Transmission ratio distortion in an interspecific cross between *Fusarium circinatum* and *Fusarium subglutinans*

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Abstract
Previously, an interspecific cross between *Fusarium circinatum* and *Fusarium subglutinans* was used to generate a genetic linkage map. A ca. 55 % of genotyped markers displayed transmission ratio distortion (TRD) that demonstrated a genome-wide distribution. The working hypothesis for this study was that TRD would be non-randomly distributed throughout the genetic linkage map. This would indicate the presence of distorting loci. Using a genome-wide threshold of a = 0.01, 79 markers displaying TRD were distributed on all 12 linkage groups (LGs). Eleven putative transmission ratio distortion loci (TRDLs), spanning eight LGs, were identified in regions containing three or more adjacent markers displaying distortion. No epistatic interactions were observed between these TRDLs. Thus, it is uncertain whether the genome-wide TRD was due to linkage between markers and genomic regions causing distortion. The parental origins of markers followed a non-random distribution throughout the linkage map, with LGs containing stretches of markers originating from only one parent. Thus, due to the nature of the interspecific cross, the current hypothesis to explain these observations is that the observed genome-wide segregation was caused by the high level of genomic divergence between the parental isolates. Therefore, homologous chromosomes do not align properly during meiosis, resulting in aberrant transmission of markers. This also explains previous observations of the preferential transmission of *F. subglutinans* alleles to the F_1 progeny.

Keywords Divergence, *Fusarium circinatum, Fusarium subglutinans*, Interspecific cross, Transmission ratio distortion

Introduction

The *Gibberella fujikuroi* species complex accommodates the sexual stage of *Fusarium* spp. collectively treated in the section *Liseola* (Leslie and Summerell 2006). This complex includes some of the most ubiquitous and economically important fungal pathogens of plants. The biological species concept had been used to formally classify species in this complex into ten mating populations or biological species (Nirenberg and O'Donnell 1998; Samuels et al. 2001; Zeller et al. 2003; Lepoint et al. 2005). Species delineation, when applying the biological species concept, implies that individual species are reproductively isolated (Mayr 1940; Dobzhansky 1951). This is somewhat complicated in fungi where interspecific crosses can occur, such as those found between some taxa in the *G. fujikuroi* species complex (Desjardins et al. 1997, 2000; Leslie et al. 2004b).
Several examples exist for interspecific crosses within this species complex. Certain isolates of *Fusarium fujikuroi* (mating population C) and *Fusarium proliferatum* (mating population D) can be interfertile and produce viable progeny (Desjardins et al. 1997, 2000; Leslie et al. 2004b). Also, a naturally occurring hybrid has been identified (Leslie et al. 2004a). The current hypothesis is that genetic isolation between these two biological species is not complete, allowing reproductive barriers to be overcome (Leslie et al. 2004b). Another example of a laboratory generated interspecific cross is one between *Fusarium subglutinans* and *Fusarium circinatum*, residing in mating

population E and H, respectively (Desjardins et al. 2000; De Vos et al. 2007; Friel et al. 2007).

De Vos et al. (2007) constructed a genetic map for the interspecific cross between *F. circinatum* and *F. subglutinans*. These authors found that ca. 55 % of the markers exhibited significant TRD (transmission ratio distortion) from the expected ratio of 1:1 of a haploid cross (P \ 0.05). Ninety-six percent of the TRD markers were skewed towards the F. subglutinans parent. There was also preferential transmission of alleles, as well as complete chromosomes, from the genome of F. subglutinans. The clear bias towards the transmission of F. subglutinans alleles led to the conclusion that the F_1 progeny that inherited F. subglutinans alleles exhibited a general fitness benefit (De Vos et al. 2007).

Mendel's postulate of segregation dictates that during the formation of gametes, the paired unit factors segregate randomly such that each gamete receives one or the other with equal likelihood (Klug and Cummings 1994). Deviations from the expected Mendelian ratio of segregation (TRD) do occur, and are more frequently observed in interspecific crosses (Zamir and Tadmor 1986). It has been demonstrated that the larger the genetic divergence between the parental lines, the higher the levels of TRD (Grandillo and Tanksley 1996; Lee et al. 2009). Interspecific crosses in *Fusarium* display the same tendency. Thus, interspecific crosses display higher levels of segregation (Jurgenson et al. 2002; Leslie et al. 2004b), than intra-specific crosses (Gale et al. 2005).

TRD has been attributed to linkage between markers and genetic factor(s) that affect the fitness of gametes leading to unbalanced transmission of parental alleles to the next generation (Zamir and Tadmor 1986). This functions during the pre- and post-zygotic stages of reproduction and can also affect the zygotic viability. The presence of non-random marker loci exhibiting TRD throughout the linkage groups (LGs), would suggest the presence of a distorting genetic factor in that region of the genome (TRD loci [TRDLs]) (Jiang et al. 2000; Myburg et al. 2004). These loci form barriers that prevent recombination from occurring in these parts of the genome, leading to unbalanced transmission of parental alleles to the zygotes.

The advent of high-throughput molecular markers such as AFLPs (Vos et al. 1995) has made it possible to construct genetic linkage maps with high levels of map coverage. This has allowed for detailed examination of the transmission of these markers to the next generation, including markers displaying TRD. The working hypothesis for this study was that TRD in an interspecific cross between *F. circinatum* and *F. subglutinans* would be non-randomly distributed throughout the genetic linkage map. The aim was, therefore, to determine the positions and effects of possible TRDLs, using a previously compiled genetic linkage map derived from an interspecific cross between *F. circinatum* and *F. subglutinans*.

Materials and methods

Identification of TRD and putative TRDL

The direction and percentage of distortion of each marker from the genetic linkage map (De Vos et al. 2007), was determined by employing the formula ((allele frequency - 0.5) 9 100 %) as explained by Myburg et al. (2004). Markers displaying TRD could have occurred by chance or by displaying linkage to genetic factor(s) that affect the fitness of gametes (Zamir and Tadmor 1986). To distinguish between a ''chance'' TRDL or a ''true'' TRDL, a genome-wide significance threshold is needed (Myburg et al. 2004). Using this method together with the results of De Vos et al. (2007), it was presumed that the 12 LGs identified correspond to the 12 chromosomes (n = 12 for F. subglutinans, Xu et al. 1995). If each chromosome contains at least two independent segregating regions, there was an expectation of a minimum of 24 independently segregating regions. To acquire a genome-wide significance level of P = 0.05, a significance threshold of 0.05/ 24 & 0.002 would be necessary. However, in order to include weak TRDLs in this study, a significance threshold of a = 0.01 (v^2 = 6.64) was used. All regions that displayed three or more distorted markers were noted. The most skewed marker in this region was considered the most likely position of the distorting factor (Lu et al. 2002).

Epistatic interactions between the TRDLs

To determine whether epistatic interactions occur between pairs of TRDLs, the most distorted marker in each TRDL was used (i.e. the most likely position of the distorting factor). Marker scores were evaluated for each pair of

markers using Fisher's exact test in Statistica (v. 10, Stat-Soft, Inc., 2011, www.statsoft.com).

Results

Identification of TRD and putative TRDL

Of the 252 markers that were placed on the genetic linkage map, 138 (55 %) showed distortion at the 5 % level of significance, 79 (31 %) at the 1 % level of significance and 37 (15 %) at the 0.1 % level of significance. Markers displaying TRD were distributed throughout the genetic linkage map; all LGs had markers that deviated from the expected 1:1 ratio (P \ 0.05, Fig. 2). Sampling error was excluded as a possible reason for distorted frequencies, as at a 5 % level of significance, only 29 markers would be expected to show TRD.

When comparing the transmission of markers on the linkage map, the distribution of the F. subglutinans genetic composition amongst the F_1 progeny showed a mean of 59.8 % (Fig. 1). This was significantly different (P = 0.049996) to the predicted value of 50 %. Also, the distribution of the F. subglutinans genome in the progeny did not follow a normal distribution as expected (Shapiro– Wilk W test; SW-W = 0.87, P = 0.00). The distribution showed two 'tails', with the second ''tail'' at the 90–100 % genomic constitution of F. subglutinans (Fig. 1). This is an indication that some (13 of 94) F_1 progeny closely resembled the F. subglutinans parental isolate in their genetic constitution, compared to *F. circinatum* (De Vos et al. 2011). In contrast, only one of the F_1 progeny showed a *F. circinatum* genomic constitution of >90 %.

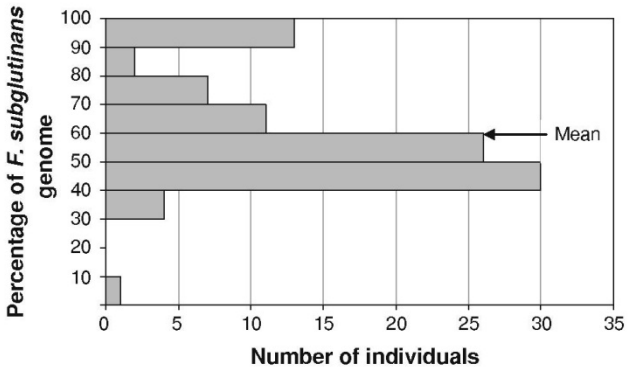

Fig. 1 Distribution of the percentage of F. subglutinans parent genome values in the F_1 progeny. The vertical axis shows the percentage of F. subglutinans genome attributed to each class, whilst the horizontal axis is representative of the number of individuals in each class

In determining the direction and percentage of distortion of each marker placed on the genetic linkage map, only12 markers from the total of 252 markers included in the genetic linkage map (4.76 %) were skewed towards the *F. circinatum* parent (Fig. 2). This directional distortion extended over whole LGs, except in LGs 2, 5, 6, 8, 9 and 11, where isolated markers were skewed towards *F. circinatum*. The exception was LG 7, where the first four of six skewed markers at the beginning of the LG were skewed towards *F. circinatum.*

Using the genome-wide significance threshold of P = 0.01, 79 markers were identified displaying TRD (Fig. 2). Eleven regions were identified that displayed three or more distorted markers (P< 0.01), with the marker displaying the highest distortion as the most probable area for the TRDL (Fig. 2, indicated with arrows). TRD regions that displayed three or more distorted markers were all unidirectionally distorted towards the F. subglutinans parent. These were located on LG 1 (markers GA/CC-353be and GA/AC-523bh), on LG 2 (marker CA/TC-463fh), LG 4 (markers AA/AC-337bh and CA/TC-263be), LG 5 (between markers CA/TC-149fh and GA/CC-111be), LG 6 (markers GA/AC-213bh and AA/AA-142fh), LG 8 (marker AG/AC-315bh), LG 10 (marker CA/TC-189be) and LG 11 (marker AG/AC-751fh) (Table 1). Thus, the putative TRDLs were not evenly distributed across the LGs, with LGs 1, 4 and 6 having two TRDLs, LGs 2, 5, 8, 10 and 11 having one TRDL and LGs 3, 7, 9 and 12 not containing any. These TRDLs covered a total of 396.5 cM which accounts for 14.29 % of the observed map length.

A haploid population has allelic frequencies that equal genotypic frequencies, and it was therefore not possible to determine whether TRD was caused by gametic or zygotic selection. However, the TRDL effects can also be expres-

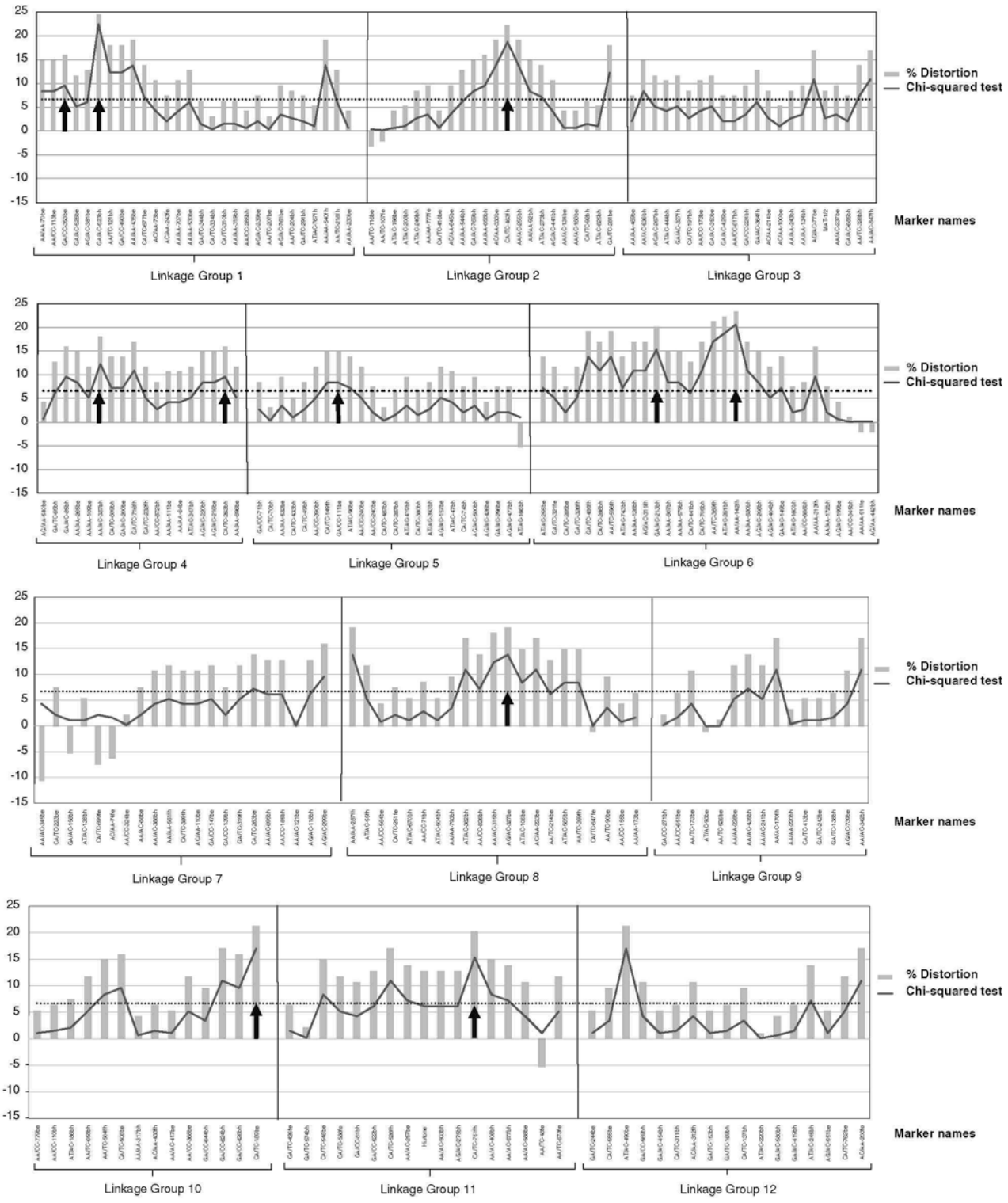

Fig. 2 The degree and direction of TRD of the F_1 hybrid. The *vertical bars* represent the percentage of distortion ([allele frequency $-$ 0.5] $\times$ 100 %) as well as the direction of distortion. The *solid lines* represent the χ^2 statistic for deviation from the expected 1:1 transmission ratio expected in a haploid F_1 cross ($P < 0.05$). The *horizontal dotted line* represents the χ^2 statistic at the 0.01 level of significance. *Arrows* represent the positions of the estimated TRDLs. The *marker names* are indicated on the *x* axis. Marker names consist of the *Mse*I selective nucleotides followed by the *Eco*RI selective nucleotides and the molecular size (bp), followed by a b (bright) or f (faint) indicating the quality of the fragment, and an 'e' and 'h' indicating markers originating from either *F. subglutinans* or *F. circinatum*, respectively. Marker data was recoded so that the direction of distortion represents that of the paternal parent (*F. subglutinans*). Intermaker distances are not shown proportionally

sed as the differential viability, t (0 \ t\1), of gametes or zygotes with alternate genotypes relative to that of normal gametes or zygotes (Cheng et al. 1998). The relative viability or fertilization ability of gametes or viability of zygotes affected by the TRDL ranged from 0.34 to 0.53 (Table 1), indicating the unidirectional skewing towards the F. subglutinans parent.

Table 1 Summary of putative TRDLs

TRDL	LGs	Map position (cM)[a]	*P* value[b]	Deviation from expected 1:1[c] (%)	Percent of F_1 individuals with allele[d]	Relative viability[e]
GA/CC-353be	1	62.1	0.002	15.96	65.96	0.52
GA/CC-523bh	1	121.4	2.09×10^{-06}	24.47	74.47	0.34
CA/TC-463fh	2	132.5	1.48×10^{-05}	22.34	72.34	0.38
AA/AC-337bh	4	71.6	0.00045	18.09	68.09	0.47
CA/TC-263bh	4	167	0.002	15.96	65.96	0.52
CA/TC-149fh and GA/CC-111be	5	77.8	0.0039	14.89	64.89	0.53
GA/AC-213bh	6	104.4	8.88×10^{-05}	20.21	70.21	0.42
AA/AA-142fh	6	139.6	5.67×10^{-06}	23.40	73.40	0.36
AG/AC-327be	8	140.4	0.00021	19.15	69.15	0.45
CA/TC-189be	10	140.7	3.70×10^{-05}	21.28	71.28	0.40
CA/TC-751fh	11	129	8.88×10^{-05}	20.21	70.21	0.42

[a] Distances in centiMorgan (Kosambi) from the top of the LG

[b] P values of the v^2 test statistic was performed on all markers to test for departure from the expected Mendelian segregation ratio expected for a haploid cross (1:1)

[c] Percentage and direction of distortion of each marker was determined by employing the formula (allele frequency - 0.5) 9 100 % (Myburg et al. 2004). All TRDL were skewed towards the F. subglutinans parent

[d] Percentage of F_1 individuals with the TRDL out of a total of 94 F_1 individuals

[e] The differential viability of gametes or zygotes calculated as the ratio of the frequency of the less frequent TRDL allele to the most frequent TRDL allele (Cheng et al. 1998)

Epistatic interactions between the TRDLs

None of the 55 possible marker pairs displayed any epistatic interaction at the 0.05 level. Thus, there was no interaction amongst the 11 TRDLs found in this study.

Discussion

In order to construct genetic linkage maps with a high level of confidence, molecular markers should be free of missing values, have no genotyping errors and display no segregation distortion (Hackett and Broadfoot 2003). This is infrequently the situation, and is confounded when examining interspecific crosses (Grandillo and Tanksley 1996; Lee et al. 2009). In this study, segregation distortion (or TRD) was analyzed in the progeny of an interspecific cross between *F. circinatum* and *F. subglutinans.*

Eleven putative TRDLs were identified that spanned eight LGs. This large number illustrates the genome-wide TRD observed in this interspecific cross. It is uncertain whether TRD was due to linkage between AFLP markers and genomic regions (TRDLs) that ensured the preferential transmission of *F. subglutinans* alleles. Rather, other hypotheses are advanced to explain the widespread TRD observed in this interspecific cross. The process of preferential transmission of alleles can be explained by either a pre- or a post-zygotic bias (Giruad et al. 2008). Such bias can be explained by three factors: (1) chromosome loss or other local rearrangements (pre-zygotic; Zolan 1995), (2) greater genomic divergence between the two parental species (Zamir and Tadmor 1986), such as that found in interspecific crosses (pre- and post-zygotic), and (3) linkage to a lethal gene (post-zygotic, Raju 1994).

Chromosome loss would lead to LGs with extreme TRD at all loci, with one genotypic class absent in that LG. In

the present study, TRD was observed throughout the genetic linkage map, with no LG displaying the absence of a genotypic class. Thus, chromosomal loss would not account for the TRD observed in this study. In fungi, chromosome rearrangements in the form of chromosome length polymorphisms, translocations and gain/loss of non-essential sequences, are widespread (Zolan 1995). Without fully assembled genomic sequence data, the presence of such local chromosomal rearrangements could not be excluded.

Other chromosomal abnormalities, such as inversions, would affect only segregation distortion in that part of the genome, and would not be visible throughout the genome (Jurgenson et al. 2002; Bowden et al. 2008), unless inversions between *F. circinatum* and F. subglutinans were prevalent throughout the genome. Inversions have been shown to play a role in speciation in Drosophila, where species grouped according to the similarity of gene order (Carson and Kaneshiro 1976). At present, three species representing the three clades within the *G. fujikuroi* species complex have genomic sequence data available (Fusarium verticillioides, Fusarium Comparative Sequencing Project 2011; *F. circinatum*, Wingfield et al. 2012; *F. fujikuroi*, http://www.fgsc.net/Fusarium/2011FusWkshp_Program.htm) and it would be interesting to determine the degree of synteny amongst these genomes.

The degree of TRD is hypothesized to equate to the level of genomic divergence between taxa (Zamir and Tadmor 1986; Jenczewski et al. 1997; Whitkus 1998; Jurgenson et al. 2002; Leslie et al. 2004b). Speciation could thus account for the TRD observed in this study, which could be linked to the presence of isolation mechanisms between these two species, i.e. barriers to gene flow (Giruad et al. 2008). These barriers may be genic in nature (see below), or due to structural differences between homologous chromosomes of the two species. In the genetic linkage map investigated in this study, parental origins of markers were non-random, i.e. LGs contained stretches of markers originating from only one parent. The implication is that homologous chromosomes from the interspecific cross did not align along their entirety during meiosis, while only small parts of chromosomes were homologous. Chiasmata (crossovers) could only occur in these homologous regions. Also, preferential inheritance of complete F. subglutinans chromosomes by the F_1 progeny (De Vos et al. 2007), provides further evidence for non-homology of chromosomes.

In this study, F_1 progeny that inherited *F. subglutinans* alleles displayed a fitness benefit, evidenced in the bias towards the transmission of *F. subglutinans* alleles. *Fusarium subglutinans* alleles could have had fewer negative interactions with the hybrid genetic background, than those of *F. circinatum* (Burke and Arnold 2001; Myburg et al. 2004). This genic incompatibility is characterized by the proper functioning of alleles in their separate genetic backgrounds, but these alleles can become incompatible when brought together in a hybrid (McDaniel et al. 2007). The observed bias could also be due to increased viability of ascospores containing F. subglutinans alleles. Hybrids can produce abnormal meiotic products, which could lead to inviability of hybrid progeny (Giraud et al. 2008). There could also be selection against certain recombinant gametes, due to co-evolved gene complexes that may be disrupted during recombination, leading to non-viable progeny (Burke and Arnold 2001; Jurgenson et al. 2002). These hypotheses should be tested in future.

Linkage to a lethal gene acts as a meiotic drive element with only those markers linked to this gene displaying TRD. One such element found in the *G. fujikuroi* species complex, is spore killer, identified in *F. verticillioides* (Kathariou and Spieth 1982). Spore killer causes the post-meiotic abortion of ascospores that did not receive the killer element and can be observed using light microscopy (Raju 1994). In the current study, viability of ascospores was high (90 %, Desjardins et al. 2000). Thus, it is unlikely that the spore killer element is present in *F. circinatum* and *F. subglutinans.*

In this study, putative TRDL regions were identified that spanned eight LGs. The presence of these TRDLs are most likely not the reason for the preferential transmission of F. subglutinans alleles. Rather, the genomic divergence between F. subglutinans and *F. circinatum* was more likely for the genome-wide segregation of markers observed in the F_1 progeny. These regions that displayed significant distortion, are most probably indicative of extreme dissimilarity at the genome sequence level between the two parental species. Thus, these could potentially harbour the 'niche-specific' genes, i.e. genes making a particular species pathogenic to a specific plant. Subsequent work should thus focus on understanding the genetic determinants of TRDL and its potential link to speciation and overall genome evolution of *F. circinatum* and *F. subglutinans* in the *G. fujikuroi* species complex.

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