression (Fig. 2; (Lafon-Placette et al.,
235 2018)). In *Solanum*, species exhibit more MEGs than PEGs, and the number of each scales
236 with effective ploidy (Florez-Rueda et al., 2016; Roth et al., 2018b, 2019). Lastly, imprinted
237 genes, particularly PEGs, show some signs of adaptive evolution (Hatorangan et al., 2016;
238 Tuteja et al., 2019).

239 Of the few studies that have quantified expression in hybrid endosperm, misexpression
240 is rampant. In *Capsella,* hybrid endosperm misexpression resembles interploidy crosses for
241 both paternal- and maternal-excess crosses (Rebernig et al., 2015). In *Solanum*, inviable
242 hybrids show extensive expression differences from intraspecific crosses (Florez-Rueda et al.,
243 2016, 2021a; Roth et al., 2019). While all hybrids exhibit maternally biassed expression

244 (Florez-Rueda et al., 2016), MEGs and PEGs tend to be overexpressed in maternal- and
245 paternal-excess crosses, respectively (Roth et al., 2019). In both *Capsella* and *Solanum*
246 paternal-excess crosses overexpress several PEGs, including AGAMOUS-LIKE Type1
247 MADS-box (AGL) genes whose overexpression is implicated in both interploidy and
248 interspecific HSI in *Arabidopsis (Rebernig et al., 2015; Roth et al., 2019)*. Hybrids also exhibit
249 complex patterns of misexpression. In *Solanum*, reciprocal F1s show a deficit of sRNA
250 expression, which contributes to greater gene expression in hybrid than intraspecific
251 endosperm (Florez-Rueda et al., 2021a). In *Capsella*, paternal-excess hybrids show reduced
252 chromatin condensation and methylation, which may cause dysregulated gene expression,
253 particularly of *PHERES1* (*PHE1*) targets (Dziasek et al., 2021). *PHE1* is a master regulator of
254 PEGs (Batista et al., 2019). How much of endosperm misexpression is a cause versus
255 consequence of inviability remains unknown, but a fundamental role of overexpression of some
256 MEGs and PEGs is evidenced by the fact that induced polyploidization of the lower effective
257 ploidy taxa can restore seed viability (Lafon-Placette et al., 2017, 2018; Tonosaki et al., 2018;
258 Sandstedt and Sweigart, 2022).

259 Although much remains unknown about the genetic basis of HSI, genetic mapping and
260 inheritance patterns suggest that HSI is caused by many moderate-to-large, parent of origin
261 effect loci ((Rebernig et al., 2015; Garner et al., 2016; Lafon-Placette et al., 2017; Dziasek et
262 al., 2021); i.e. 18 QTL control HSI between *M. guttatus* and *M. tilingii,* each of which decreases
263 viability by 20-60% (Garner et al., 2016)). Explicit links between imprinted genes and HSI
264 have been made in *A. thaliana* and *A. arenosa,* wherein loss of function *PHE1*, *AGL90,* and
265 *AGL62* mutants partially restores seed viability (Josefsson et al., 2006; Walia et al., 2009).
266 Although not uniquely supportive of parental conflict, parental conflict does predict a
267 polygenic basis of HSI. This is because paternal-excess alleles instigate the arms race, while
268 the evolution of maternal-repressive alleles are compensatory. However, in most incidences of

269 asymmetric HSI, paternal-excess crosses are more lethal. Without multiple rounds of allelic
270 replacement, paternal-excess hybrids have the same genotype as the genotype formed with the
271 initial evolution of a paternal-excess allele (Fig. 2), presenting a similar evolutionary
272 conundrum as is faced by single locus underdominance. Other aspects of the genetic basis of
273 HSI remain unknown. For example, whether HSI is governed by derived-ancestral or derived-
274 derived incompatibilities can elucidate the evolutionary pace of lower effective ploidy taxa
275 (Fig. 2). Whether HSI is caused by recurrent evolution of new MEGs/ PEGs or compensatory
276 MEG/PEG expression can inform how these arms races function at a molecular level.
277
278 *Parental conflict and effective ploidy; WISO and beyond*
279 Why should taxa differ in effective ploidy? Parental conflict suggests that variance in paternity
280 creates competition among siblings for limited maternal resources, and thus paternally-derived
281 resource acquiring alleles can evolve (Queller, 1983; Haig and Westoby, 1989). This
282 observation has sparked the WISO (weaker-inbreeder/stronger-outbreeder) hypothesis, which
283 predicts that parental conflict should be stronger in outbreeding taxa than selfing ones.
284 Subsequently, HSI should be stronger between selfing and outcrossing lineages (Brandvain and
285 Haig, 2005). Much evidence supports WISO, including an excess of HSI between selfers and
286 outcrossers (Brandvain and Haig, 2005; Rebernig et al., 2015; Lafon-Placette and Köhler,
287 2016; İltaş et al., 2021), as well as stronger HSI between mating systems than within mating
288 systems for intraspecific crosses (i.e. (İltaş et al., 2021) versus (Willi, 2013; Hämälä et al.,
289 2017)). However, recent work has also highlighted that some taxonomic groups rapidly evolve
290 HSI with no corresponding mating system shift (Roth et al., 2018a; Coughlan et al., 2020).
291 Differences in demography or life history may influence the variance in paternity by
292 influencing levels of biparental inbreeding and relatedness within a fruit. Intuitively, these
293 differences may result in similar dynamics as those seen between selfers and outcrossers (i.e.

species with high levels of biparental inbreeding may behave similarly to selfers). However, this hypothesis requires rigorous testing; including formal meta-analyses and theoretical explorations.

Conclusions and implications

HSI may play a fundamental role in plant speciation. Yet, the importance of reproductive barriers is measured by their primary role in the origin of species and their secondary role in species maintenance. Despite the potentially potent role of HSI in species formation, its role in species maintenance remains largely unexplored. Recent work in *Mimulus* suggests that hybridization in the context of mixed paternity fruits (i.e. fruits containing both hybrids and conspecific seeds), can mediate growth costs for conspecific seeds that develop alongside hybrids with higher effective ploidy fathers (Coughlan, 2022), suggesting that HSI may confer indirect costs in secondary contact. How these growth costs translate into selection coefficients requires exploration. Secondly, much remains unknown about how introgression influences the fate of HSI alleles. Whether these incompatibilities resist introgression and maintain species boundaries, or whether one set of parental alleles will introgress into another (and if so, whether this is determined by effective ploidy) remains unanswered. Lastly, earlier work proposed that HSI may serve as a rare instance of reinforcement via a postzygotic barrier, particularly if it prevented significant maternal investment (Grant, 1954; Coyne, 1974), but this idea is largely untested. A growing appreciation for the generative role of HSI has revealed much about its developmental and genetic bases and evolutionary drivers. Yet, much remains unknown about this fruitful reproductive barrier.

Acknowledgements

I graciously thank the AJB Synthesis Award committee for this opportunity. I would also like to thank the *Mimulus* community for their support and discussion of these ideas over the years. Andrius Dagilis, Adam Stuckert, and Jonathan Rader provided useful feedback on this manuscript.

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785 **Figure Captions and Tables**

786 ***Figure 1: Hybrid seed inviability can evolve rapidly.*** *The extent of premating-postzygotic*
787 *(PMPZ) isolation and hybrid seed inviability (HSI) as a function of divergence for three plant*
788 *groups; the* Mimulus guttatus *species complex, three genera within the Solanaceae, and the*
789 *genus* Streptanthus*. Data are fit with GLM with the following model: RI~Genetic Distance.*
790 *Significant relationships are indicated with a black line, while non-significant relationships*
791 *are indicated with grey. For* Mimulus *and the Solanaceae, PMPZ isolation is measured by*
792 *seed set per cross, for* Streptanthus *PMPZ is based on the ability to make a fruit. Data are*
793 *collated from:* Mimulus *crossing data: (Vickery, 1964; Garner et al., 2016; Oneal et al.,*
794 *2016; Coughlan et al., 2020; Sandstedt et al., 2020);* Mimulus *genetic data: (Brandvain et*
795 *al., 2014; Coughlan et al., 2020, 2021; Sandstedt et al., 2020), distances calculated using*
796 *(Brandvain et al., 2014); Solanaceae crossing data: (Jewell et al., 2012; Kostyun and Moyle,*
797 *2017; Roth et al., 2018a), Solanaceae divergence data: (Guerrero et al., 2013; Pease et al.,*
798 *2016; Wu et al., 2018); Streptanthus crossing and divergence data:(Christie and Strauss,*
799 *2018).*
800
801 ***Figure 2: Genetic (A) and molecular models (B) underlying HSI highlight many***
802 ***unanswered questions:*** *(A) is HSI governed predominantly by substitutions in one or both*
803 *lineages (i.e. derived-ancestral vs derived-derived incompatibilities; top vs bottom panel*
804 *respectively)? (B) Does HSI evolve via recurrent evolution of new imprinted genes or*
805 *modified expression of pre-existing imprinted genes (or a combination)? The top panel*
806 *represents the evolution of a newly imprinted gene: increased expression of a paternally*
807 *derived allele (orange) selects for reduced maternal expression (blue) at a single locus,*
808 *resulting in a bi-parentally expressed gene becoming imprinted. The bottom panel depicts a*
809 *scenario where two genes are already imprinted. Increased expression of the PEG (orange)*
810 *selects for increased expression of a compensatory MEG (blue). Green shapes represent the*
811 *origin of new transcription factors or other molecular mechanisms of increasing gene*
812 *expression. While the (C) genotypes displayed in the phenotypic outcomes depict only a*
813 *single round of paternally-derived resource acquiring alleles and maternal-derived*
814 *compensatory alleles, multiple rounds of allelic substitution (either within one species, or in*
815 *both lineages) would have to occur for the Species 2 x Species 1 cross to be lethal, as the*
816 *genotype shown in the Species 2 x Species 1 cross is the same genotype that arises with the*
817 *origin of a paternally-derived, resource acquiring allele (denoted with a *).*
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Table 1: incidences of HSI in agricultural and natural plant systems. *Group= taxonomic group, Type= endosperm type (cellular or nuclear), Strength= qualitative assessment of HSI (many older papers provide only qualitative assessments), divergence= estimate of divergence times for the taxonomic group. In some cases, the actual species have been genotyped and estimates made, but for others the crown age of the taxonomic group is given with some description of the species crossed. Ploidy= interspecific among diploids ('IS'), interploidy ('IP'), or several crosses involving both intra-diploid and interspecific crosses ('both'). Ref= reference for HSI and divergence times ('div')*

Group	**Type**	**Strength**	**Divergence**	**Ploidy**	**Ref**
Solanum sect. *Petota*	celluar	several instances; often complete or strongly asymmetric	crown age ~5.9-8.5MY; incidences between species ~3-4MY diverged	Both	(Johnston and Hanneman, 1980, 1982; Dinu et al., 2005); Div: (Särkinen et al., 2013; Fumia, 2021; Tang et al., 2022)
Solanum sect. *Lycopersicon*	celluar	several instances; often complete or strongly asymmetric	crown age ~1.2-2.6MY, incidences in species pairs <1MY diverged	Both	(Rick, 1963; Ehlenfeldt and Hanneman, 1992; Ehlenfeldt and Ortiz, 1995; Baek et al., 2016; Roth et al., 2018a; Florez-Rueda et al., 2021b)Div:(Särkinen et al., 2013; Pease et al., 2016)
Brassica	nuclear	several instances; often strong	earliest incidences between species ~2MY diverged	Both	(Nishiyama et al., 1991); Div: (Li et al., 2017)
Nicotiana	celluar	several instances; often complete or strongly asymmetric	crown age ~10-13MYA; few crosses made between recently diverged species	Both	(McCray, 1932; East, 1935; Cooper and Brink, 1940); Div (Clarkson et al., 2017; Wang et al., 2022)
Triticum	nuclear	strong HSI between *T. boeoticum* and *T. urartu*	~1MY divergd	Both	(Gill and Waines, 1978); Div (Huynh et al., 2019)
Aegilops	nuclear	strong HSI between *Ae. tauschii* (*Ae. squarrosa*) and *Ae. speltoides*	~3-4MY diverged	IS	(Gill and Waines, 1978); Div (Huynh et al., 2019)
Avena	nuclear	several strong and/or asymmetric incidences	strong HSI between different clades ~7-11MY diverged, younger pairs not tested	Both	(Nishiyama and Yabuno, 1978)Nishiyama and Yabuno 1978; Div (Liu et al., 2017; Fu, 2018)
Hordeum	nuclear	some incidences within sections, stronger incidences between sections	"sections" not monophyletic; crown age of group(s) with HSI is ~1-2MYA	Both	(von Bothmer and Jacobsen, 1986); Div (Brassac and Blattner, 2015)

Oryza	nuclear	several strong instances; strongly asymmetric	earliest incidence from species <500KY diverged	IS	(Chu and Oka, 1970; Ishikawa et al., 2011); Div (Stein et al., 2018)
Phaseolus	nuclear	two incidences, both strong and asymmetric	2-4 MY diverged	IS	(Shii et al., 1982; Geerts et al., 2002); Div (Delgado-Salinas et al., 2006)
Cucumis	nuclear	several incidences; some strong, few asymmetric	most incidences between *C. melo* and species in Sect. Sagittani, which split ~9.5MYA	Both	(John R. Deakin et al., 1971); Div (Endl et al., 2018)
Glycine	nuclear	multiple incidences, several strong/complete	multiple incidences between species ~2-4MY diverged	Both	(Singh et al., 1988; Chung and Kim, 1990; Zhang and Palmer, 1990); Div (Egan and Doyle, 2010; Sherman-Broyles et al., 2014)
Medicago	nuclear	several incidences, often strong/complete	earliest incidences are between species ~2MY diverged; crown age is 6-16MYA	Both	(Oldemeyer, 1956; Fridriksson and Bolton, 1963; McCoy and Smith, 1986; Veronesi et al., 1986); Div (de Sousa et al., 2016)
Trifolium	nuclear	multiple strong/complete incidences,	crown age for Trifolium is ~11.8-16MYA, but many sister taxa exhibit HSI	Both	(Chou and Gibson, 1968; Williams and White, 1976; Parrott and Smith, 1986; Abberton, 2007); Div (Ellison et al., 2006; Yan et al., 2022)
Datura	celluar	several highly asymmetric incidences	crown age ~15MYA, few crosses between recently diverged species	Both	(Sansome et al., 1942; Satina et al., 1950); Div (Dupin and Smith, 2018)
Helianthus	nuclear	most annual-perennial crosses fail, but can be partially restored with embryo rescue	~1.5-3.3MY diverged	IS	(Seiler and Rieseberg, 2015); Div (Mason, 2018)
Impatiens	celluar	most stronger incidences are interploidy	-	Both	(Arisumi, 1973, 1982)
Primula	nuclear	multiple strong incidences	~2-3MYA	Both	(Valentine and Woodell, 1960, 1963); Div (Li et al., 2016)
Mimulus	celluar	several instances; sometimes complete, occasionally asymmetric	earliest incidence of complete HSI is ~150KYA	Both	(Vickery, 1964; Garner et al., 2016; Oneal et al., 2016; Coughlan et al., 2020; Sandstedt et al., 2020; Kinser et al., 2022); Fig.1
Gilia	nuclear	several instances; often complete, occasionally asymmetric	several instances in <2MYA	IS	(Grant, 1954; Grant and Grant, 1954); Div (Landis et al., 2018)
Clarkia	nuclear	modest HSI between C. xantiana subsp.	65KY diverged	IS	(Davis, 1970; Briscoe Runquist et al., 2014)
Collinsia	cellular	several instances; rarely complete, often asymmetric	strong HSI between species 900KY diverged	IS	(Ahloowalia and Garber, 1961; Bell and Garber, 1961); Div Randle (unpublished)

Capsella	nuclear	strong asymmetric HSI between *C. grandiflora* and *C. rubella*; complete between each and *C. orientalis*	earliest incidence ~100KYA, oldest incidence ~1MYA	IS	(Rebernig et al., 2015; Lafon-Placette et al., 2018)
Arabidopsis	nuclear	several incidences; complete between A. arenosa and both A. thaliana and A. lyrata; variable/asymmetric within A. lyrata	earliest incidence ~35KYA; latest is ~3.8-5.8MYA	Both	(Josefsson et al., 2006; Hämälä et al., 2017; Lafon-Placette et al., 2017; İltaş et al., 2021)
Lilium	nuclear	several instance (~3% of crosses yield viable seed)	some instances as early as ~500KYA	IS	(Dowrick and Brandram, 1970; Van Tuyl et al., 1988); Div (Gao et al., 2015)
Eucalyptus	nuclear	variable: up ~35% of crosses yield no viable seed	probability of producing a hybrid is <5% by 7MY	IS	(Drake, 1975; Larcombe et al., 2015)
Silene	nuclear	several strong incidences	crown age for section Elisanthe ~1.3MYA	IS	(Prentice, 1978); Div (Moiloa et al., 2021)
Streptanthus	nuclear	common and typically strong	earliest complete incidence ~2.5MYA	IS	(Christie and Strauss, 2018).
Jaltomata	cellular	several incidences, often strong, commonly asymmetric	earliest complete incidence ~1.1MYA	IS	(Kostyun and Moyle, 2017); Div (Wu et al., 2018)
Nolana	cellular	several moderate, asymmetric incidences	earliest complete incidence ~2.2MYA	IS	(Jewell et al., 2012); Div (Guerrero et al., 2013)
Lolium	nuclear	multiple, strong incidences	~4.5MY diverged	IS	(Jenkin, 1935, 1954a; b; c); Div (Inda et al., 2014)