THE GENETIC ARCHITECTURE OF HYBRID FITNESS IN THE LOUISIANA *IRIS* SPECIES COMPLEX

THESIS

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CHAPTER I

INTRODUCTION TO REPRODUCTIVE ISOLATION IN LOUISIANA *IRIS*

The Louisiana *Iris* species complex may epitomize the taxonomic difficulty that is sometimes associated with hybridization events between divergent lineages. This was highlighted by the designation of over 80 *Iris* "species" in the Mississippi delta by Small and Alexander (1931) which were later realized to be members of a segregating hybrid swarm (Riley 1935). Initial hybrid formation is rare, however, due to numerous pre- and post-zygotic isolating barriers that act to prevent gene flow between the members of the Louisiana *Iris* species complex.

Prezygotic Isolation

As pre-zygotic barriers act first, they are often thought to be most important in preventing *current* gene flow between species (Ramsey et al. 2003). In this system, this prezygotic isolation is accomplished by reproductive asynchrony, divergent pollinator syndromes, pollinator efficacy, and various postmating isolating barriers resulting in conspecific pollen precedence.

Despite the general difference in habitat of these species, *Iris brevicaulis* and *I. fulva* are found sympatrically along bayous and other disturbed areas in southern Louisiana (Cruzan and Arnold 1993; Johnston et al. 2001). Flowering phenology is

a strong barrier to gene flow between heterospecific plants in sympatry. *I. fulva* initiates flowering in mid-March and commences as *I. brevicaulis* initiates flowering in late April (Cruzan and Arnold 1994). Flowering phenology may be a complete barrier in many years, as the two species have not co-flowered during the two years of a field experiment in their native habitat (Martin et al. 2007; N.H. Martin unpublished data). However, co-flowering is possible in natural populations with greater genotypic diversity (Cruzan and Arnold 1994).

Pollen flow between co-flowering heterospecific individuals is further limited by pollinator visitation. Hummingbirds and lepidopterans preferentially visited the red flowers with reflexed sepals exhibited by *I. fulva* (Martin et al. 2008). Worker and queen bees preferentially visited the characteristics of a "bee-pollinator syndrome" exhibited by *I brevicaulis* (blue flowers, stiff sepals, nectar guides, Martin et al. 2008). Pollinator visitation is not a complete barrier to gene flow, as pollinators of all classes still visited flowers of the other species, but under-visited them as compared to expectations of random visitation (Martin et al. 2008). The second component of pollinator isolation is caused by mechanical differences in the position of the flower parts and the pollinator's ability to successfully receive pollen from the donor plant and deposit the pollen on the recipient plant (form of mechanical isolation, Dobzhansky 1937). Preliminary results from a pollinator efficacy study suggest that both major classes of pollinators are able to successfully transfer fluorescent dye (used as a pollen analogue) from the anthers of both *I. fulva* and *I. fulva*-like hybrids to the stigma of the opposite crosstype in inter-crosstype pollination bouts (N. Martin, S. Taylor, unpublished data).

Post-mating isolation between these species exists as asymmetric pollen tube growth and pollen precedence (Emms et al. 1996). Equal pollen germination is observed on both conspecific and heterospecific plants (Emms et al. 1996), suggesting that pollen precedence is likely due to differential pollen tube growth and possible early zygote inviability (Emms et al. 1996). *I fulva* pollen tubes grow more rapidly on either maternal plant (Emms et al. 1996), and 50:50 mixtures of conspecific:heterospecific pollen yield more hybrids on *I. brevicaulis* plants than *I. fulva*, but the number of hybrids produced is still fewer than expected (Emms et al. 1996). An index of reproductive isolation due to this conspecific pollen precedence can be calculated from the data of Emms et al. (1996) as follows: $RI_{(b)} = 1-(H_b/(1-H_b)$ for *I. brevicaulis* (or $RI_{(f)} = 1-(H_f/1-H_f)$) for *I. fulva*), where H_b and H_f are the proportion of hybrids produced by the *I brevicaulis* and *I. fulva* maternal parents, respectively, when pollinated with 50:50 mixtures of conspecific:heterospecific pollen (Martin and Willis 2007). Reproductive isolation due solely to conspecific pollen precedence is $RI_{(b)} = 0.372549$ for *I brevicaulis* maternal parents and $RI_{(f)} = 0.68254$ for *I fulva* maternal parents.

Postzygotic Isolation

Intrinsic isolation is apparent in *Iris* hybrid zones where cytonuclear incompatibilities result in increased abortion of intermediate genotypes relative to conspecific embryos with *I brevicaulis* chloroplast haplotypes (Cruzan and Arnold 1994, 1999; Arnold 1997). F_1 individuals exhibit heterosis such that reproductive isolation due to postzygotic barriers ($RI_{postzygotic}$), as typically measured ($RI_{postzygotic}$ = 1-(fitness of F_1

hybrids/fitness of parents); Ramsey et al. 2003), would be negative between these species. However, hybrid breakdown is evident in post-F_1 hybrid classes (this study).

Hybrid zones between *Iris brevicaulis* and *I. fulva* conform to a mosaic model (Howard 1986; Harrison 1986) in which genotypes are partitioned in heterogeneous habitats, suggesting that, in addition to the intrinsic postzygotic isolation described above, hybrid fitness is determined by a significant extrinsic component. In order to understand the mechanisms that underlie hybrid fitness and hybrid zone structuring, we compared the fitness of pure species and hybrids in their native habitats.

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CHAPTER II

THE GENETIC ARCHITECTURE OF HYBRID FITNESS IN THE LOUISIANA *IRIS* SPECIES COMPLEX

INTRODUCTION

Speciation involves the evolution of numerous prezygotic and postzygotic isolating mechanisms that limit gene flow between genetically divergent populations (Dobzhansky 1937; Grant 1981; Coyne and Orr 2004). Although individual isolating barriers may be incomplete (e.g. partially overlapping flowering phenologies in plants), these barriers act in concert to restrict gene flow between divergent lineages. Postzygotic isolation, in the form of reduced hybrid viability or fertility, occurs when interspecific nuclear-nuclear (Orr 1995; Turelli and Orr 2000) and cytonuclear (Levin 2003) gene interactions result in maladapted hybrids. This reduced hybrid viability and / or fertility is a central tenet of speciation literature (Dobzhansky 1937) and models of hybrid zone evolution (Barton and Hewitt 1985), as most hybrids are expected to fall between the adaptive peaks occupied by the parental species (Wright 1931, 1932; Dobzhansky 1937; Schluter 1996).

Since before Darwin (1859), those who study hybridization have noticed that the degree of hybrid sterility and inviability is not uniform across all hybridizing species

pairs, as a complex genetic architecture underlies many components of fitness in hybrids (e.g. Edmands 1999; Fritz et al. 2006) . Thus, the consequence of hybridization depends on the nature of this genetic architecture (Barton 2001; Burke and Arnold 2001), and although many interspecific matings yield F_1 offspring with high fitness (e.g. Emms and Arnold 1997; Burke et al. 1998a; Campbell and Waser 2001; Milne et al. 2003), this high fitness is a poor predictor of the fitness of later generation hybrids (e.g. Milne et al. 2003), as heterosis in predominantly outbreeding species is usually due to dominance (Grant 1975) and may quickly decay to reveal hybrid breakdown in later generations.

Dobzhansky (1936, 1937) and Muller (1940, 1942) were the first to provide a model to describe the observation of reduced fitness of later-generation hybrids. In their conceptual model, reduced hybrid fitness was due to the breakup of coadapted gene complexes. According to this model, an ancestral population, fixed for the two-locus genotype *AABB,* split to form two geographically (or otherwise) isolated populations. Within one of the populations, a new mutation, *a*, arises and goes to fixation, while in the other population, a new mutation, *b*, arises and also goes to fixation. These new alleles are completely compatible with the ancestral alleles in each of the separate populations. However, since these alleles have never occupied the same genome, co-occurrences in a common genome have not been tested by natural selection. When the two novel alleles come together in a hybrid genetic background, they may interact negatively, resulting in partial hybrid sterility or inviability. These types of incompatibilities, if distributed widely throughout the genome, may ultimately lead to reproductive isolation and thus, speciation.

In hybridizing species pairs, many genomic regions have been shown to be quite resistant to introgression of foreign alleles due to negative heterospecific gene-gene interactions. Linkage mapping studies in plants, for instance, show regions of segregation distortion wherein heterospecific alleles are disfavored (e.g. Fishman et al. 2001; Kuittinen et al. 2004; Bouck et al. 2005). However, not all heterospecific alleles decrease the fitness of hybrids, and numerous studies have revealed that at least some portions of the genome are permeable to introgression of advantageous and/or neutral genomic regions (Sweigart and Willis 2003; Bouck et al. 2005; Martin et al. 2005, 2006; see Arnold 2006, 2008 for reviews). Thus, the "porosity" of a species' genome will likely depend on a number of ecological and genetic factors. First, the possibility for introgression of genomic regions across species boundaries will depend on the actual formation of at least minimally fit F_1 hybrids *in nature*. Further, later generation hybrids must also possess the potential to form offspring. The degree to which these hybrids have the capacity to produce offspring will depend on the genetic architecture that underlies fitness components. While F_1 hybrids may demonstrate extremely high fitness due to heterosis, the breakup of coadapted gene complexes in later generation hybrids will likely prevent a large portion of heterospecific DNA (including neutral genomic regions linked to those genes causing hybrid incompatibilities) from crossing species boundaries. In order to gain a clear understanding of the evolutionary dynamics underlying the formation and maintenance of hybrid zones, it is thus necessary to know the 1) effectiveness of prezygotic barriers preventing gene flow between species in sympatry, 2) fitness of F_1 and later generation hybrids *in nature*, and 3) the genetic architecture of this

fitness. Natural hybridization in the Louisiana *Iris* species complex allows for an investigation of the evolutionary dynamics of introgression in nature.

The Louisiana *Iris* system consists of three widespread species, *I. brevicaulis*, *I. fulva*, and *I hexagona*, of which *I. fulva* and *I. brevicaulis* are the most ecologically similar (Viosca 1935). Hybrid zones between the latter two species are located in southern Louisiana (Cruzan and Arnold 1993; Johnston et al. 2001b). In these areas, hybrids are formed during a period of minimal overlap in flowering time (Cruzan and Arnold 1994). The formation of F_1 individuals is extremely rare likely due to strong prezygotic isolation (Cruzan and Arnold 1994; Emms et al. 1996; Martin et al. 2007, 2008) and abortion of intermediate seeds (Cruzan and Arnold 1994, 1999; Burke et al. 1998b). However, the few F_1 individuals that are formed are viable and fertile and, thus, able to facilitate the formation of later generation hybrid classes, resulting in widespread introgression between the species (Arnold et al. 1990, 1992). However, the limited number of markers used to detect introgression in the early hybrid zone studies provided neither estimates of the extent nor the adaptive consequences of this introgression.

The potential porosity of the *Iris* genome was first determined by Bouck et al. (2005) using mapping populations derived from crosses between *Iris brevicaulis* and *I. fulva*. Only a minority of markers exhibited significant segregation distortion (15.7% of the markers in the BC*Ib* mapping population and 15.3% of the markers in the BC*If* mapping population). In fact, most of these distortions (71.9% in BC*Ib;* 56.8% in BC*If*) were caused by *over*representation of the heterospecific allele in the mapping population.

Adaptive introgression was investigated by a series of Quantitative Trait Locus (QTL) mapping studies by Martin et al. (2005, 2006, 2008). First, QTLs were detected that were associated with increased survival of the introgressed genotypes in a greenhouse setting (Martin et al. 2005). The second study detected QTLs associated with increased survival in natural, flooded conditions (Martin et al. 2006). The third study detected QTLs associated with pollinator visitation, potentially allowing the hybrid to utilize a wider array of pollinators than the parental species (Martin et al. 2008). As these previous studies suggested that the *Iris* genome is quite permeable to introgression, we examined the potential for adaptive introgression of other fitness-related traits, including measures of both sexual and clonal reproduction in these perennial *Iris* species. Specifically, we first compared the fitness of F_1 and BC_1 hybrids with that of *I. brevicaulis* and *I. fulva* genotypes. We then determined the models of gene action that are most likely to result in the observed patterns of fitness and identified regions of the genome (QTL) responsible for much of the observed variation in hybrid fitness. Finally, we identified and estimated the effects of epistasis between QTLs.

METHODS

Construction of Mapping Populations and Linkage maps

One genotype each of *I. fulva* (If174, collected from Terrebonne Parish, Louisiana) and *I. brevicaulis* (Ib72, collected from St. Martin Parish, Louisiana) were used to produce reciprocal backcross mapping populations (BC*If* and BC*Ib*). The *I. fulva* and *I. brevicaulis* individuals were collected from markedly different habitats - the

former from the margin of a bayou and the latter from a much drier, mixed hardwood forest (M. L. Arnold, unpublished data). If174 (paternal parent) and Ib72 (maternal parent) were crossed in the greenhouse to produce F_1 hybrids. In subsequent years, clones of a one F_1 hybrid were backcrossed to clones of *I. fulva* (again If174) to produce the BC*If* mapping population, while a different F_1 genotype was backcrossed to clones of *I. brevicaulis* (again Ib72) to produce the BC*Ib* mapping population. Ultimately, several hundred BC*If* and BC*Ib* individuals were produced in order to perform linkage mapping (Bouck et al. 2005). Two independent linkage maps were constructed (Bouck et al. 2005) using dominant *Iris* retroelement (IRRE) transposon display markers (Kentner et al. 2003) in Mapmaker 3.0 (Lander et al. 1987; Lincoln et al. 1992). Bouck et al. (2005) and Martin et al. (2007) provide detailed descriptions of both the crossing design and the mapping protocols used to produce the two linkage maps.

Assaying fitness in the field

Two plots were selected in southern Louisiana that represent the general habitat of both species (cypress-mixed hardwood forests, Viosca 1935). These plots (ca. 1 km apart) are located near the Chopique Bayou in the U. S. Army Corps of Engineers Atchafalaya Basin Floodway in south-central Louisiana, USA. These are the same plots that were observed for phenology (Martin et al. 2007) and pollinator visitation (Martin et al. 2008), but not the plots described in Martin et al. (2006), as extensive flooding resulted in high mortality in those sites. We refer to the current plots as either the "dry" plot or the "wet" plot (see Martin et al. 2007, 2008) based on field observations that much

of the "wet" plot remains inundated after heavy rains long after the "dry" plot. The "wet" plot also retains moisture longer than the "dry" site. This has been the case for the field seasons encompassing both 2006 and 2007 described in the current study (S. Taylor and N. Martin, unpublished data).

The clonal reproduction of these species allowed planting of the same genotype into both environments. In October 2005, up to five clones (i.e. ramets) of each genotype of the mapping populations (BC*If*: 172 genotypes; BC*If*: 243 genotypes), the parental species (*I. brevicaulis*: 62, clones of seven wild-collected individuals; *I. fulva*: 43; clones of five wild collected individuals), and the F_1 hybrids used in the crossing design (47 clones) were planted in random order at 0.5 meter intervals into each experimental plot. A total of 1000 individual ramets were planted and subsequently assayed for fitness during the 2006 and 2007 field seasons (January – June).

Fitness Components

Lifetime fitness in long-lived perennial plants, such as irises, is difficult to capture. Here, we chose to assay components of post-seedling fitness, as Johnston et al. (2003) found that hybrids between these species germinate at rates equal or superior to those of the parents, followed by high fitness in early life-history stages. These observations suggested that a large proportion of selection in this system is associated with adult life history stages (but also see Cruzan and Arnold 1994).

In order to assess the fitness of pure species and hybrid classes, we recorded: 1) number of ramets produced before the flowering season (January 2006, March 2007), 2)

presence/absence of flowering stalks, 3) number of flowering stalks produced (per growth point), 4) number of flower nodes, 5) number of flowers (per node), 6) presence/absence of fruit, and 7) number of fruits. Seed viability was not assayed, as Johnston et al. (2003) found that hybrid seeds did not differ from parental individuals in germination or early life history fitness. We then devised a measure of maternal and paternal fitness based on a multiplicative function of the above fitness measures (described in detail in the results section).

Data Analyses

For continuous variables, we utilized a fully saturated three-way analysis of covariance which included: a ''cross type'' main effect (*I. brevicaulis*, BC*Ib*, F_1, BC*If*, and *I. fulva*), a ''habitat'' main effect ("wet" or "dry" site), and initial rhizome weight (covariate), as well as all possible interactions between the main effects. This model was also used in logistic regressions for the nominal variables ("stalk / not" and "fruit / not"). Post-hoc Tukey HSD tests were used to detect differences between crosstypes for all traits when a significant effect for "cross type" was detected. Data were analyzed separately for each year.

Line-Cross Analysis

We used planned linear contrasts to detect deviations from the expected crosstype mean given the null assumption of models of gene action (Mather and Jinks 1982). Under an additive model, the mean of the F_1 individuals is expected to equal the midparent

value. If the F_1 differed from the midparent value (at $P = 0.05$), an additive-dominance model was tested by comparing the mean of the BC_1 generations to the expectation of $BC_1 = 0.5(F_1) + 0.5$(recurrent parent). Deviations from expectations of these models were used to test for the effect of epitasis on the fitness of hybrids for that component.

QTL Analysis

For each fitness trait examined, four separate QTL analyses were performed in each of the BC*If* and BC*Ib* mapping populations: separately for each site ("dry" and "wet") and separately for each year of the study (2006 and 2007). In each site, up to five copies of each of the BC_1 genotypes were planted and assayed for each fitness trait, and the means of each genotype were used to perform QTL mapping. No transformations were performed on any of the traits in order to normalize the data, as this makes QTL effect sizes difficult to interpret (R. Doerge, Z.-B. Zeng, personal communication). All analyses were carried out in Windows QTL Cartographer version 2.5 (Wang et al. 2007).

Composite interval mapping (CIM, Zeng 1994) was performed at 2-cM intervals using a forward and backward regression method along both maps. A10-cM window size was used to exclude closely linked cofactors, with the number of control markers set to five (the program's default setting). Experiment-wise threshold values for declaring the significance of a QTL ($P = 0.05$) were determined using 1000 permutation tests (as suggested by Churchill and Doerge 1994; Doerge and Churchill 1996). A drop below the permutation threshold (or a change in the directionality of the QTL effect) was used as an

indicator of a boundary between multiple QTL peaks on the same linkage group. Significant QTLs were assigned based on these permutation-test criteria.

We further refined our CIM QTL models with Multiple Interval Mapping (MIM, Kao et al. 1999) in order to 1) detect additional significant QTLs (since MIM has greater power and precision for detecting significant QTL; Kao et al. 1999) and 2) search for epistatic interactions between detected QTL. Specifically, MIM was performed for all traits using MIM default settings as follows. First, potential QTL that were initially detected by CIM (inclusively defined as peaks exceeding two-LOD thresholds, regardless of whether those peaks were significant as defined by CIM) were used as the initial model in MIM. Second, tests for epistasis between QTL included in the initial model were performed, and significant interactions were included in this subsequent model. Third, tests for significance were performed on the main-effect QTL and then the epistatic interactions. All non-significant QTL were removed from the model. Finally, a "model summary" report was made which estimates both the individual QTL effects as well as the proportion of the variance explained by each of the QTL and significant interactions. In addition to the QTL estimates of effect sizes, we also calculated two-LOD support limits for each significant QTL (detected by MIM).

RESULTS

Comparison of Cross type Means and Line-cross Analysis

Unlike the field plots assayed for survivorship by Martin et al. (2006), 97% of our plants survived during the two years of the study. This survival did not differ by cross type ($\chi^2 = 0.131114$, $P = 0.997943$) or site ($\chi^2 = 0.001627$, $P = 0.967823$). All other traits differed significantly by cross type (Table 1). Only two traits were significantly influenced by a cross type x site interaction ($fitness_{(M)}$ 2006 [overall maternal fitness], flowers per node 2007). For these two traits, line-cross analyses were conducted separately for each site and charts for both sites are reported (Figure 1).

According to line-cross analyses, only three fitness components (proportion that flowered 2006, stalks per growth point 2006, fruits per flower 2007) were free of the effects of epistasis. However, the negative epistasis was only rarely "strong" enough to lower the hybrid means below the lowest mean of the pure-species. Also, although we utilized crosstype means for statistical comparison and line-cross analyses, recombination can result in genotypes that are capable of producing values that are extreme to those of the pure species. Thus, we reported the minimum and maximum values of each fitness component in Table 2.

Of all traits assayed, heterosis was most prevalent in the clonal growth component of fitness (Figure 1). F_1 hybrids differed from the midparent value and produced significantly more growth points than did pure species individuals in both years; however, the mean of each BC_1 class was significantly lower than expectations of an

additive-dominance model, suggesting that interactions in the hybrid genome are important in affecting asexual fitness. Despite the lower than expected BC_1 means, the best performing individuals from both BC_1 generations (i.e. BC*Ib* and BC*If*) outperformed the best performing individuals of the parental species in both years (Table 2).

F_1 hybrids were consistently equivalent or superior or equal to *I. brevicaulis* and *I. fulva* individuals in terms of sexual fitness, and were not inferior to the least fit species for any fitness component. Like the estimates of clonal fitness, the BC_1 generations exhibited reduced fitness when compared to expectations of the null model (additive or additive-dominance) for all components. The model of gene action responsible for fitness did not only differ between traits, but also differed between years (Figure 1, 2).

As these are long-lived plants, each genotype does not flower in every year. In both years, a higher proportion of F_1 and BC*If* hybrids flowered than did *I. brevicaulis*. In 2006, the hybrids followed expectations of an additive-dominance model for the proportion of plants that flowered, but during the next flowering season, both BC_1 generations were lower than expected under this model (Figure 1).

Of those plants that produced a flowering stalk, the mean number of stalks produced by the F_1 hybrids (corrected for the number of growth points produced) was significantly lower than both the midparent value and the lowest parent (*I. brevicaulis*). However, in 2007, F_1s did not differ from the highest parent (*I. fulva*). BC_1 means conformed to an additive-dominance model and were equivalent to pure species in 2006, and equal or superior to pure species in 2007. In 2007, the F_1 did not differ from the

midparent; both BC_1 generations were lower than expected under an additive model, however, only the BC*If* generation differed significantly from expectations (Figure 1).

The iris inflorescence consists of one to five flowering nodes distributed along the length of the stalk (Wesselingh and Arnold 2003). BC*If* hybrids produced the fewest nodes in 2006, but did not differ from the pure species in 2007. In 2006, the F_1 was significantly lower than the midparent value and BC_1 generations were lower than expectations of an additive-dominance model for the number of flower nodes. In 2007, the F_1 was higher than the midparent value, but BC_1 generations were lower than expected under an additive-dominance model (Figure 1).

Hybrids produced at least as many flowers per node as did the lowest parent (*I. brevicaulis*). In 2006, the F_1 and BC*Ib* conformed to expectations of an additive model, but BC*If* hybrids produced fewer flowers, on average, than expected under that model. In 2007, the *I. fulva* and BC*If* classes performed better in the wet site than the dry site, resulting in a significant crosstype x site interaction ($F_{4,1099}$= 4.74626957, P <0.001). Due to the interaction, contrasts were conducted separately for each plot. In both plots, F_1s were inferior to the midparent value and BC*If* individuals were lower than expected under an additive-dominance model. The maximum number of flowers per node produced by the BC_1 generations exceeded that of the parental species in 2006 (Table 2).

Neither model could fully explain the variation in the proportion of plants that produced a fruit, as BC*Ib* hybrids were lower than expected in both 2006 and 2007. More F_1 and *I. brevicaulis* plants produced fruits than other genotypic classes in 2006. In 2006, the proportion of plants that set fruit did not conform to an additive-dominance model, as

the BC*Ib* mean was lower than expected. In 2007, the BC*Ib* class was significantly lower than expectations of an additive model, although the BC*Ib* mean did not differ from that of *I. brevicaulis* or *I. fulva*.

Of those plants that set fruit in 2006, F_1s produced the highest proportion of fruits, followed by the parental species. In 2007, all classes were superior to *I. fulva* in the number of fruits produced (per flower). An additive-dominance model explained variation in the number of fruits produced in 2007, but not in 2006, as BC*Ib* plants produced fewer fruits than expected under this model.

Fitness Summaries

Although we have analyzed the above fitness components separately, a discussion of total fitness contribution to the next generation for each of the years examined must include all components listed above. As such, we have calculated a summary of paternal fitness for both years separately as follows:

$Fitness_{(P)}$ = [Growth Points / Initial Weight (g)] x [Stalks / Growth Point (including zero)] x [Nodes / Stalk] x [Flowers / Node]

This represents the total number of flowers produced corrected for the initial weight of the rhizome planted in October 2005. No attempts to examine pollen viability or pollen number were made, and thus all flowers are assumed to have equal paternal fitness. However, the BC*Ib* class exhibits reduced pollen viability (Bouck 2004), such that our estimates of hybrid breakdown in paternal fitness (Figure 2) are conservative. Overall, *I. fulva* and the F_1 hybrids were the most paternally-fit in 2006, while *I. fulva* was superior

to all other genotypic classes in 2007. The two BC_1 classes produced the fewest numbers of flowers (corrected for initial rhizome weight) in 2007, but were superior to *I. brevicaulis* in 2006.

Furthermore, we calculated an estimate of maternal fitness as follows:

$$Fitness_{(M)} = [Fitness_{(P)}] \times [Fruits / Flower]$$

This represents the total number of fruits produced, corrected for the initial weight of the rhizome planted in October 2005. All fruits are assumed to have equal maternal fitness. Maternal fitness of cross types varied over the two years of the study as well as across sites in 2006 ($F_{4,1860} = 8.386$, $P < 0.001$). Of all genotypic classes, *I. fulva* and the F_1 hybrids produced the highest number of fruits (per gram of tissue initially planted) in the wet site during 2006 (Figure 2). However, *I. fulva* suffered from greatly reduced fruit formation in the dry site in that of all plants that flowered, only one successfully set fruit. In the dry site, the pure species and BC_1 generations did not differ from pure species. In 2007, maternal fitness was highest in F_1 hybrids, followed by pure species.

Genetic Architecture

Using a QTL approach, we estimated the number of loci responsible for variation in each trait. The number of QTLs identified should be considered a minimum, as there are likely other QTLs that we were unable to detect due to small sample size. Also, due to the limited detection power for some fitness traits, we focus solely on the direction of QTL, as the magnitude of the QTL effects (both additive effects and proportion of the variance explained) is certainly inflated (Beavis 1994). Furthermore, our identification of

interactions between QTLs was limited to those QTL detected by CIM. As there are potentially more epistatically acting QTLs than those that act additively (Malmberg and Mauricio 2005), we also consider our estimates of the number of interacting loci to be a minimum value.

Significant BC*Ib* fitness QTLs

The total number of additive QTL detected for each trait in the BC*Ib* mapping population ranged from 1-4, with a maximum of three epistatic interactions detected by MIM (Table 3a; Figure 3a). Of the thirteen traits for which we were able to detect more than one significant QTL, ~69% were affected by QTLs with individually opposite effects on the trait. The direction of the effect of epistasis between QTLs was inconsistent, as some were in opposite directions to the additive effects (traits $11_{C \times D}$ and 25), some enhanced the additive effects (BC*Ib*: $11_{B \times C}$), and some were between QTLs of opposing effects (BCIb: traits 6, $11_{A \times C}$). We only attempted to identify interactions between QTL that had already been detected by CIM. We were unable to detect significant QTL in the BC*Ib* mapping population for the following traits in 2006: growth points (wet site), stalk / not (wet site), flowers per node (wet site), and 2007: stalk / not (wet site); stalks per growth points (wet site).

Significant BC*If* fitness QTLs

The total number of additive QTL detected for traits in the BC*If* mapping populations ranged from 1-5, with a maximum of one epistatic interaction detected by

MIM (Table 3b; Figure 3b). The direction of most QTL effects was consistent with expectations, given the difference between the means of *I. brevicaulis* and *I. fulva*. However, of the thirteen traits for which we were able to detect more than one significant QTL, ~54% were determined by QTLs with individually opposite effects on the trait. Interactions between the additive QTLs were detected for four traits in the BCIF mapping population. Of these, one was in the opposite direction to the additive effects (trait 25) and three enhanced the additive effects (traits 7, 8, 11). We were unable to detect significant QTL in the BC*If* mapping population for the following traits in 2006: growth points (wet site), stalks per growth point (wet site), fruits per flower (dry site), and 2007: stalk / not (wet site), stalks per growth point (wet site), fruit / not (wet site).

Colocalization of QTLs

We searched for overlapping QTLs by comparing the confidence intervals around the most-likely location of each QTL. However, the confidence intervals of many QTLs on each linkage group were overlapping (Table 3), so we discuss those QTLs that share a common "nearest marker" on a linkage group. Using these discussion criteria, we detected overlapping QTLs (Figure 3) for traits in both mapping populations. In the BC*Ib* mapping population, all detected overlapping QTLs were responsible for variation in the different traits. QTL for nodes per stalk (dry 2007, trait 21) overlapped with QTLs for flowers per node from both sites in 2007 (traits 23-24) on LG6. LG7 contained overlapping QTL for flowers / node (dry 2006, trait 9) and fruits / flower (wet 2006, trait 14). QTLs for stalk / not (dry 2007, trait 17) and fruit / not (dry 2007, trait 25) overlapped

on LG9. Variation in trait in the proportion of plants that set fruit (wet 2006, trait 12) and the amount of fruits produced (wet 2006, trait 14) was affected by QTLs that overlapped on LG14. Lastly, a detected QTL for stalk /not (dry 2007, trait 17) colocalized with a QTL for fruit / not (dry 2006, trait 11) and a QTL for growth points / wt (wet 2007, trait 16).

In the BC*If* mapping population, many linkage groups contained colocalized QTLs that were responsible for variation in the same trait, but in different sites or years. For example, variation in clonal growth in the dry site during both years (traits 1, 15, LG10) was controlled by overlapping QTLs, as were QTLs for flower / node in both sites during 2007 (traits 23-24, LG11). Also, the QTL detected for nodes / stalk (dry 2006, trait 7) colocalized with the QTL detected for variation in the same trait in the dry site in the previous year (trait 21). However, not all colocalized QTLs were responsible for variation in the same trait. QTLs for nodes / stalk (dry, wet 2006) and stalks / gp (dry 2007, trait 19) shared a common nearest marker on LG1. QTLs responsible for node / stalk (wet 2006, trait 8) and flower / node (wet 2006, trait 10) overlapped on both LG3 and LG9. Finally, on LG16, QTLs for nodes / stalk (dry 2007, trait 21) and fruit / flower (wet 2007, trait 28) were found to overlap.

DISCUSSION

Iris hybrid zones consist of *I. brevicaulis*-like and *I. fulva*-like hybrids interspersed with *I. brevicaulis* and *I. fulva* genotypes (Cruzan and Arnold 1993; Johnston et al. 2001b). In these "mosaic" hybrid zones (Howard 1986; Harrison 1986), a

genotypic cline exists from one type of hybrid to another. Although a sharp genotypic cline is characteristic of a traditional tension zone (Barton and Hewitt 1985), Arnold (1997) noted that such a cline may correspond to a change in habitat, emphasizing the importance of the environment in determining the degree of postzygotic isolation between species. This is apparent in the Louisiana *Iris* system, as well as in other systems that contain naturally hybridizing species pairs (see Arnold 1997, 2006 for reviews).

F_1 hybrids between *I. brevicaulis* and *I. fulva* consistently show equal or superior fitness to the parental species, both in experimental conditions (e.g. dry, field capacity, and flooded substrates, Johnston et al. 2001a), and natural conditions (this study). Although heterosis is not unusual in early generation hybrids between divergent lineages, the systems that present cases of F_1 heterosis often do demonstrate common evolutionary outcomes of hybridization due to differences in the fitness of later generation hybrids *in nature*. For example, although natural F_1 hybrids between *Rhododendron ponticum* and *R. caucasicum* exhibit high fitness, hybrid zones may be is completely devoid of post-F_1 hybrids, apparently due to strong hybrid breakdown (Milne et al. 2003). However, in the *Rhododendron* system, no hybrid breakdown was evident in greenhouse conditions (Milne et al. 2003). Thus, it is important that any attempt to examine the degree of postzygotic isolation between divergent lineages be conducted *under natural conditions*.

We examined the fitness of F_1 and first-generation backcross individuals, along with *I. brevicaulis* and *I. fulva* genotypes, in plots characteristic of the habitat of each parent (i.e. "dry" and "wet"; Viosca 1935) in southern Louisiana. In irises, F_1 heterosis is followed by substantial hybrid breakdown, resulting in backcross hybrids revealing

significantly reduced fitness compared to that expected given an additive-dominance model (this study). However, unlike in *Rhododendron*, this breakdown in *Iris* is not so severe as to lower the fitness of backcross generations below that of the parental species, and, thus result in hybrid zones between *I. brevicaulis* and *I. fulva* that are dominated by backcrosses, but devoid of F_1s. The production of fertile F_1s between these species allows for the potential for introgressive hybridization (Anderson 1948). The evolutionary potential of introgression will depend on: 1) the formation of fertile F_1s; 2) the fitness of the F_1 and backcross generations in nature; and 3) the genetic architecture of this fitness.

Formation of F_1 hybrids

Barriers to the formation of F_1 hybrids between *I brevicaulis* and *I. fulva* have been documented by Cruzan and Arnold (1994), Emms et al. (1996), Martin et al. (2007), and Martin et al. (2008). Briefly, *I. brevicaulis* and *I. fulva* occupy large ranges in the along the Mississippi River and central U.S.; however, they are sporadically sympatric along bayous in southern Louisiana. In sympatric populations, the species presumably hybridize during an extremely small period of flowering overlap in April. Although no adult F_1 hybrids have been found in nature (Cruzan and Arnold 1993), experimental F_1s exhibit high fitness (Johnston et al. 2003), are intermediate in flowering time compared to the two pure-species populations (Martin et al. 2007), are attractive to pollinators (Martin et al. 2008) and are thus able to facilitate the creation of later generation hybrids.

Fitness of hybrids in nature

Asexual growth of clonal plants is included in measures of reproductive output because clonal growth increases both the potential for survival of a genotype (Cook 1979; Gardner and Mangel 1999), and the genotype's sexual output by facilitating the production of flowering stalks, flowers, and fruits (Watson 1984; Gardner and Mangel 1999). In the present study, Louisiana *Iris* hybrids were able to produce as many (in BC*If* or BC*Ib* hybrids), or substantially more (in F_1 hybrids), clonal growth points than the pure-species plants, thus allowing for survival and increased sexual output of the hybrids. Also in this system, the clonal fitness of hybrids may have facilitated the stabilization of *I. nelsonii*, a purported hybrid species between *I. fulva*, *I. hexagona*, and *I. brevicaulis* (Randolph 1966; Arnold 1993; Burke et al. 2000).

Gene flow between allopatric populations in Louisiana *Iris* primarily occurs by pollen transfer across long distances rather than by long-distance seed dispersal (Arnold et al. 1991, 1992; Cornman et al. 2004). Therefore, the production of flowers that produce viable pollen is important in allowing for gene flow and possible dispersed introgression, especially because hybrid genotypic classes are equally or more attractive to pollinators than parental genotypes (Martin et al. 2008). However, although the BC_1 generations appear to be only slightly less fit than parental species in potential paternal fitness, members of this backcross generation suffer from reduced pollen viability (Bouck 2004). Thus, our estimates of hybrid breakdown in the BC*Ib* fitness are conservative.

Genetic Architecture

The backcross design utilized for this QTL analysis was advantageous because it allowed an examination of the initiation of introgression between these species. However, due to the lack of an F_2 generation for our study, we were limited in our analysis of genetic mechanisms underlying fitness. For instance, dominance effects cannot be estimated in a backcross design, and all main effects are assumed to be completely additive. Still, we were able to detect significant heterosis in the F_1 generation followed by breakdown in the BC_1 generations, which we attribute to the breakup of coadapted gene complexes (Dobzhansky 1937).

No trait followed the same model of gene action in both years; furthermore, no QTLs were detected that overlapped for both environments, in both years. These results further emphasize the role of the environment on the effects of postzygotic isolation and potential introgression (Bordenstein and Drapeau 2001).

For most traits, at least one heterospecific genomic region increased the trait mean (and resulting fitness of the individuals that received introgressed DNA). This result occurred even when the donor parent mean fitness was lower than that of the BC_1 generation's recurrent parent, suggesting the possibility of adaptive trait introgression for many traits, thus increasing the fitness of the recipient individuals in native and potentially novel habitats. Indeed, hybrid classes of Louisiana *Iris* have been found that are capable of occupying novel habitats (Randolph 1966; Cruzan and Arnold 1993).

However, for most traits, the introgression of the majority of heterospecific genomic regions decreased trait means. For these genomic regions, introgression of

heterospecific DNA would likely be strongly disfavored. An examination of the BC*If* and BC*Ib* linkage maps reveals QTLs affecting both prezygotic (Bouck et al. 2005, 2007; Martin et al. 2007, 2008) as well as postzygotic barriers (Bouck et al. 2005; Martin et al. 2005, 2006; Figure 3) widely dispersed across the entire genome (in both linkage maps). By examining these maps, it is quite clear that the genome likely acts as a "genetic sieve", allowing for the introgression of certain regions, and preventing the introgression of others.

The QTLs reported in the present and previous studies of Louisiana irises (Martin et al. 2005, 2006, 2007, 2008; Bouck et al. 2007) form good "hypotheses" to test in natural hybrid zones. For example, we can ask whether or not the patterns of introgression predicted by these QTL analyses are detected in natural hybrid populations. The body of data concerning the biology and genetic architecture of pre- and postzygotic reproductive isolation in Louisiana irises thus represents a unique and powerful resource for testing the process of speciation in the face of gene flow (Arnold 2006).

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TABLES

Table 1a: ANCOVA and Nominal Logistic Results for continuous and nominal variables, respectively, in 2006. * Test Statistic: F-ratio for continuous response variables; $\chi 2$ for nominal variables. # Main effect "site" was excluded due to low sample size.

Response	**SOV**	**df**	**MS**	**TS***	***P***
Growth Points	Crosstype	4	37.044	8.71	**<0.001**
	Site	1	0.013	0.003	0.955
	Wt	1	3310.4	778.37	**<0.001**
	crosstype*site	4	5.307	1.248	0.289
	crosstype*wt	4	27.361	6.433	**<0.001**
	site*wt	1	0.376	0.088	0.766
	crosstype*site*wt	4	0.602	0.141	0.967
	Error	1851	4.253		
Flower / Not	Crosstype	4		35.764	**<0.001**
	Site	1		1.503	0.22
	Wt	1		40.009	**<0.001**
	crosstype*site	4		0.894	0.925
	crosstype*wt	4		6.844	0.144
	site*wt	1		2.565	0.109
	crosstype*site*wt	4		5.609	0.23
Stalks per growth point	Crosstype	4	0.207	4.355	**0.002**
	Site	1	0.025	0 526	0.47
	Wt	1	2.359	49.553	**<0.001**
	crosstype*site	4	0.027	0.573	0.682
	crosstype*wt	4	0.046	0.963	0 427
	site*wt	1	0.13	2.741	0.098
	crosstype*site*wt	4	0.075	1 573	0.179
	Error	802	0.009		
nodes per stalk	Crosstype	4	2.802	5.849	**< 0.001**
	Site	1	0.712	1.485	0.223
	Wt	1	0.001	0.002	0.967
	crosstype*site	4	0.487	1.017	0.397
	crosstype*wt	4	0.295	0.616	0.651
	site*wt	1	0.191	0.399	0.528
	crosstype*site*wt	4	0.753	1.572	0.18
	Error	802	0.479		

Table 1a - Continued

Response	**SOV**	**df**	**MS**	**TS***	***P***
Flowers per Node	Crosstype	4	0.389	11.022	**<0.001**
	Site	1	0.104	2.955	0.086
	Wt	1	0.018	0.506	0.477
	crosstype*site	4	0.011	0.304	0.875
	crosstype*wt	4	0 077	2.183	0.069
	site*wt	1	0.118	3.332	0.068
	crosstype*site*wt	4	0.072	2.039	0.087
	Error	802	0.035		
Fruit / Not	Crosstype	4		38.319	**<0.001**
	Site	1		1.104	0.293
	Wt	1		0 892	0 345
	crosstype*site	4		8.974	0.062
	crosstype*wt	4		1.927	0.749
	site*wt	1		3.311	0.069
	crosstype*site*wt	4		6 35	0.174
Fruits per Flower	Crosstype	4	0.467	7.19	**<0.001**
	Wt	1	0.162	2.495	0.115
	crosstype*wt	4	0.071	1.091	0.361
	Error	362	0.065		
Paternal Fitness	Crosstype	4	0.056	8.162	**<0.001**
	Site	1	0.03	4.342	**0.037**
	crosstype*site	4	0.008	1.201	0.308
	Error	1860	0.007		
Maternal Fitness	Crosstype	4	0.062	13.958	**<0.001**
	Site	1	0 075	16.961	**<0.001**
	crosstype*site	4	0.037	8.386	**<0.001**
	Error	1860	0.004		

Table 1b: ANCOVA and Nominal Logistic Results for continuous and nominal variables, respectively, in 2007. * Test Statistic: F-ratio for continuous response variables; $\chi 2$ for nominal variables.

Response	**SOV**	**df**	**MS**	**TS***	***P***
Growth Points	Crosstype	4	879.15	52.481	**<0.001**
	Site	1	190.86	11.394	**<0.001**
	Wt	1	8903.4	531.49	**<0.001**
	crosstype*site	4	9.697	0.579	0.678
	crosstype*wt	4	248.52	14.834	**<0.001**
	site*wt	1	1.2	0.072	0.789
	crosstype*site*wt	4	23.193	1.385	0.237
	Error	1832	14.043		
Flower / Not	Crosstype	4		42.716	**<0.001**
	Site	1		19.179	**<0.001**
	Wt	1		11.654	**<0.001**
	crosstype*site	4		1.552	0.817
	crosstype*wt	4		11.352	**0.023**
	site*wt	1		0.01	0.752
	crosstype*site*wt	4		3.993	0.407
Stalk per Growth Point	Crosstype	4	0.109	11.002	**<0.001**
	Site	1	0.209	20.996	**<0.001**
	Wt	1	0.224	22.569	**<0.001**
	crosstype*site	4	0.008	0.84	0.5
	crosstype*wt	4	0.017	1.746	0.138
	site*wt	1	0.053	5.327	**0.021**
	crosstype*site*wt	4	0.008	0.827	0.508
	Error	1117	0.01		
Nodes per Stalk	Crosstype	4	9.74	21.781	**<0.001**
	Site	1	1.176	2 631	0.105
	Wt	1	0.058	0.13	0.718
	crosstype*site	4	0.196	0.439	0.781
	crosstype*wt	4	0.138	0.309	0.872
	site*wt	1	0.381	0.851	0.356
	crosstype*site*wt	4	0.143	0.32	0.864
	Error	1100	0.447		

Table 1b - Continued

Response	SOV	df	MS	TS*	P
Flowers per Node	Crosstype	4	5.387	74.805	**<0.001**
	Site	1	0.166	2.299	0.13
	Wt	1	0.422	5.853	**0.016**
	crosstype*site	4	0.342	4.746	**<0.001**
	crosstype*wt	4	0.232	3.22	**0.012**
	site*wt	1	0.03	0.419	0.518
	crosstype*site*wt	4	0.043	0.591	0.669
	Error	1099	0.118		
Fruit / Not	Crosstype	4		23.337	**<0.001**
	Site	1		0.273	0.601
	Wt	1		1.169	0.28
	crosstype*site	4		1.72	0.787
	crosstype*wt	4		4.664	0.324
	site*wt	1		0.443	0.506
	crosstype*site*wt	4		6.455	0.168
Fruits per Flower	Crosstype	4	2 01	40.193	**<0.001**
	Site	1	0.452	9.04	**0.003**
	Wt	1	0.201	4.018	**0.045**
	crosstype*site	4	0.051	1.023	0.394
	crosstype*wt	4	0.024	0.476	0.753
	site*wt	1	0.001	0.0148	0.903
	crosstype*site*wt	4	0.029	0.58	0.677
	Error	790	0.05		
Flower Product	Crosstype	4	4.055	45.285	**<0.001**
	Site	1	6.061	67.681	**<0.001**
	crosstype*site	4	0.159	1.78	0.13
	Error	1832	0.09		
Fruit Product	Crosstype	4	0.8	50.984	**<0.001**
	Site	1	0.5	31.851	**<0.001**
	crosstype*site	4	0.014	0.865	0.484
	Error	1786	28.04		

Table 2: Summary statistics of fitness components for all cross types, averaged across plots for both years.

	2006					2007				
	N	Min	Max	LSM	SE	N	Min	Max	LSM	SE
Growth Points										
I brevicaulis	82	1	15	3.77	0.25	82	1	23	6.721	0.49
BC*Ib*	881	1	24	3.87	0.07	888	1	32	7.623	0.14
F_1	107	1	19	5.08	0.2	108	1	42	13.2	0.4
BC*If*	718	1	40	3.86	0.08	719	1	31	7.149	0.16
I fulva	83	1	16	3.89	0.26	84	1	24	6.967	0.49
Stalk / Growth Point										
I brevicaulis	18	0.08	1	0.42	0.05	34	0 06	0.33	0.203	0.02
BC*Ib*	376	0.06	1	0.34	0.01	494	0.05	0.6	0.216	0.01
F_1	74	0.11	1	0.25	0.03	96	0.06	1.5	0.259	0.01
BC*If*	342	0.06	1	0.36	0.01	469	0 04	1	0.247	0.01
I. fulva	22	0.11	1	0.36	0.06	59	0.11	0.75	0.291	0.01
Node / Stalk										
I. brevicaulis	18	2	5	3.43	0.17	33	2.33	4	3.281	0.16
BC*Ib*	376	1	4	2.99	0.04	487	1	5	3.082	0.03
F_1	74	1	4	3.1	0.08	92	2.75	4.67	3.659	0.07
BC*If*	342	1	5	2.87	0.04	465	1	5	3.387	0.03
I fulva	22	3	4	3.45	0.18	58	2	5	3.58	0.1
Flower / Node										
I brevicaulis	18	0.88	1.5	1.26	0.05	33	1.14	2	1.32	0.06
BC*Ib*	376	0.5	3	1.34	0.01	487	1	2.5	1.364	0.01
F_1	74	1.2	2.5	1 36	0.02	92	1.19	1.89	1.331	0.03
BC*If*	342	0.75	3	1.4	0.01	464	1	3.5	1.529	0.01
I fulva	22	1.13	2	1.57	0.05	58	1.25	4	1.989	0.04
Fruit / Flower										
I brevicaulis	10	0.17	1	0.65	0.08	26	0.13	1	0.545	0.06
BC*Ib*	167	0.07	1	0.6	0.02	312	0.06	1	0.55	0.01
F_1	59	0.21	1	0.76	0.03	87	0.05	1	0.645	0 02
BC*If*	128	0.11	1	0.55	0.02	355	0.03	1	0.391	0.01
I fulva	9	0.33	1	0.38	0.16	40	0.08	0.71	0.237	0.04

Table 3a: BC*Ib* QTL summary report. QTL underlying the fitness of hybrids for seven fitness components in two plots in southeastern Louisiana in 2006 and 2007.

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
1	2006	Dry	GP/WT	5	4	34-79 (63)	0.14	0.0404
2	2006	Wet	GP/WT	x	x	x	x	x
3	2006	Dry	Stalk/Not	3	9	53-86 (75)	0.056	-0.1928
4	2006	Wet	Stalk/Not	x	x	x	x	x
5	2006	Dry	Stalk/GP	5	2	0-62 (25)	0.103	0.1432
6	2006	Wet	Stalk/GP (A)	2	8	85-135 (112)	0.099	-0.1246
6	2006	Wet	Stalk/GP (B)	7	9	58-78 (60)	0.129	0.1544
6			A X B				0.081	-0.2194
7	2006	Dry	Node/Stalk	1	1	0-12 (0)	0.149	-0.6537
7	2006	Dry	Node/Stalk	13	3	12-53 (27)	0.12	-0.5362
7	2006	Dry	Node/Stalk	15	1	0-18 (0)	0.142	-0.5737
8	2006	Wet	Node/Stalk	13	5	36-53 (53)	0.126	-0.4739
8	2006	Wet	Node/Stalk	17	1	0-14 (0)	0.213	0.606
9	2006	Dry	Flower/Node	7	10	68-88 (88)	0.197	-0.1442
9	2006	Dry	Flower/Node	11	5	25-50 (37)	0.105	-0.1093
10	2006	Wet	Flower/Node	x	x	x	x	x
11	2006	Dry	Fruit/Not *	1	n.s.			
11	2006	Dry	Fruit/Not (A)	3	1	0-18 (0)	0.62	-0 2301
11	2006	Dry	Fruit/Not (B)	4	6	89-91 (91)	0.097	0.2276
11	2006	Dry	Fruit/Not (C)	10	1	6-16 (10)	0.012	0.2487
11	2006	Dry	Fruit/Not (D)	17	1	0-39 (0)	0.063	0.2587
			AXC				0.048	0.4602
			BXC				0.634	1.5447
			CXD				0.056	-0.5173

Table 3a - Continued

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
12	*2006*	*Wet*	*Fruit/Not*	*2*	*n s*			
12	2006	Wet	Fruit/Not	14	4	33-47 (41)	0.693	0.7987
13	2006	Dry	Fruit/Flower	6	9	61-85 (73)	0.208	0.2611
13	2006	Dry	Fruit/Flower	13	4	10-53 (32)	0.111	-0.1924
13	2006	Dry	Fruit/Flower	15	2	0-30 (14)	0.176	0.2442
13	2006	Dry	Fruit/Flower	22	1	0-12 (0)	0.283	-0.3024
14	*2006*	*Wet*	*Fruit/Flower*	*4*	*n s*			
14	2006	Wet	Fruit/Flower	7	10	60-88 (74)	0.256	0.2572
14	2006	Wet	Fruit/Flower	11	1	0-12 (0)	0.342	-0.3069
14	2006	Wet	Fruit/Flower	13	5	36-53 (53)	0.283	0.2671
14	2006	Wet	Fruit/Flower	14	4	29-45 (39)	0.374	-0.3035
14	2006	Wet	Fruit/Flower	17	3	8-39 (27)	0.231	0.2993
15	2007	Dry	GP/Wt	1	6	73-88 (87)	0.172	0.1178
15	2007	Dry	GP/Wt	1	8	106-116 (106)	0.124	-0 1016
16	2007	Wet	GP/Wt	17	1	0-18 (0)	0.109	0.0927
17	2007	Dry	Stalk/Not	9	1	0-23 (14)	0.165	0 3278
17	2007	Dry	Stalk/Not	9	4	33-57 (35)	0.225	-0.3774
17	2007	Dry	Stalk/Not	21	2	0-14 (7)	0.084	0.2158
18	2007	Wet	Stalk/Not	X	x	x	x	x
19	2007	Dry	Stalk/Gp	6	7	45-73 (62)	0.098	-0.0444
20	2007	Wet	Stalk/Gp	X	x	x	x	x
21	2007	Dry	Node/Stalk	6	4	25-55 (45)	0.164	-0.4932

Table 3a – Continued

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
22	2007	Wet	Node/Stalk	2	8	60-114 (96)	0.143	0.5696
23	2007	Dry	Flr/Node	6	4	26-55 (45)	0.095	0.0595
23	2007	Dry	Flr/Node	19	2	0-35 (30)	0.105	-0.0629
24	2007	Wet	Flr/Node	2	8	85-147 (106)	0.11	-0.105
24	2007	Wet	Flr/Node	6	4	25-38 (45)	0.085	0.0928
25	2007	Dry	Fruit/Not (A)	2	2	14-42 (28)	0.329	0.4549
25	2007	Dry	Fruit/Not (B)	9	4	39-65 (65)	0.36	0.5044
			A X B				0.259	-0.9176
26	2007	Wet	Fruit/Not	2	4	12-58 (41)	0.146	0.3405
27	2007	Dry	Fruit/Flr	4	6	61-91 (81)	0.372	0.279
27	2007	Dry	Fruit/Flr	21	1	0-8 (0)	0.264	0.2404
28	2007	Wet	Fruit/flr	17	3	27-39 (35)	0.303	-0.3284

Table 3b: BC*If* QTL summary report: QTL underlying the fitness of hybrids for seven fitness components in two plots in southeastern Louisiana during 2006 and 2007.

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
1	2006	Dry	GP/Wt	10	1	0-17 (0)	0.109	-0.039135
2	2006	Wet	GP/Wt	X	x	x	x	x
3	2006	Dry	Stalk/Not	7	3	39-65 (50)	0.102	-0.268576
4	2006	Wet	Stalk/Not	3	1	0-48 (18)	0.308	0.4681096
5	2006	Dry	Stalk/GP	13	2	0-29 (11)	0.171	-0.22796
6	2006	Wet	Stalk/GP	X	x	x	x	x
7	2006	Dry	Node/Stalk (A)	1	1	0-28 (10)	0.133	-0.4711
7	2006	Dry	Node/Stalk (B)	9	4	2-56 (40)	0 117	-0.5899
7	2006	Dry	Node/Stalk (C)	15	1	0-13 (0)	0.237	-0.7878
			BXC				0.07	-0.775
8	2006	Wet	Node/Stalk (A)	3	4	54-74 (61)	0.14	-0.7906
8	2006	Wet	Node/Stalk (B)	1	1	10-39 (28)	0.182	-0.8392
8	2006	Wet	Node/Stalk (C)	9	1	8-32 (20)	0.287	-0.7354
8	2006	Wet	Node/Stalk (D)	9	4	32-48 (40)	0.09	-0.3461
8	2006	Wet	Node/Stalk (E)	17	1	0-9 (0)	0.22	0.9438
			B X D				0.021	-0.45
9	2006	Dry	Flr/Node	18	12	0-12 (12)	0.139	-0.199102
10	2006	Wet	Flr/Node	3	4	48-74 (61)	0.147	0.138027
10	2006	Wet	Flr/Node	9	4	32-58 (40)	0.179	0.14735
11	2006	Dry	Fruit/Not (A)	4	4	8-41 (21)	0.075	0.2169
11	2006	Dry	Fruit/Not (B)	11	4	0-43 (25)	0.238	0.338
			A X B				0.087	0.3569

Table 3b - Continued

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
12	2006	Wet	Fruit/Not	12	1	0-27 (12)	0.339	-0.517579
12	2006	Wet	Fruit/Not	2	6	40-51 (45)	0.215	0.528848
13	2006	Dry	Fruit/Flr	X	x	x	x	x
14	2006	Wet	Fruit/Flr	6	3	2-62 (42)	0.074	-0.124791
14	2006	Wet	Fruit/Flr	11	5	20-43 (35)	0.192	0.1867818
14	2006	Wet	Fruit/Flr	2	8	54-85 (65)	0.107	-0.146933
14	2006	Wet	Fruit/Flr	20	1	0-4 (0)	0.158	0.186
14	2006	Wet	Fruit/Flr	15	3	0-28 (14)	0.3	0.24009
15	2007	Dry	Gp/Wt	11	1	0-18 (8)	0.123	0.1524781
15	2007	Dry	Gp/Wt	10	1	0-17 (0)	0.092	-0.075333
16	2007	Wet	Gp/Wt	13	3	10-40 (30)	0.107	0.1062864
17	2007	Dry	Stalk/Not	2	5	26-53 (40)	0.111	0.2756036
18	2007	Wet	Stalk/Not	X	x	x	x	x
19	2007	Dry	Stalk/Gp	1	1	0-20 (0)	0.339	0 0997292
19	2007	Dry	Stalk/Gp	1	7	66-94 (80)	0.165	-0.070541
20	2007	Wet	Stalk/Gp	X	x	x	x	x
21	2007	Dry	Node/Stalk	1	3	2-60 (39)	0.137	-0.569066
21	2007	Dry	Node/Stalk	16	1	0-26 (0)	0.138	0.5810528
21	2007	Dry	Node/Stalk	15	1	0-28 (0)	0.11	-0.4726

Table 3b - Continued

Trait	Year	Site	Fitness	Chromosome	Nearest Marker	Location	PVE	Additive
22	2007	Wet	Node/Stalk	8	4	43-75 (57)	0.187	-0.508657
23	2007	Dry	Flr/Node	11	2	0-21 (10)	0.212	-0.315677
24	2007	Wet	Flr/Node	4	7	82-100 (100)	0.255	0.3111877
24	2007	Wet	Flr/Node	11	2	0-21 (10)	0.206	-0.304187
25	2007	Dry	Fruit/Not (A)	3	6	87-105 (105)	0.102	0.1935
25	2007	Dry	Fruit/Not (B)	6	1	0-22 (0)	0.089	0.2397
			A X B				0.227	-0.5795
26	2007	Wet	Fruit/Not	X	x	x	x	x
27	2007	Dry	Fruit/Flr	4	3	0-43 (17)	0.164	0.1880124
27	2007	Dry	Fruit/Flr	9	5	46-64 (64)	0.155	0.1736234
28	2007	Wet	Fruit/Flr	5	6	51-86 (66)	0.144	0.1432753
28	2007	Wet	Fruit/Flr	8	1	0-16 (0)	0.133	0.1389642
28	2007	Wet	Fruit/Flr	16	1	0-26 (14)	0.175	0.1583894

FIGURES

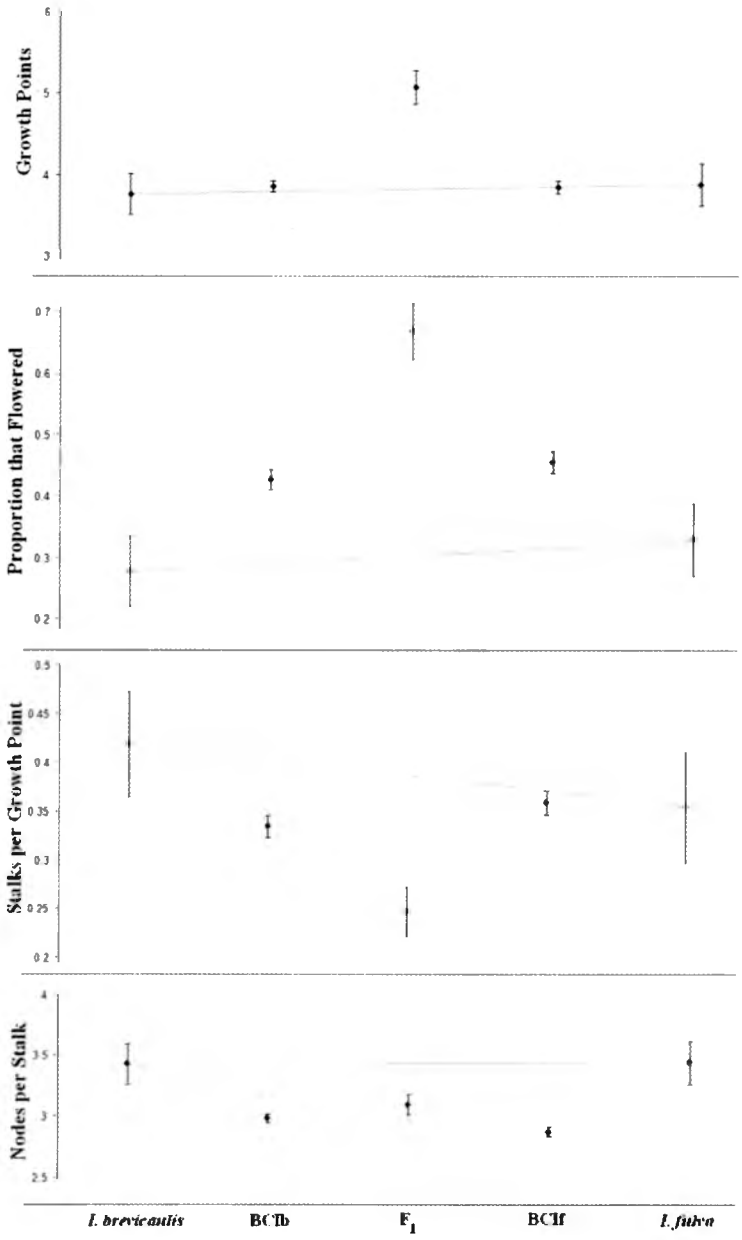

Figure 1a: Least squares means (± SE) for fitness components during 2006. Dotted lines represent assumptions given additivity.

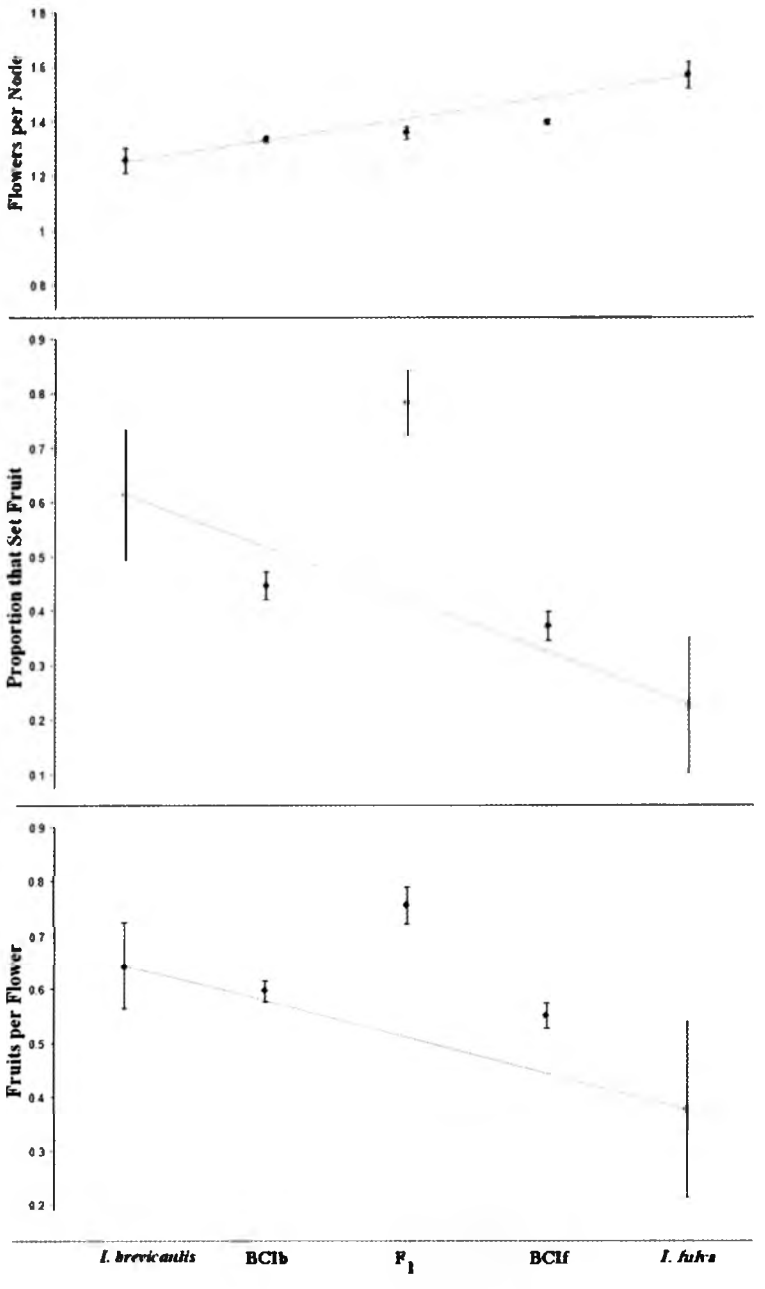

Figure 1a - Continued

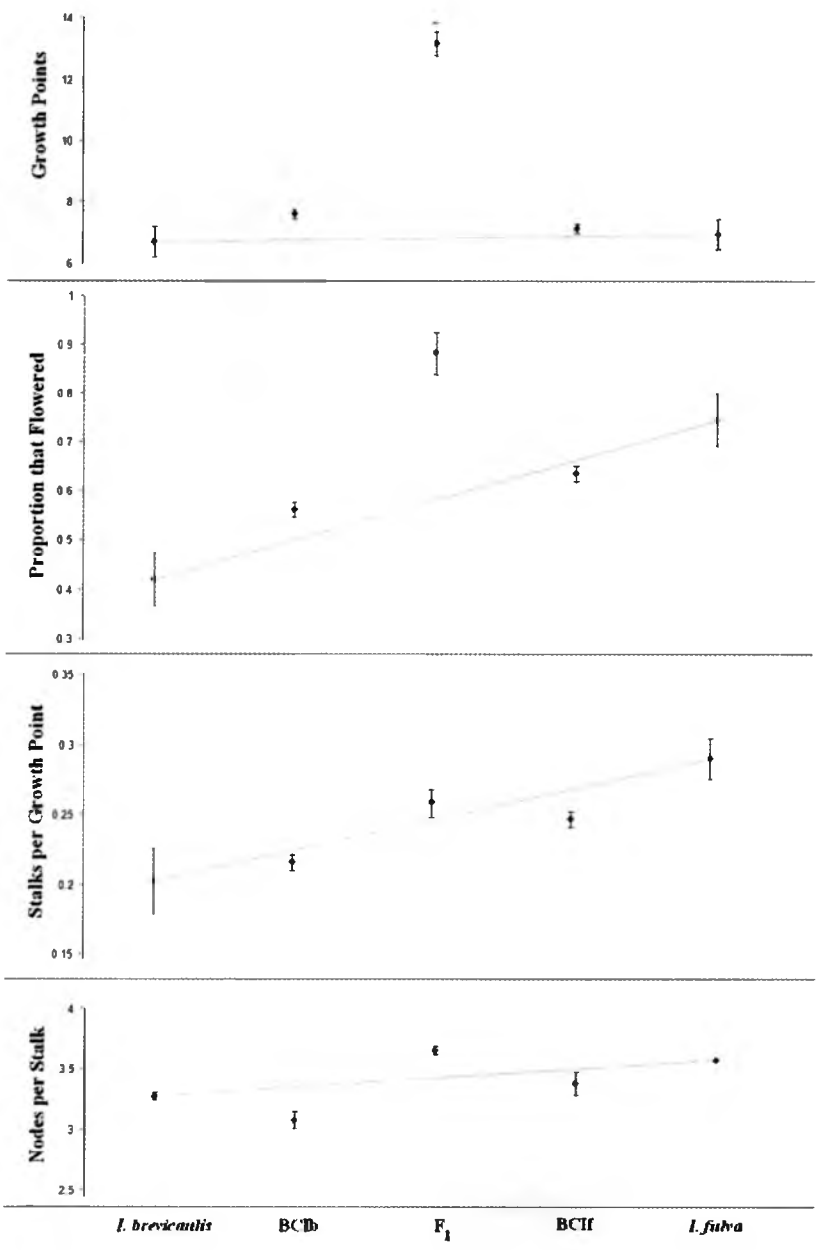

Figure 1b. Least squares means (± SE) for fitness components during 2007. Dotted lines represent assumptions given additivity.

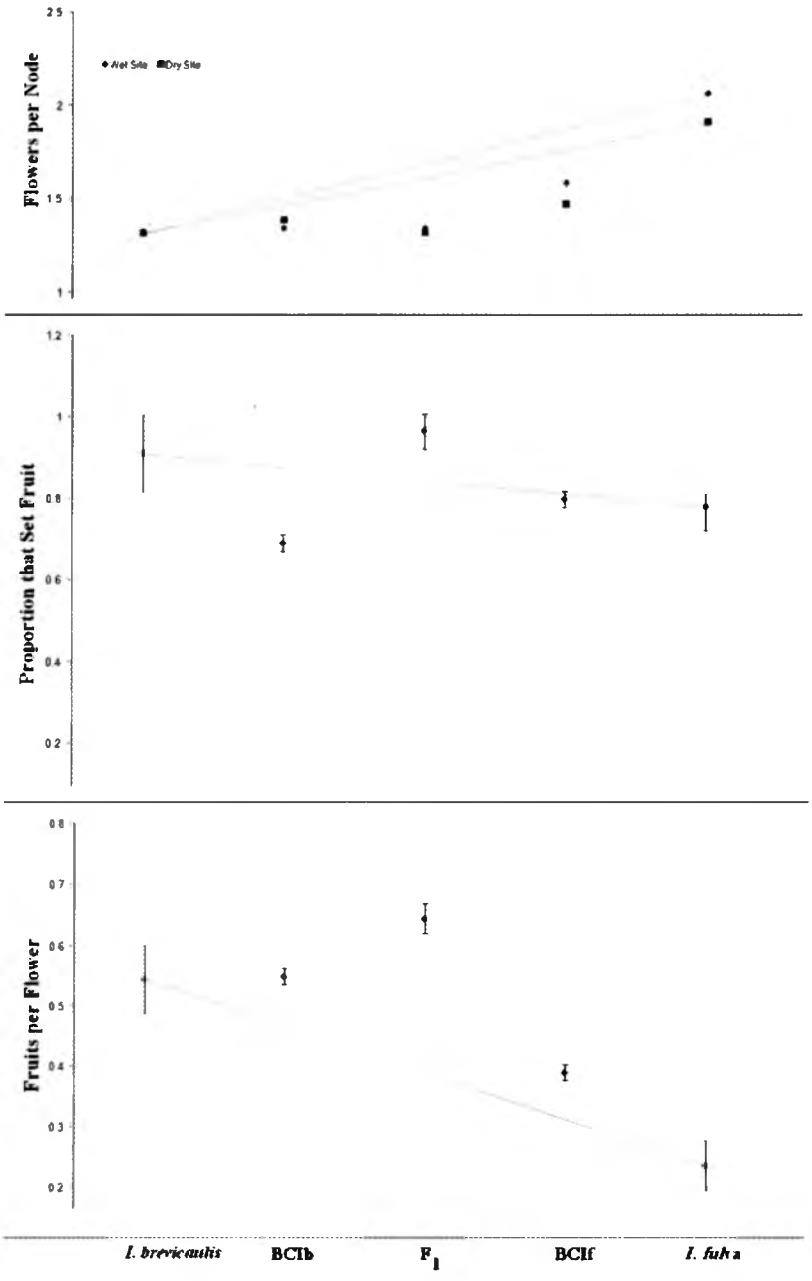

Figure 1b - Continued

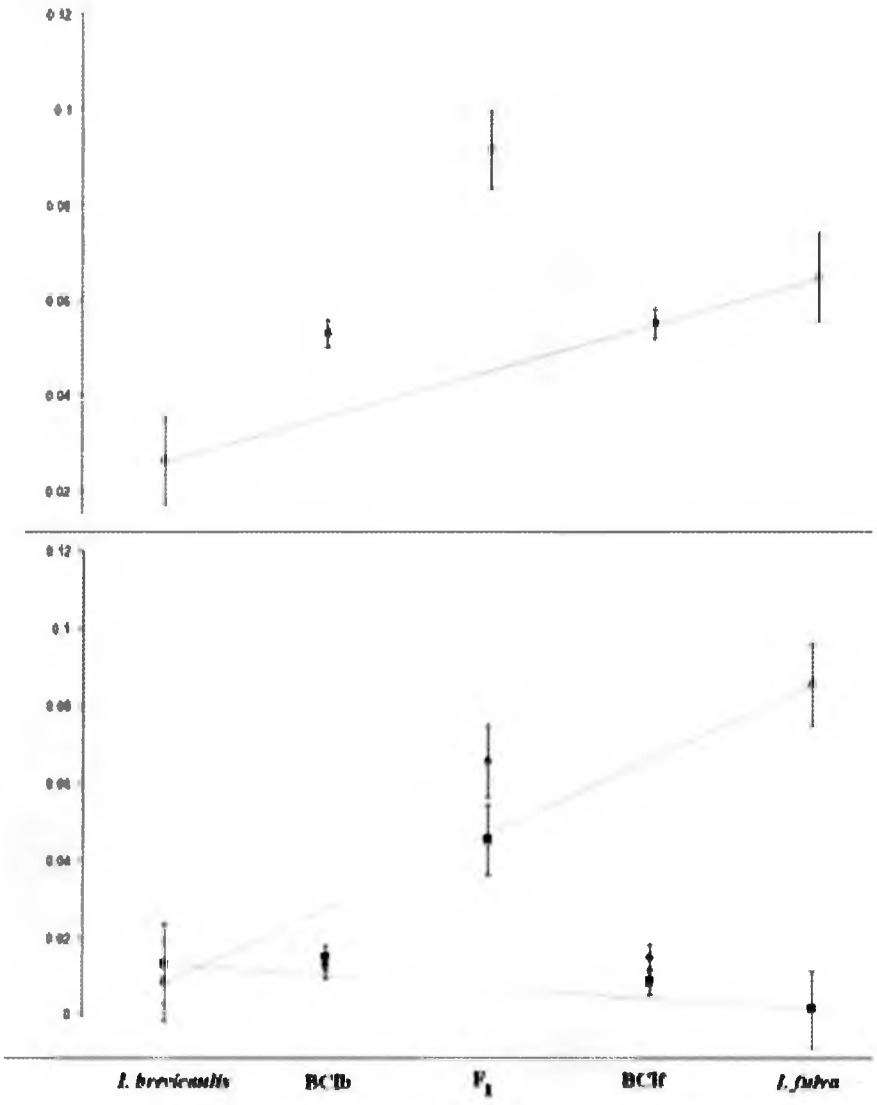

Figure 2a Summary of paternal (flower production) and maternal (fruit production) fitness in 2006.

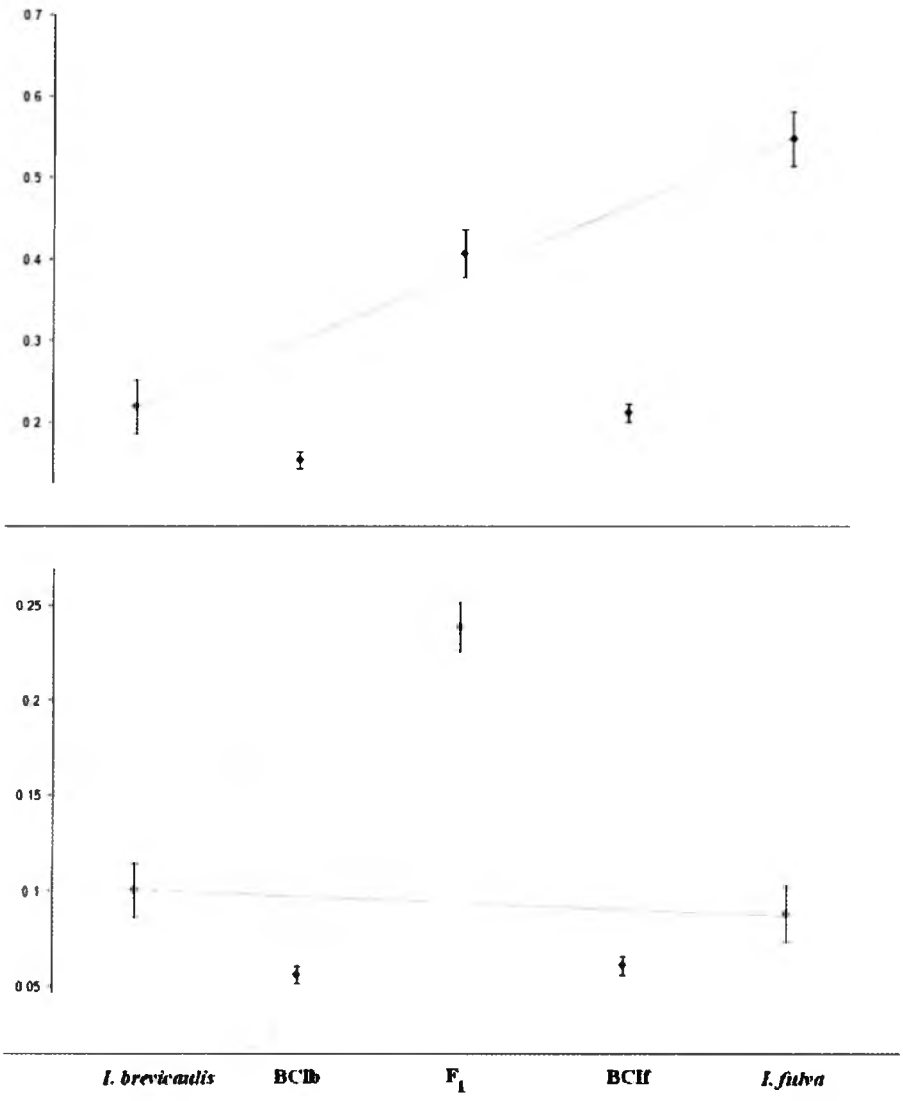

Figure 2b Summary of paternal (flower production) and maternal (fruit production) fitness in 2007.

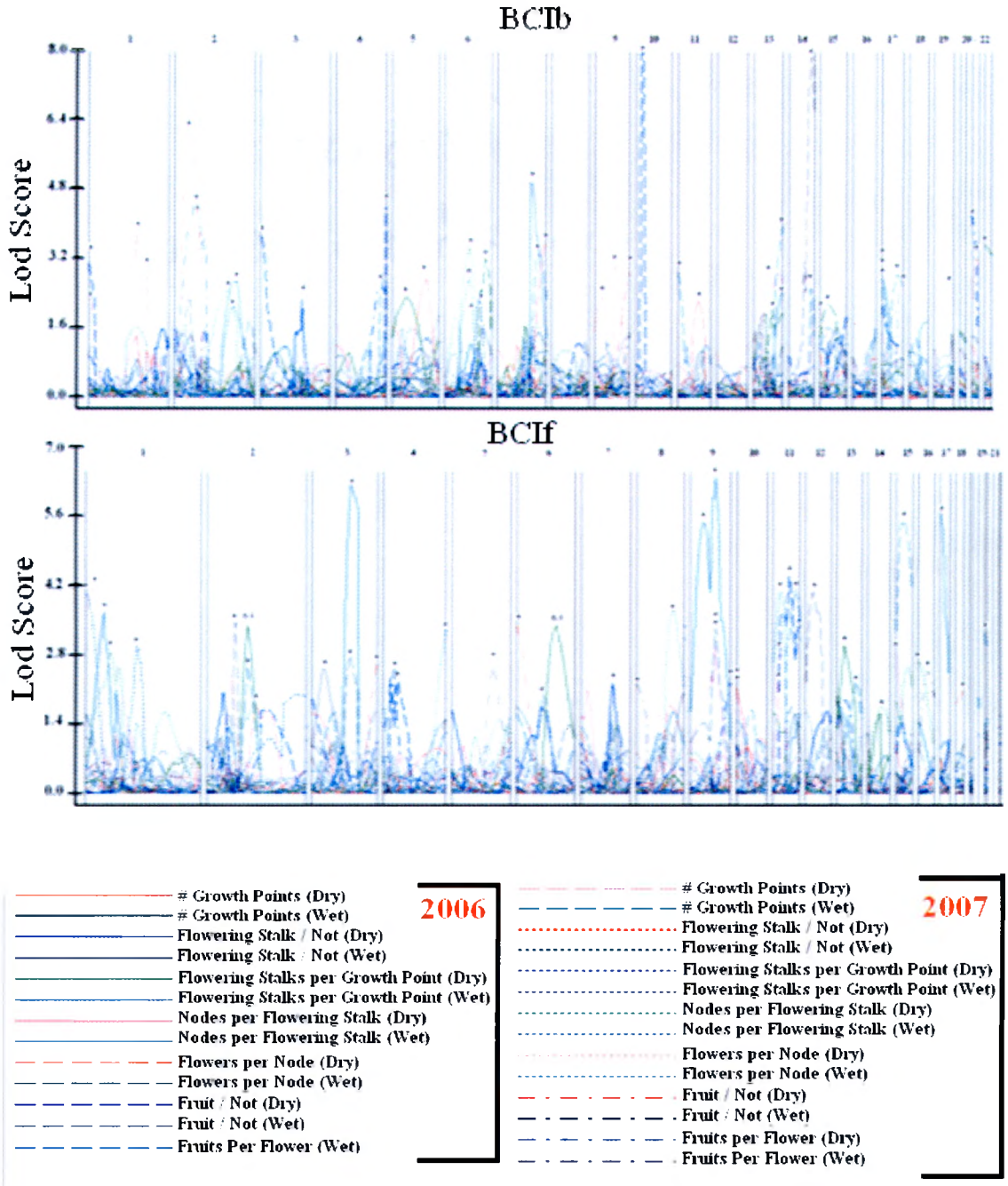

Figure 3: QTL locations for fitness components in BCIb (Fig. 3A) and BCIf (Fig. 3B) mapping populations. LOD-scores are shown for all traits. Map distances (cM) are shown on the x-axis. Significant QTLs are denoted by an asterisk. Fruit per Flower Dry 2006 (trait 13) is excluded from the BC*If* chart due to low sample size.

VITA

Sunni Taylor graduated from Pettus High School as valedictorian in 2003. She went on to pursue a BS in Biology from Tarleton State University. As an undergraduate, she worked in Dr. Russell Pfau's lab, which was focused on detecting hybridization between lineages of the hispid cotton rat. After graduating magna cum laude in 2006, Sunni applied to Texas State to work with Noland Martin. Throughout her tenure at Texas State, Sunni has received grants from Sigma Xi, the American Iris Society Foundation, and the Botanical Society of America, as well a Durrenberger scholarship from Texas State. Sunni has been accepted into Texas State's PhD program in Aquatic Resources where she will be studying the ecological genetics of homoploid hybrid formation in the Martin lab.

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