

The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations

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Segregating hybrids often exhibit phenotypes that are extreme or novel relative to the parental lines. This phenomenon is referred to as transgressive segregation, and it provides a mechanism by which hybridization might contribute to adaptive evolution. Genetic studies indicate that transgressive segregation typically results from recombination between parental taxa that possess quantitative trait loci (QTLs) with antagonistic effects (i.e. QTLs with effects that are in the opposite direction to parental differences for those traits). To assess whether this genetic architecture is common, we tabulated the direction of allelic effects for 3252 QTLs from 749 traits and 96 studies. Most traits (63.6%) had at least one antagonistic QTL, indicating that the genetic substrate for transgressive segregation is common. Plants had significantly more antagonistic QTLs than animals, which agrees with previous reports that transgressive segregation is more common in plants than in animals. Likewise, antagonistic QTLs were more frequent in intra- than in interspecific crosses and in morphological than in physiological traits. These results indicate that transgressive segregation provides a general mechanism for the production of extreme phenotypes at both above and below the species level and testify to the possible creative part of hybridization in adaptive evolution and speciation.

Keywords: adaptive evolution; directional selection; hybridization; quantitative trait locus

1. INTRODUCTION

Most evolutionary studies focus on how populations diverge, but evolution is not just about divergence. If populations come into contact before reproductive barriers are fully developed, they may form hybrids and exchange genes via backcrossing or introgression. Some of the consequences of these genetic contacts include the origin and transfer of genetic adaptations, the origin of new ecotypes or species and the breakdown of reproductive barriers and merger of species (Arnold 1997). Hybridization has been shown to play an important part in both the origin and merger of species (Rieseberg 1997; Otto & Whitton 2000; Wolf *et al.* 2001), but its contribution to adaptation is less clear.

Hybridization does appear to be sufficiently frequent in plants for it to be at least plausible that it has a significant role in adaptive evolution. In a survey of five major biosystematic floras, the frequency of natural hybrids compared to the total number of species in the flora ranged from *ca.* 22% for the British flora to 5.8% for the intermountain flora of North America (Ellstrand *et al.* 1996). Of course,

only a small fraction of the hybrids that exist in nature (or have existed in the past) are likely to have been detected or reported, so these are minimum estimates of natural hybridization frequencies.

A more difficult question is whether hybridization, when it occurs, actually contributes to adaptive evolution. The most promising evidence that it might play a critical creative role derives from frequent reports of individuals with extreme or novel phenotypes in segregating hybrid populations (Grant 1975; Rieseberg & Ellstrand 1993). The generation of these extreme phenotypes in hybrids (i.e. phenotypes that exceed those of either parental line) is referred to as transgressive segregation (Grant 1975; de Vicente & Tanksley 1993). Transgressive segregation is particularly attractive as a mechanism for large and rapid evolutionary transitions because hybridization generates variation at many genes simultaneously and the variant alleles have already been tested by selection.

A recent review of phenotypic variation in hybrids indicates that transgressive segregation occurs frequently in segregating plant and animal populations (Rieseberg *et al.* 1999). Out of 171 studies reviewed, 155 (91%) reported at least one transgressive trait and 44% out of 1229 traits examined were transgressive. Transgressive segregation was found to be more frequent in plants than in animals, in intraspecific than in interspecific crosses, in inbred than in outbred populations, and in domesticated than in wild populations.

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One contribution of 21 to a Discussion Meeting Issue 'Mechanisms regulating gene flow in flowering plants'.

Table 1. Hypothetical example of transgressive segregation owing to the complementary action of genes with additive effects. (Letters in parentheses indicate the species' origin of QTL alleles in F₂ individuals.)

QTLs	phenotypic values			
	species A (AA genotype)	species B (BB genotype)	transgressive F ₂	transgressive F ₂
1	+1	-1	+1 (AA)	-1 (BB)
2	+1	-1	+1 (AA)	-1 (BB)
3	+1	-1	+1 (AA)	-1 (BB)
4	-1	+1	+1 (BB)	-1 (AA)
5	-1	+1	+1 (BB)	-1 (AA)
total	+1	-1	+5	-5

Genetic studies indicate that transgressive segregation mostly results from the appearance, in individual genotypes, of combinations of alleles from both parents that have effects in the same direction (complementary gene action; de Vicente & Tanksley 1993; Rieseberg *et al.* 1999). That is, hybrid individuals that combine 'plus' alleles from both parents or 'minus' alleles from both parents are likely to have extreme phenotypes (table 1). Other mechanisms have been proposed for transgressive segregation such as an increased mutation rate, the exposure of recessive alleles in segregating hybrid populations, epistasis and overdominance, but these alternative mechanisms have received little support (Rieseberg *et al.* 1999). Given the simple, additive genetic basis of transgressive segregation in the complementary gene action model, it should be feasible to predict the likelihood of transgression in a given cross or trait based on the distribution of plus and minus alleles for QTLs in the parental species. That is, the magnitude and frequency of transgressive phenotypes should increase as the proportion of QTLs with opposing effects increases (i.e. as the ratio of plus to minus QTLs approaches 0.5).

Several authors have theorized that the ratio of +/- QTLs reflects the history of selection or genetic drift at the trait in question (Coyne 1996; Laurie *et al.* 1997; True *et al.* 1997; Orr 1998). If most or all QTL alleles for a given trait have effects in the same direction within a line, this would imply that the trait has experienced fairly constant directional selection. By contrast, if QTL alleles have opposing effects within the line (i.e. antagonistic QTLs), then trait differences may have arisen through drift and/or selection that fluctuates in direction. Orr (1998) has formalized these observations with the creation of a QTL sign test that compares observed numbers of +/- QTL alleles in a given line with those predicted under neutral conditions.

A recent application of Orr's (1998) test to the QTL literature in both wild and domesticated plants and animals revealed that QTL ratios were significantly reduced relative to neutral expectations, suggesting that directional selection was the primary cause of phenotypic diversification (Rieseberg *et al.* 2002). Because traits with a consistent history of directional selection are less likely to exhibit transgressive segregation than those with a mostly neutral pattern of evolution, the results appear to represent a challenge to the earlier report of widespread transgressive segregation (Rieseberg *et al.* 1999).

Here, we review the QTL literature to determine the distribution of plus and minus QTL alleles for different categories of organisms and traits. Our goals were to estimate the likelihood of transgressive segregation for these different categories, to compare these predictions with the earlier review of phenotypic variation in hybrids (Rieseberg *et al.* 1999) and to account for the seeming paradox of pervasive directional natural selection and widespread transgressive segregation.

2. MATERIAL AND METHODS

(a) Literature review

In an earlier study of the role of directional selection in phenotypic evolution, we compiled the estimated direction of effects of 2684 QTLs from 572 traits and 84 studies (Rieseberg *et al.* 2002). Because we were primarily interested in the genetics of adaptive evolution, we excluded studies involving domesticated species only or laboratory strains that had been subjected to artificial selection for the trait(s) of interest. Also, we did not include studies of disease or disease resistance traits.

Exactly half of the studies examined in this initial survey employed wild × domesticated crosses and half used wild × wild crosses. However, there was a large imbalance in the number of traits analysed in these two kinds of crosses: 188 traits were analysed in the studies of wild × wild crosses versus 384 from crosses involving wild × domesticated populations. To rectify this imbalance, we surveyed the literature for additional QTL studies involving wild × wild crosses that had been published over the past year, using the same criteria as were employed previously. An additional 12 studies were found that reported results from 177 traits and 568 QTLs (see electronic Appendix A, available on the Royal Society's Publications Web site). Thus, the present analysis employs a roughly equivalent sample of traits from wild × wild crosses (365) versus wild × domesticated crosses (384).

Although the tabulation of +/- QTLs from many studies was straightforward, the following complexities were introduced by a few studies (see also Rieseberg *et al.* 2002).

- (i) In some instances, the same trait was phenotyped in multiple environments or in multiple studies involving the same or closely related taxa. In general, if little overlap was detected in the QTLs in different environments, we reported the results from each environment separately. However, if many of the QTLs detected mapped to the same position, we combined them into a single ratio with

each different QTL counted once. We did not combine QTLs for the same trait from multiple studies because different lines and markers often were used, making it difficult to assess whether the QTLs detected were the same or different. A possible consequence of these scoring decisions is that a small fraction of the QTL ratios reported here are not independent. However, removal of potentially redundant traits or QTLs does not significantly affect QTL ratios (Rieseberg *et al.* 2002).

- (ii) Owing to the reduced information content associated with dominant markers in F_2 populations, some studies mapped QTLs onto two coupling-phase maps derived from the same segregating population (Bradshaw *et al.* 1998; Hawthorne & Via 2001). To avoid redundancy, we arbitrarily reported QTL ratios from just one of the coupling phase maps.
- (iii) Finally, owing to a lack of parental phenotypic information for many studies, we have simply reported the proportion of QTL alleles with opposing effects within a line. This differs subtly from the proportion of QTL alleles with effects in the opposite direction to those predicted based on the trait differences between the parental lines. That is, the former proportion can never be greater than 0.5, but the latter proportion could theoretically exceed 0.5, particularly if the phenotypic differences between the parental lines were small or if there was a large QTL in the predicted direction and many small QTLs in the opposing direction. Fortunately, these proportions were nearly always identical in the QTL studies examined here.

(b) Classification of organisms and traits

Each study was classified with respect to kingdom (animal versus plant), nature of populations crossed (wild \times wild versus wild \times domesticate), divergence of cross (intra- versus interspecific cross), and mating system (self \times self, self \times outcross and outcross \times outcross). In addition, each trait was placed in one of four categories: behaviour; life history; morphology; or physiology. Although most traits were easily classified, some fit equally well in multiple categories. For example, traits related to fecundity could be defined as either morphological or life-history traits. We arbitrarily classified offspring number as a life-history trait, but characteristics of the offspring (e.g. size, weight, shape, etc.) as morphological traits.

(c) Data analyses

We analysed the number of QTLs per trait via multifactor ANOVA with kingdom, population type, cross type, mating system and trait type as the main effects. Owing to the small sample size, behavioural traits were excluded from this and all following analyses. The total number of QTLs per trait was Box–Cox transformed prior to analysis (Box & Cox 1964), and all main effects were tested against the residual error. We then analysed the proportion of antagonistic QTLs per trait as a multifactor ANCOVA with kingdom, population type, cross type, mating system and trait type as main effects, and the total number of QTLs per trait (following Box–Cox transformation) as a covariate. All proportions were arcsine-square root transformed prior to analysis (Sokal & Rohlf 1995), and traits with a single detected QTL were excluded from this analysis. Once again, all main effects as well as the covariate were tested against the residual error. In addition, Orr's (1998) sign test (eqn (7)) was employed to determine whether the proportion of antagonistic QTLs for the organismal/trait categories main effects in the

ANCOVA deviated significantly from neutral expectations, and a logistic analysis was employed to test whether or not each trait had at least one antagonistic QTL. As in the ANOVA, the main effects in the model were kingdom, population type, cross type, mating system and trait type. The transformed total number of QTLs per trait was included as a covariate and, once again, traits with only a single detected QTL were excluded from this analysis. All analyses were performed in JMP (v. 5; SAS Institute, Cary, NC, USA).

3. RESULTS

(a) Representation of organisms and traits

Out of the 96 studies included in this review, 27 (28%) concerned animals and 69 (72%) concerned plants (electronic Appendix A; Rieseberg *et al.* 2002). Likewise, only 96 out of 749 traits scored (13%) were from animal studies compared with 653 traits (87%) from plants (table 2). The unequal representation between plants and animals results mostly from the more widespread use of QTL methods in plants, but it may also reflect unconscious author bias (we all work with plants). In addition, more than twice as many traits were analysed per plant study (9.1 ± 1.3) than per animal study (3.6 ± 0.6).

As might be expected, most of the studies employed model or domesticated organisms (table 2). In animals, for example, 51 out of the 96 traits examined derive from *Drosophila*. The remaining 44 traits were from seven other animal genera that span three phyla and four classes. Plant studies were also highly skewed toward a handful of genera and families. Indeed, out of the 18 genera and eight families examined, the tomato genus (*Lycopersicon*) accounts for 222 of the 653 plant traits. Other well-represented taxa include *Arabidopsis thaliana* (118 traits), pines (*Pinus*, 78 traits), sunflowers (*Helianthus*, 74 traits) and rice (*Oryza*, 52 traits).

In general, there was fairly even representation between wild \times wild (365 traits) and wild \times domesticated crosses (384 traits) and between intra- (349 traits) and interspecific crosses (400 traits). The representation of different mating systems was skewed toward crosses between selfers and outcrossers (336 traits), primarily because many selfing crop plants have outcrossing progenitors (table 2). Unsurprisingly, morphological traits have been most commonly analysed in QTL studies (461 traits), followed by life-history (142 traits), physiological (138 traits) and behavioural traits (eight traits). Indeed, there were too few behavioural traits to make any general conclusions about their evolution. All other trait categories, however, have sufficient representation for meaningful comparisons (table 2).

(b) Quantitative trait locus numbers

The total number of QTLs detected per trait was found to differ substantially among different categories of organisms and traits (table 3). In particular, more QTLs were detected in animals (4.76 ± 0.29 , least squares mean \pm s.e.) than in plants (4.09 ± 0.11), and in interspecific (5.02 ± 0.20) than in intraspecific crosses (3.83 ± 0.18), and in selfers (4.78 ± 0.27) than in outcrossers (4.06 ± 0.20). Likewise, life-history and morphological traits were controlled by significantly more QTLs (4.72 ± 0.22 and 4.60 ± 0.16 QTLs, respectively) than physiological traits (3.97 ± 0.24).

Table 2. Proportions of antagonistic QTLs for various categories of organisms and traits in crosses involving wild species and tests for significant deviations from neutrality.

trait category	total traits	proportion of traits with antagonistic QTLs	total QTLs	proportion of antagonistic QTLs	least-square means (\pm s.e.) ^a
animals	96	0.595	419	0.220 ^b	0.145 (0.025)
plants	653	0.641	2833	0.221 ^b	0.230 (0.010)
wild	365	0.684	1359	0.263 ^b	0.196 (0.018)
wild \times domesticate	384	0.594	1893	0.191 ^b	0.180 (0.020)
interspecific	400	0.596	1999	0.194 ^b	0.155 (0.018)
intraspecific	349	0.685	1253	0.265 ^b	0.221 (0.015)
outcross	242	0.655	938	0.241 ^b	0.216 (0.018)
outcross \times self	336	0.580	1658	0.189 ^b	0.150 (0.022)
self	171	0.732	656	0.274 ^b	0.197 (0.024)
life-history	142	0.609	648	0.215 ^b	0.181 (0.019)
morphology	461	0.669	2053	0.237 ^b	0.213 (0.014)
physiology	138	0.541	530	0.168 ^b	0.169 (0.021)
total	749	0.635	3252	0.221 ^b	

^a Means are adjusted for the effects of factors in the ANOVA model in table 5.

^b $p < 0.001$, corrected for multiple tests by a sequential Bonferroni (30).

Table 3. ANOVA of the effects of kingdom, population type, cross type, mating system and trait type on the total number of QTLs per trait.

source	d.f.	SS	MS	F	p value
kingdom	1	25.54	25.54	4.76	0.0294 ^a
population type	1	16.92	16.92	3.16	0.0761
cross type	1	150.90	150.90	28.13	0.0001 ^b
mating system	2	35.94	17.97	3.35	0.0356 ^c
trait type	2	48.18	24.09	4.49	0.0115 ^d
error	733	3931.36	5.36		

^a The total number of QTLs per trait is lower for plants than it is for animals.

^b The total number of QTLs per trait is lower for intraspecific crosses than for interspecific crosses.

^c Outcrossers had significantly fewer QTLs per trait than did selfers; outcross \times self mapping populations were intermediate to and not significantly different from the others.

^d Physiological traits had fewer QTLs than did morphological or life-history traits, which were not significantly different from each other.

(c) *Antagonistic quantitative trait loci*

Only a single antagonist QTL is needed to generate transgressive phenotypes, so we initially estimated the proportion of traits that had at least one antagonist QTL. Overall, 63.6% of traits had one or more antagonist QTL (table 2). Comparisons among categories of organisms and traits revealed that more plant traits have antagonistic QTLs than animal traits, and traits from intraspecific crosses are more likely to have at least one antagonistic QTL than traits from interspecific crosses (table 4). Mating system, population type (domesticated versus wild) and trait type did not affect the proportion of traits with antagonistic QTLs.

Another way to predict the occurrence and magnitude of transgressive segregation comes from the ratio of $+/-$ QTLs rather than just the presence or absence of antagonistic QTLs (see previous paragraph). As alluded to in § 1, the ratio of $+/-$ QTLs may reflect the history of directional selection on a particular trait, and this was the focus of a previous paper (Rieseberg *et al.* 2002). As reported previously, all categories of traits have QTL ratios closer to zero than expected under neutrality (table 2), a result

Table 4. Logistic analysis of whether or not each trait had at least one antagonistic QTL as a function of kingdom, population type, cross type, mating system, trait type and the total number of QTLs per trait.

source	d.f.	χ^2	p value
kingdom	1	4.64	0.0312 ^a
population type	1	0.40	0.5292
cross type	1	6.15	0.0131 ^b
mating system	2	1.41	0.4939
trait type	2	4.27	0.1182
total QTLs	1	66.84	0.0001

^a Plants are more likely than animals to harbour antagonistic QTLs.

^b Intraspecific crosses are more likely than interspecific crosses to reveal antagonistic QTLs.

consistent with the view that most phenotypic differences are caused by directional selection (Rieseberg *et al.* 2002). Comparison of QTL ratios for different kinds of traits and organisms revealed, as previously reported, that traits from

Table 5. ANCOVA of the effects of kingdom, population type, cross type, mating system and trait type on the proportion of antagonistic QTLs per trait. (The total number of QTLs per trait was included as a covariate.)

source	d.f.	SS	MS	F	p value
kingdom	1	2676.05	2676.05	8.98	0.0028 ^a
population type	1	120.93	120.93	0.41	0.5243
cross type	1	2986.47	2986.47	10.02	0.0016 ^b
mating system	2	1157.79	578.80	1.94	0.1441
trait type	2	1934.99	967.50	3.25	0.0395 ^c
total QTLs	1	10 301.10	10 301.10	34.58	0.0001
error	633	188 586.96	297.93		

^a The proportion of antagonistic QTLs per trait was lower for animals than for plants.

^b The proportion of antagonistic QTLs per trait was lower for interspecific crosses than for intraspecific crosses.

^c Physiological traits had a lower proportion of antagonistic QTLs per trait than did morphological traits; life-history traits were intermediate to and not significantly different from the other two trait types.

intraspecific crosses and morphological traits have higher QTL ratios (weaker selection) and thus are more prone to transgressive segregation than interspecific traits and physiological traits, respectively (table 5). Life-history traits are intermediate between and not significantly different from the other two categories in this analysis. The one surprise from the analysis of the larger dataset is a significant effect of kingdom, with plants having significantly higher QTL ratios than animals (table 5).

4. DISCUSSION

Quantitative trait locus studies typically focus on the number of QTLs and the size of their effects. Few generalizations are possible from these studies, however, because QTL numbers and magnitudes are influenced by the size of the mapping population (Beavis 1994) and the density of genes along chromosomes (Noor *et al.* 2001). The ratio of QTL alleles with opposing effects represents another kind of information that can be mined from QTL studies. Unlike QTL numbers and magnitudes, the direction of QTL effects appears to be robust with respect to experimental design. Also, as emphasized in § 1, the direction of QTL effects can provide information about fundamentally important issues such as:

- (i) the history of the evolutionary forces that have shaped phenotypic diversity (Orr 1998; Rieseberg *et al.* 2002); and
- (ii) the potential for transgressive segregation in segregating hybrids.

(a) *Transgressive segregation*

Because transgressive segregation appears to result mostly from complementary gene action (table 1), the widespread distribution of antagonistic QTLs (63.6% of traits examined) implies that it should be common (table 3). This expectation is concordant with an earlier review of transgressive segregation, in which significant transgression was reported for 58% of plant traits and 35% of animal traits (Rieseberg *et al.* 1999). The somewhat lower realized transgression may be owing to the small phenotypic effects of some antagonistic QTLs, the small hybrid populations employed in some of the phenotypic studies,

and/or high levels of phenotypic variance in the parental lines.

In agreement with the earlier review of transgressive phenotypic expression (Rieseberg *et al.* 1999), antagonistic QTLs were more common in plants than in animals and in intraspecific than in interspecific crosses (see tables 3–5). However, contrary to expectations from observations of phenotypic transgression (Rieseberg *et al.* 1999), in which crosses involving selfers and/or domesticated organisms exhibited higher levels of transgression, these categories were not associated with an increased frequency of antagonistic QTLs. This apparent conflict may be a statistical artefact of the low phenotypic variance associated with parental lines in selfing or domesticated organisms, which increases the likelihood of detecting significant transgression.

In a previous paper, we showed that all categories of traits examined had fewer antagonistic QTLs than would be expected under neutrality, implying an important part for directional selection in phenotypic diversification (Rieseberg *et al.* 2002). If directional selection is ubiquitous, however, then transgressive segregation should be rare rather than common. This puzzle has a simple solution. QTL ratios must merely be significantly below 0.5 to provide evidence of directional selection, but only a single antagonistic QTL is necessary for transgressive segregation. It is easy to see how this sort of genetic architecture could be achieved if there were transitory shifts in the direction of selection or if major QTLs fixed during initial bouts of natural selection overshoot the phenotypic optimum, and minor QTLs with effects in the opposite direction evolve later to bring the trait back to the optimum value (Orr 1998; Rieseberg *et al.* 2002). In addition, the selective fixation of major QTLs that have pleiotropic effects on other traits may generate antagonistic QTLs for the affected traits and inflate QTL ratios.

From an evolutionary standpoint, the frequent occurrence of QTL alleles with opposing effects indicates that transgressive segregation may be a common mechanism for producing extreme phenotypes at both above and below the species level. We have argued elsewhere that extreme phenotypes generated by hybridization may play an important part in adaptation and speciation (Rieseberg *et al.* 1999; Welch & Rieseberg 2002). Unlike mutation,

hybridization provides variation at numerous traits simultaneously, which may be critical for evolutionarily difficult steps that require changes at multiple loci. Colonization of discrete and highly divergent habitats, which appears to have been facilitated by hybridization in annual sunflowers (Welch & Rieseberg 2002; Lexer *et al.* 2003a,b), may represent one such step. Of course, hybridization is unlikely to produce useful transgressive phenotypes for traits that already have a continuous history of directional selection in the parental species. Thus, it is worth noting that the habitats colonized by hybrid sunflower species are novel rather than more extreme versions of the parental species' habitats (Rosenthal *et al.* 2002).

(b) *Quantitative trait locus ratios in animals versus plants*

The proportion of QTL alleles with opposing effects in animals is significantly smaller than that found in plants (tables 3–5), implying that animals traits have had a more constant history of directional selection than plants. This may have a biological explanation. Owing to lower vagility, plants may be less able to minimize temporal changes in their environment than animals. A non-biological explanation relates to the discrepancy in the number of traits scored in animal versus plant studies. Fewer than four traits were scored on average in the animal studies, compared with more than nine in plants. Possibly, zoologists are more discriminating in trait choice, restricting their analyses to traits of perceived importance, whereas botanists may be more willing to score any measurable trait.

(c) *Quantitative trait locus numbers*

Although the focus of this review is on the direction(s) of QTL effects rather than QTL numbers, we also found significant differences among organisms and traits in terms of the total numbers of QTLs per trait. In particular, more QTLs were associated with animals, interspecific crosses, domesticated plants, selfers and life-history/morphological traits (table 2). It is tempting to interpret these differences in a biological fashion. For example, it might be argued that phenotypic differences between species are likely to be larger and to have accumulated over a longer time period than intraspecific differences, and that both factors might contribute to a more complex genetic architecture. Likewise, many of the physiological traits represent simple biochemical differences that are likely to have a simple genetic basis. Alternatively, the differences observed may simply reflect the greater power for detecting QTLs if their effects are in the same direction (Liu 1998). With respect to this hypothesis, note that animal traits and interspecific differences have significantly reduced QTL ratios; i.e. most QTLs are in the same direction (see tables 2 and 5). Another explanatory factor may be the heterozygosity of the parental lines. Parental heterozygosity reduces power for detecting QTLs if multiple parents or multiple F₁s are employed to create the mapping population, and selfers and domesticated lines tend to be highly homozygous.

(d) *Conclusions*

Information derived from variation in the direction(s) of QTL effects can be viewed as an unexpected bonus from QTL studies that provides an estimate of both the

history of selection and the likelihood of transgressive segregation for a particular trait or trait group. In this study, we showed that although QTL proportions are significantly below neutral expectations for all categories of traits and organisms, a genetic architecture favourable for transgressive segregation is common.

The finding that antagonistic QTLs are widespread is more than just an intellectual curiosity. Plant and animal breeders have long recognized that wild populations of organisms sometimes contain cryptic variation that cannot be predicted by the phenotype of the population. This cryptic variation, which may be exposed in crosses through the generation of transgressive phenotypes, is sometimes exploited in breeding programmes (Tanksley & McCouch 1997). Our results indicate that cryptic variation is common, further validating the importance of wild germplasm that seemingly lacks useful phenotypic variation.

With respect to evolutionary theory, our results lend credence to the view that hybridization may serve as a source of genetic variation for adaptive evolution (Anderson 1949; Stebbins 1959; Lewontin & Birch 1966; Grant 1981; Arnold 1997; Barton 2001), at least in hybridizing groups (Ellstrand *et al.* 1996). Given the high proportion of traits with antagonistic QTLs, hybridization may generate useful variation for multiple traits simultaneously, providing a mechanism for large and rapid evolutionary transitions such as the colonization of extreme niches by hybrid sunflower lineages (Lexer *et al.* 2003a,b).

The authors' research on the genetics of adaptation, speciation and hybridization has been supported by National Institutes of Health, the National Science Foundation, the US Department of Agriculture and the Swiss National Science Foundation.

REFERENCES

- Anderson, E. 1949 *Introgressive hybridization*. New York: Wiley.
- Arnold, M. L. 1997 *Natural hybridization and evolution*. New York: Oxford University Press.
- Barton, N. H. 2001 The role of hybridization in evolution. *Mol. Ecol.* **10**, 551–568.
- Beavis, W. D. 1994 The power and deceit of QTL experiments: lessons from comparative QTL studies. In *49th A.I. Corn Sorghum Res. Conf.* pp. 250–266. Washington, DC: American Seed Trade Association.
- Box, G. E. P. & Cox, D. R. 1964 An analysis of transformations. *J. R. Stat. Soc. B* **26**, 211–243.
- Bradshaw Jr, H. D., Otto, K. G., Frewen, B. E., McKay, J. K. & Schemske, D. W. 1998 Quantitative trait loci affecting differences in floral morphology between two species of monkeyflower (*Mimulus*). *Genetics* **149**, 367–382.
- Coyne, J. A. 1996 Genetics of a difference in male cuticular hydrocarbons between two sibling species, *Drosophila simulans* and *D. sechellia*. *Genetics* **143**, 1689–1698.
- de Vicente, M. C. & Tanksley, S. D. 1993 QTL analysis of transgressive segregation in an interspecific tomato cross. *Genetics* **134**, 585–596.
- Ellstrand, N. C., Whitkus, R. & Rieseberg, L. H. 1996 Distribution of spontaneous plant hybrids. *Proc. Natl Acad. Sci. USA* **93**, 5090–5093.
- Grant, V. 1975 *Genetics of flowering plants*, 2nd edn. New York: Columbia University Press.
- Grant, V. 1981 *Plant speciation*. New York: Columbia University Press.

- Hawthorne, D. J. & Via, S. 2001 Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* **412**, 904–907.
- Laurie, C. C., True, J. R., Liu, J. & Mercer, J. M. 1997 An introgression analysis of quantitative trait loci that contribute to a morphological difference between *Drosophila simulans* and *D. mauritiana*. *Genetics* **145**, 339–348.
- Lewontin, R. C. & Birch, L. C. 1966 Hybridization as a source of variation for adaptation to new environments. *Evolution* **20**, 315–336.
- Lexer, C., Welch, M., Durphy, J. L. & Rieseberg, L. H. 2003a Natural selection for salt tolerance QTL in wild sunflower hybrids: implications for the origin of *Helianthus paradoxus*, a homoploid hybrid species. *Mol. Ecol.* (In the press.)
- Lexer, C., Welch, M., Raymond, O. & Rieseberg, L. H. 2003b The origins of ecological divergence in *Helianthus paradoxus* (Asteraceae): selection on transgressive characters in a novel hybrid habitat. *Evolution* (In the press.)
- Liu, B. H. 1998 *Statistical genomics*. Boca Raton, FL: CRC Press.
- Noor, M. A. F., Cunningham, A. L. & Larkin, J. C. 2001 Consequences of recombination rate variation on quantitative trait locus mapping studies: simulations based on the *Drosophila melanogaster* genome. *Genetics* **159**, 581–588.
- Orr, H. A. 1998 Testing natural selection vs. genetic drift in phenotypic evolution using quantitative trait locus data. *Genetics* **149**, 2099–2104.
- Otto, S. P. & Whitton, J. 2000 Polyploid incidence and evolution. *A. Rev. Genet.* **34**, 401–437.
- Rieseberg, L. H. 1997 Hybrid origins of plant species. *A. Rev. Ecol. Syst.* **28**, 359–389.
- Rieseberg, L. H. & Ellstrand, N. C. 1993 What can morphological and molecular markers tell us about plant hybridization? *Crit. Rev. Pl. Sci.* **12**, 213–241.
- Rieseberg, L. H., Archer, M. A. & Wayne, R. K. 1999 Transgressive segregation, adaptation, and speciation. *Heredity* **83**, 363–372.
- Rieseberg, L. H., Widmer, A., Arntz, M. A. & Burke, J. M. 2002 Directional selection is the primary cause of phenotypic diversification. *Proc. Natl Acad. Sci. USA* **99**, 12 242–12 245.
- Rosenthal, D. M., Schwarzbach, A. E., Donovan, L. A., Raymond, O. & Rieseberg, L. H. 2002 Phenotypic differentiation between three ancient hybrid taxa and their parental species. *Int. J. Pl. Sci.* **162**, 387–398.
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*, 3rd edn. New York: Freeman.
- Stebbins, G. L. 1959 The role of hybridization in evolution. *Proc. Am. Phil. Soc.* **103**, 231–251.
- Tanksley, S. D. & McCouch, S. R. 1997 Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* **277**, 1063–1066.
- True, J. R., Jianjun, L., Lynn, F. S., Zeng, Z. B. & Laurie, C. C. 1997 Quantitative genetic analysis of divergence in male secondary sexual traits between *Drosophila simulans* and *Drosophila mauritiana*. *Evolution* **51**, 816–832.
- Welch, M. E. & Rieseberg, L. H. 2002 Habitat divergence between a homoploid hybrid sunflower species, *Helianthus paradoxus* (Asteraceae), and its progenitors. *Am. J. Bot.* **89**, 472–478.
- Wolf, D. E., Takebayashi, N. & Rieseberg, L. H. 2001 Predicting the risk of extinction through hybridization. *Conserv. Biol.* **15**, 1039–1053.

Discussion

D. E. C. Carr (*Blandy Experimental Farm, University of Virginia, Boyce, VA, USA*). Are the QTLs detected in natural hybrid populations the same from population to population within a taxon of annual sunflowers?

L. H. Rieseberg. The QTL analyses to date have been confined to a single cross within each taxon, and differences among populations have not yet been explored.

R. J. Abbott (*Division of Environmental and Evolutionary Biology, School of Biology, University of St Andrews, St Andrews, UK*). Do you have any new ideas on why balanced polygenic systems are so common in animal and plant species, i.e. composed of ‘+’ and ‘-’ QTLs?

L. H. Rieseberg. Several possibilities were described.

T. R. Meagher (*Division of Environmental and Evolutionary Biology, School of Biology, University of St Andrews, St Andrews, UK*). You showed that blocks of parental genomes stay together. Looking to future evolution, if one came in at a much later time and tried to work out the phylogeny, different parts of the genome would give different, but equally correct, answers. The same is true of contemporary species that are the product of general hybridization. Do you have any comment?

L. H. Rieseberg. Yes, that is a good point.

GLOSSARY

QTL: quantitative trait locus

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