Heredity **83** (1999) 363–372 *Received 10 June 1999, accepted 9 July 1999*

Short Review

Transgressive segregation, adaptation and speciation

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The production of extreme or 'transgressive' phenotypes in segregating hybrid populations has been speculated to contribute to niche divergence of hybrid lineages. Here, we assess the frequency of transgressive segregation in hybrid populations, describe its genetic basis and discuss the factors that best predict its occurrence. From a survey of 171 studies that report phenotypic variation in segregating hybrid populations, we show that transgression is the rule rather than the exception. In fact, 155 of the 171 studies (91%) report at least one transgressive trait, and 44% of 1229 traits examined were transgressive. Transgression occurred most frequently in intraspecific crosses involving inbred, domesticated plant populations, and least frequently in interspecific crosses between outbred, wild animal species. Quantitative genetic studies of plant hybrids consistently point to the action of complementary genes as the primary cause of transgression, although overdominance and epistasis also contribute. Complementary genes appear to be common for most traits, with the possible exception of those with a history of disruptive selection. These results lend credence to the view that hybridization may provide the raw material for rapid adaptation and provide a simple explanation for niche divergence and phenotypic novelty often associated with hybrid lineages.

Keywords: adaptation, complementary genes, hybridization, introgression, speciation, transgressive segregation

Introduction

Studies of quantitative traits in segregating hybrid populations sometimes report the presence of phenotypes that are extreme relative to those of either parental line (deVicente & Tanksley, 1993; Rieseberg & Ellstrand, 1993; Cosse *et al*., 1995). The generation of these extreme phenotypes is referred to as transgressive segregation, and this is a major mechanism by which extreme or novel adaptations observed in new hybrid ecotypes or species are thought to arise. If transgressive segregation is frequent, then an important evolutionary role for hybridization is more easily explained. Note that transgressive segregation is a phenomenon specific to segregating hybrid generations and refers to the fraction of individuals that exceed parental phenotypic values in either a negative or positive direction. This is caused in part by heterosis, which is most pronounced in first-generation hybrids, and is implicated when the mean trait value of the hybrids exceeds (in a positive direction only) the phenotypic values of both parental lines. As will be shown below, the genetic basis of transgressive segregation appears to be largely distinct from that underlying heterosis.

Evidence that transgressive segregation facilitates the successful establishment of hybrid lineages is indirect and comes principally from research on plants. Theoretical and empirical studies identify niche separation between hybrid and parental genotypes as the single most important factor favouring hybrid establishment (Lewontin & Birch, 1966; Grant, 1981; Templeton, 1981; Buerkle *et al*. in review). Without niche differentiation, new hybrid genotypes are likely to be overcome by competition and/or gene flow from parental populations. These predictions are supported by reports that most stabilized introgressants or hybrid species are ecologically divergent with respect to their parental species (Abbott, 1992; Arnold, 1997; Rieseberg, 1997). Presumably, the niche separation that is so critical to hybrid lineage establishment arises via selection for an extreme or transgressive phenotype in the initial hybrid population. However, this has not yet been shown.

Numerous explanations have been offered to account for observations of transgressive phenotypes in segregating hybrid populations (Rick & Smith, 1953; Grant, 1975; Voigt & Tischler, 1994). These include: (i) an elevated mutation rate in hybrids; (ii) reduced developmental stability; (iii) nonadditivity of allelic effects between loci or epistasis; (iv) nonadditivity of allelic effects within a locus or overdominance; (v) the unmasking of rare recessive alleles that are normally heterozygous in the parental taxa; (vi) chromosome number variation; and (vii) the complementary action of additive alleles that are dispersed between the parental lines. The latter explanation assumes that parental lines are often fixed for sets of alleles that have opposing effects within lines (Table 1). If this were the case, then extreme phenotypes are the predicted result of recombination in segregating hybrid generations (Table 1).

The nature of the genetic mechanism(s) responsible for transgressive segregation is critical to any predictions regarding the role of transgression in adaptive evolution. For example, if transgressive segregation results from reduced developmental stability in hybrids (explanation ii), it is unlikely to be heritable or to contribute to adaptive evolution. Likewise, transgressive phenotypes resulting from overdominance

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Table 1 Hypothetical example of transgressive segregation due to the complementary action of genes with additive effects

	Phenotypic values			
QTL	Species A	Species B	Transgressive F2	Transgressive F2
1	+1	−1	+1 (A)	−1 (B)
2	+1	−1	+1 (A)	−1 (B)
3	+1	−1	+1 (A)	−1 (B)
4	−1	+1	+1 (B)	−1 (A)
5	−1	+1	+1 (B)	−1 (A)
Total	+1	−1	+5	−5

Letters in parentheses after values indicate the species origin of a given QTL in the *F*2 s.

(explanation iv) could not be fixed in sexual, diploid hybrids and thus would be unlikely to contribute to adaptive evolution. On the other hand, it is easy to see how extreme phenotypes generated by epistasis (explanation iii) or the recombination of sets of alleles with opposing effects (explanation vii) could become fixed in stabilized hybrid lineages through either selection or drift.

Here, we assess the frequency of transgressive segregation in hybrid populations, describe results from recent quantitative trait locus (QTL) studies that have elucidated the genetic basis of transgressive segregation in plants, and discuss the implications of these data for adaptive evolution and speciation in hybrid lineages. Because we have compiled data from both animal and plant crosses, we also can ask whether animal hybrids are less likely to exhibit transgressive segregation than their botanical counterparts. A positive answer might partially explain the perceived greater importance of hybridization in plant vs. animal evolution. Other questions that are addressed include: (a) is transgressive segregation most frequent in wide than narrow crosses, and (b) what factors best predict the occurrence of transgression for a given cross or a given character?

Methods

We examined 171 studies that report phenotypic variation in segregating hybrid populations (58 animal, 113 plant; Appendix 1). To increase the explanatory power of this list, we also included information on the mating system of the parental lines, the genetic basis of transgressive segregation, the divergence of the cross (intraspecific vs. interspecific), and whether the parental lines were derived from wild or domesticated stock. The list is by no means exhaustive, and we undoubtedly missed many excellent studies. Nonetheless, it is adequate for asking whether transgressive segregation in interpopulational crosses is common.

In all of the plant studies, phenotypes were assayed under common or greenhouse garden conditions. Likewise, all but one of the plant studies examined hybrids derived from experimental crosses. In the one exception, individuals from a wild sunflower hybrid zone were propagated and measured in the Indiana University greenhouses (L. Rieseberg, unpubl. data).

Of the animal studies, 30 examined hybrids in hybrid zones, two examined hybrids in the species' natural environment, 23 examined hybrids derived from experimental crosses, and three compared artificial hybrids with their natural counterparts (Appendix 1). Most natural animal hybrids were verified with genetic markers, but a small minority were inferred to be hybrids based on their phenotype. We recognize that the inclusion of hybrids raised in natural populations increases the probability that some of the extreme phenotypes reported have an environmental rather than genetic basis. Likewise, natural hybrids are more likely than experimental hybrids to be misidentified, and it is sometimes difficult to distinguish between F1 and later generation hybrids. Nonetheless, given the small number of artificial crosses in animals that report appropriate phenotypic data, the inclusion of natural hybrids seemed justified.

In animals and plants there was considerable variation in how phenotypic data were reported. Most of the studies provided information on the ranges of character values in both the parental and hybrid populations. However, in several instances, descriptive rather than quantitative data were provided. Likewise, in some of the animal studies, mean values were given rather than ranges. Our rationale was that if the hybrid mean exceeded that of either parental line in a negative or positive direction (whether significantly so or not) then the range of hybrid phenotypic values was likely to be transgressive. Of course, we recognize this assumption will not hold in all cases, and that in other instances hybrid means will be intermediate, yet ranges will be transgressive. However, because of the small number of relevant animal studies, we felt that reports of mean values would be useful. Finally, there was substantial heterogeneity among studies in the presence or kinds of statistical analyses conducted. Many studies only provided character ranges, and it was not possible to calculate significance, whereas other studies used fairly stringent criteria to declare significant transgression. Both are included in Appendix 1. Thus, the frequencies of transgression reported here should be viewed as rough estimates.

Frequency and taxonomic distribution of transgressive segregation

Plants

Transgressive segregation appears to be ubiquitous in plant hybrids. Only three of 113 studies failed to report extreme phenotypes for at least one character, and of 579 traits examined across the 113 studies, 336 (58%) exhibited transgression. Transgressive segregation was much more common in crosses between domesticated lines than in crosses between wild populations (92% vs. 38% of traits; d.f. = 1, $G = 155$, $P < 0.001$). Likewise, hybrids from crosses between inbred populations were more likely to exhibit transgression than those from crosses between outbred or mixed-mating populations (92% vs. 39% of traits; d.f. = 1, $G = 149$; $P < 0.001$).

Of course, these two comparisons are not strictly independent because most domesticated plants are inbreeders and most wild plants are outcrossers or mixed breeders. Nonetheless, analyses of the frequency of transgression in only wild plants reveals that the association between inbreeding and transgression remains (86% vs. 14% of traits; d.f. = 1; $G = 14.3$; $P < 0.001$).

Although evolutionists typically view transgressive segregation as a consequence of interspecific hybridization (Stebbins, 1959; Lewontin & Birch, 1966), according to Appendix 1, transgression actually occurs more frequently in intraspecific crosses (44% vs. 82% of traits; d.f. = 1; $G = 84.2$; $P < 0.001$). However, this result is compromised by the fact that most reported studies of interspecific plant hybrids involve wild, outcrossing species, whereas most studies of intraspecific hybrids involved inbred, domesticated lines. If we restrict our analysis to a less heterogeneous sample of outcrossing or mixed-mating wild populations, there is no difference (d.f. = 1; $G = 2.4$; $P > 0.1$).

Animals

Transgressive segregation does occur in animals, but it appears to be much less frequent than in plants. Of 58 animal studies examined, 45 (78%) report transgressive segregation as compared to 97% for plants (d.f. = 1; $G = 16.8$; $P < 0.001$). Likewise, only 200 of 650 animal traits examined (31%) exhibit transgression vs. 58% for plants (d.f. = 1; $G = 93.6$; $P < 0.001$). Although these values are substantially lower than those reported in plants, differences in plants and animals may be exaggerated by breeding system and human selection. Most of the animal studies report on wild outcrossers, whereas the plant data set includes a substantial number of domesticated species, many of which are inbred. Thus, a comparison between wild plant and animal species with similar breeding systems (i.e. outcrossing) is appropriate. The results from this more realistic comparison reveals that transgression actually occurs at only a slightly higher frequency for plant than animal traits (36% vs. 23%; d.f. = 1; $G = 15.0$; $P < 0.001$).

Domesticated animal hybrids were significantly more likely to exhibit transgressive segregation than wild animal hybrids (45% vs. 24% of traits; d.f. = 1; $G = 14.0$; $P < 0.001$), as was previously observed in plants. Likewise, intraspecific animal hybrids were significantly more likely to exhibit transgressive segregation than interspecific ones (50% vs. 28% of traits; d.f. = 1; $G = 17.8$; $P < 0.001$). However, unlike plants, this correlation remains even when comparisons are restricted to crosses between wild animals (79% vs. 25% of traits; d.f. = 1; $G = 49.4$; $P < 0.001$).

The nature of transgressive segregation

Plants

A remarkable diversity of traits have been shown to exhibit transgression in plants. The bulk of these are morphological traits (65%), whereas the remainder are fairly evenly divided among trait categories such as fecundity, the biochemical composition of organs and tissues, physiology, life history, and tolerances to various biotic and abiotic factors (Appendix 1). This latter category may be most important to the success of hybrids, because transgressive segregation for ecological tolerances seems most likely to facilitate niche divergence. Examples of transgressive segregation for abiotic factors include increased cold, salt, drought, heat, and heavy metal tolerances. Likewise, transgressive phenotypes for resistance to pathogens and herbivores are often reported. Of course, we recognize that expanded ecological tolerances may be a secondary consequence of transgressive changes in morphology, life history, physiology, or biochemical composition.

Transgressive segregation may also contribute to the development of reproductive isolation between a hybrid lineage and its progenitors. The niche differentiation discussed in the preceding paragraph may lead to habitat isolation, which can act as either a premating or postmating barrier. Transgressive segregation has also been reported for potential premating barriers such as flowering time and floral differences that contribute to pollinator discrimination. In this context, it is noteworthy that the reproductive barrier between a well-documented natural hybrid species, *H. paradoxus*, includes both habitat isolation (salt tolerance) and a shift in flowering time (Rieseberg, 1997). However, it has not yet been shown that transgressive segregation has facilitated the development of either adaptation.

Animals

The 650 traits measured in animals also represent a diverse array, including 471 morphological traits, 72 life-history traits, 16 behavioural traits, 32 qualitative traits, and 59 traits that were not easily classified (Appendix 1). Only 26% of the morphological traits assayed were transgressive. These included morphometric or meristic traits from hybrid populations of different fish species, wing length, bill length, and bill width in hybrids between bird species, mandible dimensions in cattle-bison hybrids, body weights and dimensions of hybrid mice, skull indices of dogs, and body and reproductive morphological measurements in insects.

Of the 72 life-history traits examined, 27 (38%) were transgressive. One noteworthy example that might conceivably contribute to niche divergence involves hybridization between two schistosoma species whose shedding patterns have single emergence peaks. By contrast, their hybrids are characterized by two unequal emergence peaks (Theron, 1989).

Four of 16 behavioural traits were transgressive, one of which was novel and involved the disruption of genetic correlations between antennae types and response to pheromone blends in F2 corn borer hybrids (Cosse *et al.*, 1995). Likewise, of seven transgressive qualitative traits examined, six represented novel attributes. These included novel colour patterns in hybrid landsnail populations, unique combinations of carina and antennal groove colours in *Drosophila* F2 and backcross hybrids, and novel body colouration in hybrid cichlid fishes. Finally, of the 59 traits that were difficult to classify, 41 (69%) were transgressive. These included lower infection rate in hybrid toads, higher oxygen uptake in crab hybrids, and lower energy consumption in

backcrossed progeny of the African honey bee and the European bee, all of which could contribute to niche divergence of hybrid lineages.

The genetic basis of transgressive segregation

As discussed in the introduction, many different explanations have been put forward to account for transgressive segregation. Although each may contribute to transgression in specific instances, some seem unlikely to provide a general explanation for this phenomenon. For example, mutation rates are known to be elevated in hybrid populations (Barton & Hewitt, 1985), perhaps in part due to the activation of previously quiescent transposable elements (Engels, 1983), but novel mutations seem unlikely to account for the high frequency of transgression in segregating hybrid populations or for the fact that transgressive segregation is often reported for the same traits in replicate crosses (Cox & Frey, 1985). Likewise, chromosome number variation (Voigt & Tischler, 1994) can only possibly account for transgression in populations that segregate for chromosome number, which represent less than 3% of the studies listed in Appendix 1. Finally, selection experiments demonstrate that transgressive phenotypes are highly heritable, indicating that transgression cannot be due to developmental instability alone (Lewontin & Birch, 1966).

Results from classical genetic studies have provided fairly convincing evidence for the hypotheses that transgressive segregation can result from the expression of rare recessive alleles (Rick & Smith, 1953) and/or from complementary gene action (Vega & Frey, 1980). The best evidence that rare recessive alleles exist in wild populations whose phenotypes are masked by common alleles comes from crosses between the domesticated tomato, *Lycopersicon esculentum* and its wild relative, *L. chilense* (Rick & Smith, 1953). A single plant from an F2 population between the species was found to have dull orange flowers, a phenotype never before seen in either parental species or for that matter any other species of *Lycopersicon*. Additional crosses revealed that this trait is controlled by a rare recessive allele in the self-incompatible wild species, *L. chilense*, as predicted by the recessive allele theory. However, it seems unlikely that rare recessives account for more than a small fraction of the transgressive phenotypes reported in the literature because transgressive segregation is most frequently reported in crosses involving inbred lines in which recessive alleles are likely to be fixed in the homozygous condition.

Complementary gene action has been a more popular general explanation for transgressive segregation in the plant genetics literature (Grant, 1975; Vega & Frey, 1980). In fact, some researchers have taken observations of transgressive segregation as *prima facie* evidence for complementary genes (e.g. Lee & Shaner, 1985). However, most early studies lacked sufficient power to test alternative explanations involving nonadditive gene action.

Recently, marker-based QTL studies have confirmed that complementary genes are the major cause of transgression, at least in plants (Appendix 1). Critical to this conclusion is the somewhat surprising discovery that different species or different parental lines are often fixed for sets of alleles with opposing effects (see Table 1), which results in transgressive segregation in hybrids. This is illustrated by a QTL analysis of 11 quantitative traits in an interspecific tomato cross (deVicente & Tanksley, 1993). Alleles at 36% of the detected QTL had effects that were in the opposite direction of the species differences for those traits. That is, alleles reducing a trait were sometimes derived from the species that had the highest value for that trait and vice versa. These complementary alleles generated extreme phenotypes for eight of the 11 traits assayed. deVicente & Tanksley (1993) also examined the possibility that nonadditive gene action might have contributed to transgressive segregation. However, the number of significant pairwise digenic interactions did not exceed that expected by chance, indicating that epistasis was unlikely to be a major cause of transgression in this cross.

Most other QTL mapping studies that report transgressive segregation (all in plants) have also implicated the action of complementary genes as the primary cause of transgression (Appendix 1). For example, 25% and 17% of QTL effects were opposite in sign from the parental differences in interspecific tomato (Weller *et al*., 1988) and sunflower crosses (Kim & Rieseberg, 1999), respectively, and transgressive segregation due to complementary alleles was observed for all 15 traits assayed in hybrids from a cross between two phenotypically similar soybean cultivars (Mansur *et al*., 1993). However, in several of these studies (e.g. deVicente & Tanksley, 1993; Kim & Rieseberg, 1999), allelic effects opposite to those predicted by the parental values were also detected for traits that did not exhibit significant transgression. This result may be due to the stringency of the statistical tests used in these studies to declare significant transgression. Alternative explanations include the possibility that the most transgressive QTL combinations were not found in any of the progeny assayed or that transgressive segregation was masked by nonadditive gene action. Another puzzle is that transgressive segregation was sometimes observed for traits which appear to lack complementary alleles in the parental lines (e.g. Monforte *et al*., 1997; Kim & Rieseberg, 1999). These observations might be taken as evidence for nonadditive gene action (Monforte *et al*., 1997). However, the possibility that the observed transgression may be due to undetected complementary alleles cannot be ruled out.

Predictions

Assuming that complementary gene action is the main cause of transgression, several predictions can be made about the kinds of traits and kinds of crosses that are most likely to result in transgressive segregation. We can also ask whether the empirical evidence complied in this review accords well with these predictions.

Prediction 1: Transgressive segregation will be most frequent in crosses between inbred or selfing lineages because genetic and phenotypic variation will occur among lineages rather than within them. That is, the fixed differences required for transgressive segregation will build up more rapidly between selfing than outcrossing populations. Presumably, this at least partially explains the higher frequencies of transgressive

segregation reported here for domesticated plant and animal species and for wild populations of selfing plants.

Prediction 2: The frequency of transgression will be positively correlated with the genetic divergence of the parental lines. Again, the rationale for this prediction is that greater genetic divergence will be accompanied by an increase in the number of fixed differences between the parental lines, resulting in transgressive segregation for a larger number of traits. Comparative data in Appendix 1 provide little support for this prediction, but sampling is heterogeneous and genetic distances are poorly known. Studies that have asked this question by comparing wide and narrow crosses from the same organismal groups between populations also report mixed results. Greater numbers of transgressive progeny have been reported for matings between more distantly related species of oats (Cox & Frey, 1984) and barley (Vega & Frey, 1980), but no correlation was observed between genetic distance and numbers of transgressive segregants in wheat intraspecific crosses (Fabrizius *et al*., 1998). One possible explanation for this puzzle may relate to an apparent trade-off between phenotypic and genetic divergence, which is described below. An alternative explanation is that heterosis may play a larger role in transgressive segregation than has been suggested by the initial genetic studies reported here. Heterosis is known to decline with the genetic divergence of the cross (Moll *et al*., 1965), and if it is related to transgressive segregation, then a similar decline might be predicted for transgression.

Prediction 3. The more similar the phenotype of the parents, the greater the likelihood transgressive segregation will be observed in the F2. This prediction at first seems counterintuitive, but as genetic differences accumulate between lineages, the maintenance of similar phenotypes (i.e. stabilizing selection) appears to require the accumulation of allelic differences with effects that differ in sign from those predicted by the parental phenotypes (deVicente & Tanksley, 1993). This prediction has been confirmed repeatedly by empirical study (deVicente & Tanksley, 1993; Mansur *et al*., 1993; Kim & Rieseberg, 1999). Not only do traits with similar parental phenotypes exhibit transgression most frequently, but a negative correlation has been observed between parental mean differences and the proportion of QTL with allelic effects that differ in sign from parental phenotypic predictions (deVicente & Tanksley, 1993). These observations provide a possible explanation for the lack of a strong correlation between parental genetic divergence and the frequency of transgression. If genetic and phenotypic divergence proceed at similar rates, genetically more divergent crosses will also be more phenotypically divergent, possibly muting the transgressive effects that presumably accompany the accumulation of genetic differences.

Prediction 4. Traits with a history of directional selection are less likely to exhibit transgressive segregation than those with a history of genetic drift or stabilizing selection. This prediction overlaps with the previous one and is based on the observation that directional selection on a trait often appears to result in the fixation of alleles whose effects are in the same direction as predicted from the parental phenotypes (Paterson *et al*., 1991; True *et al*., 1997; Orr, 1998). For example, Paterson *et al*. (1991) mapped 11 QTL responsible for differences in fruit weight between the domesticated tomato, *Lycopersicon esculentum* and its wild relative, *L. cheesmanii*. In all cases, the *L. esculentum* allele increased fruit weight. This makes sense. The domestication of tomato presumably involved strong and consistent directional selection for increased fruit weight. Similarly, the area of the posterior genital lobe distinguishing *Drosophila simulans* from its close relative *D. mauritiana* is controlled by a minimum of eight QTL, all with allelic effects consistent with parental differences (True *et al*., 1997). Presumably this pattern is due to directional sexual selection. As predicted based on the complementary gene model, neither trait exhibits transgressive segregation.

Discussion

In his introduction to the *The Origin of Species by Means of Natural Selection*, Darwin (1859) argued that '…a careful study of domesticated animals and cultivated plants would offer the best chances of making out this obscure problem.' However, of the two engines that drive conventional plant and animal breeding programmes (selection and hybridization), Darwin focused his attention almost exclusively on selection. Selection continues to be the central theme of evolutionary biology, and rightly so. Nonetheless, it is puzzling that, with the exception of the botanical literature, possible contributions of hybridization to adaptive evolution and speciation in nature are rarely considered (although see Lewontin & Birch, 1966; Bullini, 1994; Arnold, 1997; Dowling & Secor, 1997; Grant & Grant, 1998). At least part of this neglect may relate to the common assumption that hybrids are intermediate phenotypically with respect to their parental species and thus have little to contribute to adaptive evolution. Even when extreme characters are reported, they are sometimes considered to be rare or to be a byproduct of developmental instability.

The data summarized in this review indicate that not only is transgressive segregation frequent, but that it is an expected consequence of the genetic architecture of differentiated populations or species. This result lends credence to the view that hybridization may provide the raw material for rapid adaptation (Stebbins, 1959; Lewontin & Birch, 1966; Arnold, 1997; Grant & Grant, 1998) and provides a simple explanation for the niche divergence and phenotypic novelty often associated with hybrid lineages (Stebbins, 1959; Grant, 1981; Abbott, 1992; Rieseberg, 1997).

Although it seems likely that transgressive segregation contributes to the evolutionary success of hybrid lineages, a full understanding of this phenomenon and its evolutionary role will require further study. For example, a direct link between observations of transgression in a synthetic hybrid population and adaptation in nature has yet to be made. Fortunately, experimental verification should be fairly straightforward. One possible experiment, for example, would be to compare the set of QTL combinations required to achieve the most transgressive phenotypes in synthetic populations to those found in a natural hybrid lineage. A match would provide compelling evidence that transgressive segregation had facilitated the evolution of that lineage.

From a genetic standpoint, the possible contributions of epistatic interactions to transgressive segregation are poorly understood. Although the QTL studies listed in Appendix 1 suggest that epistasis rarely contributes to transgressive segregation, this might reflect the general difficulty of detecting epistasis rather than biological reality. QTL studies that employ larger sample sizes or that use recombinant inbred lines (which control for genetic background effects outside of the region of interest) may be required for an accurate assessment of the contributions of epistasis.

While we were able to make some fairly simplistic predictions regarding the factors that cause the occurrence of transgression for a given cross or a given character, additional information would be useful. We need a better understanding, for example, of the relationship between the genetic differentiation of the parental lines and the frequency of transgression. Predictive power also would be enhanced by computer simulation studies that directly explore the effects of mating design (e.g. BC1 vs. F2), gene number and magnitudes, and extent of phenotypic differentiation between the parental lines on the expression of transgressive phenotypes.

It also would be useful to consider transgressive segregation in theoretical models that explore hybrid zone dynamics and hybrid speciation. Most hybrid zone models assume that hybrids are less fit than either parent (Barton & Hewitt, 1985; Harrison, 1986) or that hybrids exceed their parents only in intermediate habitats in the centre of the hybrid zone (Moore, 1977). One exception is Arnold's evolutionary novelty model (Arnold, 1997), but this model has not been formalized mathematically and does not provide a genetic mechanism for the origin of novelty. Two homoploid hybrid speciation models have been developed (McCarthy *et al*., 1995; Buerkle *et al*. in review). The McCarthy *et al*. model does not assume ecological divergence between the hybrid neospecies and its parents. By contrast, Buerkle *et al*. explicitly model the evolution of niche divergence between a new hybrid lineage and its parental progenitors. Although niche divergence in the Buerkle *et al*. model is not based on transgressive segregation, they report on unpublished simulations which suggest that outcomes are largely unaffected when complementary gene action is considered.

Lastly, it is not clear why transgressive segregation is more common in plants than in animals. Perhaps developmental canalization is more likely to mask extreme phenotypes in animals than plants. Another possible explanation is that the majority of animals are bisexual and thus may be more likely to have a history of directional sexual selection. Alternatively, the lower reported frequencies of transgression may be an artifact of the small sample sizes in most animal hybrid populations (for traits controlled by many genes, the most transgressive individuals are likely to be rare). A final possibility is investigator or publication bias. If zoologists assume that hybrids should be phenotypically intermediate, extreme hybrid phenotypes might be misinterpreted as resulting from experimental error or phenotypic plasticity and thus go unreported. By contrast, plant breeders may be less likely to publish the results from crossing studies that do not exhibit transgression, since this might be viewed as a negative result.

In summary, we have shown that segregating hybrids often exhibit extreme phenotypes when compared to parental values for those traits. Most of these extreme or transgressive phenotypes appear to arise as a consequence of recombination between lines that are fixed for sets of complementary alleles that have opposing effects within lines. Because these transgressive phenotypes are heritable, it is argued that transgressive segregation often accounts for the niche divergence and phenotypic novelty characteristic of most hybrid lineages. Nonetheless, several puzzles remain such as the relationship between genetic differentiation and transgressive segregation and the observation that transgression appears to be more frequent in plants than in animals.

Acknowledgements

We thank Alex Buerkle and John Burke for helpful comments on the manuscript. L. Rieseberg's research on hybridization has been supported by the NSF and the USDA.

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Appendix 1

Expression of extreme phenotypes in segregating hybrid populations

Taxa[1]	Mating system[2]	No. Traits measured	No. Traits transgressive	Genetic basis[3]	Reference[4]
Plants					
[W]*Aegilops umbellulata* (intraspecific crosses)	I	1	1	—	Morrison *et al.* (1989)
[D]*Asparagus officinalis* (intraspecific crosses)	O	1	1	—	Johnson & Peaden (1993)
[W]*Arabidopsis thaliana* (intraspecific crosses)	I	1	1	CG	Clarke *et al.* (1995)
[D]*Arachis hypogaea* (intraspecific crosses)	I	2	2	—	Anderson *et al.* (1993)
[W]*Atylosia lineata* × *A. scarabaeoides*	?	2	1	—	Pundir & Singh (1986)
[D × W]*Avena sativa* × *A. maroccana*	I	22	19	—	Pachuari & Choubey (1994)
[D × W]*Avena sativa* × *A. sterilis*	I	6	6	—	[5]
[D]*Avena sativa* (intraspecific crosses)	I	4	4	—	[6]
[D]*Beta vulgaris* (intraspecific crosses)	O	1	1	—	Wang & Goldman (1997)
[D]*Brassica napus* (intraspecific crosses)	I	3	3	CG	Ecke *et al.* (1995), Toroser *et al.* (1995)
[W]*Calamagrostis* (interspecific crosses)	M	5	1	—	Nygren (1948)
[D]*Carthamus tinctorius* (intraspecific crosses)	I	2	2	—	Fernandez-Martinez *et al.* (1986)
[D]*Cucumis melo* (intraspecific crosses)	I	1	1	—	Rajamony *et al.* (1990)
[D]*Cucurbita maxima* (intraspecific crosses)	I	1	1	—	Maluf *et al.* (1997)
[D]*Eragrostis curvula* (intraspecific crosses)	A × I	4	3	CNV	Voigt & Tischler (1994)

Appendix 1 (*Continued*)

Taxa[1]	Mating system[2]	No. Traits measured	No. Traits transgressive	Genetic basis[3]	Reference[4]
[D]*Fragaria chiloensis* (intraspecific crosses)	O	1	1	—	Shaw & Sacks (1995)
[W]*Gilia capitata* (intraspecific crosses)	M	9	0	—	Grant (1950)
[W]*Gilia malior* × G. *modocensis*	M	11	2	—	Grant (1966)
[D]*Glycine max* × *G. soja*	I	1	1	—	Bailey *et al.* (1997)
[D]*Glycine max* (intraspecific crosses)	I	3	2	—	[7]
[D]*Glycine max* (intraspecific crosses)	I	18	17	CG	[8]
[D]*Gossypium barbadense* (intraspecific crosses)	M	2	2	—	Percy & Turcotte (1988)
[D]*Gossypium hirsutum* (intraspecific crosses)	M	1	1	—	Muhammad & Jones (1990)
[W]*Helianthus annuus* × *H. petiolaris**	I(O)	6	6	—	L. Rieseberg (unpubl.)
[D × W]*Helianthus annuus* × *H. debilis*	O	15	7	CG	Kim & Rieseberg (in press)
[W]*Helianthus grosseserratus* × *H. nuttallii*	O	8	6	—	Long (1966)
[D]*Hordeum vulgare* (intraspecific crosses)	I	13	11	—	[9]
[D]*Hordeum vulgare* (intraspecific crosses)	I	27	26	CG	[10]
[W]*Lesquerella perforata* × *L. lyrata*	O	23	10	—	Rollins & Solbrig (1973)
[W]*Lesquerella perforata* × *L. stonensis*	O	23	5	—	Rollins & Solbrig (1973)
[W]*Lesquerella perforata* × *L. lescurii*	O	23	8	—	Rollins & Solbrig (1973)
[W]*Lesquerella perforata* × *L. densipila*	O	23	9	—	Rollins & Solbrig (1973)
[W]*Lesquerella stonensis* × *L. lyrata*	O	23	9	—	Rollins & Solbrig (1973)
[W]*Lesquerella stonensis* × *L. lescuriia*	O	23	5	—	Rollins & Solbrig (1973)
[W]*Lesquerella stonensis* × *L. densipila*	O	23	7	—	Rollins & Solbrig (1973)
[W]*Lesquerella lyrata* × *L. lescurii*	O	23	7	—	Rollins & Solbrig (1973)
[W]*Lesquerella lyrata* × *L. densipila*	O	23	10	—	Rollins & Solbrig (1973)
[W]*Lesquerella lescurii* × *L. densipila*	O	23	9	—	Rollins & Solbrig (1973)
[D]*Linum usitatissimum* (intraspecific crosses)	I	2	2	—	Green (1986)
[D]*Lolium perenne* (intraspecific crosses)	O	8	5	—	[11]
[D × W]*Lycopersicon esculentum* × *L. pennellii*	I × ?	11	8	CG, O	de Vicente & Tanksley (1993)
[D × W]*L. esculentum* × *L. pimpinellifolium*	I	3	3	CG, O?, E?	Monforte *et al.* (1997)
[D]*Lycopersicon esculentum* (intrasp. crosses)	I	1	1	—	Poysa (1993)
[W]*Malva oxyloba* × *M. parviflora*	O	16	5	—	Kristofferson (1925,26)
[?]Medicago polymorpha × *M. murex*	M	2	1	—	Pathiapanawat *et al.* (1997)
[W]*Microseris pygmaea* (intraspecific crosses)	I	10	8	CG	[12]
[W]*Microseris douglasii* × *M. bigelovii*	I	1	1	CG	Hombergen & Bachmann (1995)
[W]*Mimulus lewisii* × *M. cardinalis*	O	12	9	CG	Bradshaw *et al.* (1998)
[W]*Nicotiana sanderae* × *N. langsdorfii*	O	7	1	—	Smith (1950)
[W]*Nicotiana langsdorfii* × *N. alata*	O	1	1	—	Stebbins (1966)
[D]*Nicotiana tabacum* (intraspecific crosses)	I	1	1	—	Campbell & Wernsman (1994)
[D]*Oryza sativa* (intraspecific crosses)	I	15	14	—	[13]
[D]*Oryza sativa* (intraspecific crosses)	I	3	3	CG	Li *et al.* (1995), Xu *et al.* (1998)[1]
[D]*Papaver somniferum* (intraspecific crosses)	M	1	1	—	Singh *et al.* (1995)
[D]*Phaseolus vulgaris* (intraspecific crosses)	I	8	6	—	[14]
[D]*Pisum sativum* (intraspecific crosses)	I	4	1	CG	Dirlewanger *et al.* (1994)
[W]*Populus deltoides* (intraspecific crosses)	O	3	3	—	Prakash & Heather (1989)
[D]*Potentilla glandulosa* (intraspecific crosses)	O	18	4	—	Clausen & Hiesey (1958)
[D]*Sorghum bicolor* (intraspecific crosses	I	1	1	CG	Dixon *et al.* (1991)
[D]*Sorghum bicolor* (intraspecific crosses)	I	1	1	—	Wenzel & Van Den Berg (1995)
[D]*Theobroma cacao* (intraspecific crosses)	M	2	2	—	Iwaro *et al.* (1997)
[D]*Triticum aestivum* × *Secale cereale*	I × O	1	1	—	Nkongolo (1996)

Appendix 1 (*Continued*)

Taxa[1]	Mating system[2]	No. Traits measured	No. Traits transgressive	Genetic basis[3]	Reference[4]
[D]*Triticum aestivum* × *T. dicoccoides*	I	1	1	—	Carver *et al.* (1989)
[D]*Triticum aestivum* (intraspecific crosses)	I	26	25	—	[15]
[D]*Triticum dicoccoides* (intraspecific crosses)	I	1	1	—	Grama *et al.* (1984)
[D]*Triticum turgidum* (intraspecific crosses)	I	1	1	—	Singh *et al.* (1993)
[D]*Vigna mungo* (intraspecific crosses)	I	4	4	—	Reddy & Singh (1989)
[D]*Vigna radiata* (intraspecific crosses)	I	7	7	—	[16]
[D]*Vitis vinifera* (intraspecific crosses)	M	3	3	—	Sandhu *et al.* (1984)
[D]*Zea mays* (intraspecific crosses)	I	3	3	—	[17]
Animals					
[W]*Agrotis segetum* × *A. ipsilon*	O	12	2	—	Gadenne *et al.* (1997)
[D]*Allonemobius fasciatus* × *A. socius**	O	1	1	—	Howard *et al.* (1993)
[W]*Ambystoma talpoiduem* (intraspecific crosses)	O	3	3	—	Harris *et al.* (1990)
[W]*Anas platyrhynchos* × *A. americana**	O	3	0	—	Fedynich & Rhodes *et al.* (1993)
[D]*Apis mellifera* (intraspecific crosses)	O	5	3	—	Harrison & Hall (1993)
[W × D]*Bison bonasus* × *Bos taurus*	O	48	32	—	[18]
[W]*Bombina bombina* × *B. variegata**	O	8	2	—	Nurnberger *et al.* (1995)
[D]*Bos taurus* × *B. grunniens*	O	2	1	—	Tumennasan *et al.* (1997)
[W]*Bufo microscaphus* × *B. woodhousii**	O	1	1	—	Goldberg *et al.* (1996)
[W]*Caledia captiva* × intraspecific crosses	O	1	1	—	Shaw *et al.* (1983)
[D]*Canis familiaris* × intraspecific crosses	I	42	8	—	Stockard (1941)
[W]*Catostomus insignis* × *Pantosteus clarki chalcoides**	O	22	2	—	Clarkson & Minckley (1988)
[D]*Choristoneura occidentalis* × *C. retiniana*	O	1	0	—	Liebhold (1986)
[W]*Chorthippus parallelus* (intraspecific crosses)	O	6	6	—	Hewitt *et al.* (1987)
[W]*Chrysopa quadripunctata* × *C. slossonae*	O	23	12	—	Tauber *et al.* (1995)
[W]*Cnemidophorus tesselatus* × *C. sexlineatus**	O	22	0	—	Walker *et al.* (1994)
[W]*Cottus bairdi* × *C. cognatus**	O	5	3	—	Strauss (1986)
[W]*Culicoides variipennis* (intraspecific crosses)	O	1	1	—	Velten & Mullens (1997)
[W]*Cyprinodon variegatus* × *C. pecosensis**	O	12	6	—	Wilde & Echelle (1997)
[W]*Daphnia cucullata* × *D. galeata**	O	7	0	—	Giessler (1997)
[W]*Daphnia cucullata* × *D. hyalina**	O	7	0	—	Giessler (1997)
[W]*Daphnia galeata* × *D. cucullata**	O	36	8	—	Spaak & Hoekstra (1995)
[W]*Daphnia galeata* × *D.hyalina**	O	20	2	—	Weider (1993)
[W]*Daphnia hyalina* × *D. galeata**	O	7	0	—	Giessler (1997)
[W]*Dendroica magnolia* × *D. coronata coronata**	O	4	1	—	Latta *et al.* (1998)
[W]*Drosophila heteroneura* × *D. silvestris**	O	9	0	—	Carson *et al.* (1989)
[D]*Drosophila heteroneura* × *D. silvestris*	I	3	3	—	Val (1977)
[D]*Drosophila subobscura* × *D. madeirensis*	I	1	1	—	Papaceit & Prevosti (1991)
[W]*Etheostoma crossopterum* × *E. nigripinne**	O	1	0	—	Page *et al.* (1992)
[W]*Geospiza fuliginosa* × *G. fortis**	O	8	0	—	Grant & Grant (1994, 1996)
[W]*Geospiza scandens* × *G. fortis**	O	8	0	—	Grant & Grant (1994, 1996)
[D × W]*Haplochromis burtoni* × *H. nubilus*	O	8	6	—	Crapon de Caprona & Fritzsch (1984)
[W]*Hyla cinerea* × *H. gratiosa**	O	4	0	—	Gerhardt *et al.* (1980)
[W]*Laupala paranigra* × *L. kohalensis*	O	5	2	—	Shaw (1996)
[W]*Leuciscus cephalus* × *Chalcalburnes**	O	39	12	—	Economidis & Sinis (1988)
[W]*Mandarina mandarina* × *M. chichijimana**	O	2	1	—	Chiba (1997)
[W]*Menippe mercenaria* × *M. adina**	O	24	18	—	Combs *et al.* (1997)
[W]*Mercenaria mercenaria* × *M. campechiensis**	O	1	1	—	Arnold *et al.* (1996)

Appendix 1 (*Continued*)

Taxa[1]	Mating system[2]	No. Traits measured	No. Traits transgressive	Genetic basis[3]	Reference[4]
[W]*Micropterus salmides* (intraspecific crosses)	O	1	1	—	Fields *et al.* (1987)
[D × W] *Morone saxatilis* × *M. chrysops*	O	11	4	—	Harrell & Dean (1988)
[D × W]*Mus musculus* (intraspecific crosses)	O	1	1	—	Hauffe & Searle (1993)
[W]*Mus musculus* (intraspecific crosses)	I	4	2	—	Bateson & D'udine (1986)
[D]*Mus musculus* (intraspecific crosses)*	O	6	5	—	Alibert *et al.* (1994)
[W]*Mytilus edulis* × *M. galloprovincialis**	O	1	0	—	Gardner (1996)
[D]*Oreochromis aureus* × *O. niloticus*	O	6	1	—	Behrends *et al.* (1990)
[W]*Ostrinia nubilalis* (intraspecific crosses)	O	1	1	—	Cosse *et al.* (1995)
[W]*Passerina cyanea* × *P. amoena**	O	5	3	—	Baker & Johnson (1998)
[W]*Peromyscus leucopus* (intraspecific crosses)	O	16	13	—	Wichman & Lynch (1991)
[D]*Peromyscus maniculatus* × *P. polionotus*	O	15	13	—	Dawson (1965)
[W]*Phoxinus oreas* × *Semotilus atromaculatus**	O	42	0	—	Maurakis & Woolcott (1992)
[W]*Rutilus rutilus* × *Abramis brama*	O	2	1	—	Wood & Jordan (1987)
[W]*Salvelinus confluentus* × *S. fontinalis**	O	10	2	—	Leary *et al.* (1983)
[W]*Saxicola torquata rubicola* × *S. t. axillaris*	O	6	0	—	Starck *et al.* (1995)
[W]*Sceloporus grammicus* complex*	O	7	2	—	Reed *et al.* (1995), Sites *et al.* (1993)
[D]*Schistosoma mansoni* × *S. rodhaini*	O	1	1	—	Theron (1989)
[W]*Semotilus atromaculatus* × *Phoxinus cumberlandensis**	O	29	0	—	Eisenhour & Piller (1997)
[W]*Semotilus atromaculatus* × *Phoxinus tennesseensis**	O	29	0	—	Eisenhour & Piller (1997)
[W]*Solenopsis invicta* × *S. richteri**	O	15	6	—	Ross & Robertson (1990)
[W]*Tilapia zilli* × *T. mariae**	O	31	2	—	Taylor *et al.* (1986)

*Natural hybrids.
[1]W = wild; D = domesticated (domesticated populations are defined as populations that have been maintained under artificial conditions for two or more generations).
[2]A = Asexual (facultative); I = Inbred; O = Outbred; M = Mixed-mating. Information on plant breeding systems was obtained from the following general sources: Goodspeed (1954), Fryxell (1957), Free (1993), and Smart & Simmonds (1995). In some instances, domesticated populations have a mixed mating system, but inbred lines were used for the crosses reported in the Appendix (e.g. domesticated *Helianthus annuus*). In these cases, we classified the populations as inbred.
[3]Genetic data are reported for marker-assisted QTL studies only. CG = complementary gene action; CNV = chromosome number variation; E = epistasis; O = overdominance
[4]A full list of references is provided on the *Heredity* web site (*http://www.blackwell-science.com/her*), where a link to the database can be found under the relevant table of contents.
[5]Cox & Frey (1984, 1985), Thro & Frey (1985)
[6]Kuenzel & Frey (1985), Pixley & Frey (1991)
[7]Fehr *et al.* (1991), Luzzi *et al.* (1994), Wilcox *et al.* (1994)
[8]Mansur *et al.* (1993, 1996), Mian *et al.* (1996, 1998)
[9]Miles *et al.* (1989), Newton (1990), Minella & Sorrells (1992), Cherif & Harrabi (1993), Hadjichristodoulou (1993), Hou *et al.* (1994)
[10]Backes *et al.* (1995), Thomas *et al.* (1995), Mano *et al.* (1996)
[11]Rose-Fricker *et al.* (1986), Opsahl-Ferstad *et al.* (1994), Waldron *et al.* (1998)
[12]Battjes *et al.* (1993); Van Houten *et al.* (1994)
[13]Mahmoud *et al.* (1984), Ekanayake *et al.* (1985), Jun (1985), Jun & Yea (1988), Oard *et al.* (1991), Oshima *et al.* (1993), Roumen (1994), Ahmed *et al.* (1995), Oard & Hu (1995), Xue & Deng (1998)
[14]Weaver *et al.* (1985), Kornegay & Temple (1986), Morales & Niessen (1988), Miklas & Grafton (1992), Beaver & Rosas (1998)
[15]Lee (1984), Lee & Shaner (1985), Milus & Line (1986), Hautea *et al.* (1987), Poulos & Allan (1987), Agache *et al.* (1988), Van Ginkel & Scharen (1988), Broers & Jacobs (1989), Gulyan (1990), Paull *et al.* (1991), Zwer & Qualset (1991), Schultz & Line (1992), Yadav *et al.* (1992), Bhagwat & Bhatia (1993), Bergman *et al.* (1998), Campbell *et al.* (1998), Fabrizius *et al.* (1998), Suge *et al.* (1998)
[16]Bhatnagar *et al.* (1988), Singh & Murty (1988)
[17]Schön *et al.* (1993), Campbell & White (1995)
[18]Kobrynczuk & Krasinska (1987), Krasinska (1988), Kobrynczuk & Krasinska (1991)