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DEPARTMENT OF PLANT PATHOLOGY AND ENVIRONMENTAL MICROBIOLOGY

Phylogeny of Mating Type Locus in The *Fusarium oxysporum* Species Complex

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ABSTRACT

The *Fusarium oxysporum* species complex (FOSC) is an a very pertinent group of plant pathogenic filamentous ascomycotan fungi. The wide host range of this fungus is reflected in the diversity of recognized FOSC lineages. Prior phylogenetic studies in *F. oxysporum* have concluded that a multiplicity of different clades, and even different species, exist within the FOSC. Determining if the genetic differences found between distinct groups in the FOSC qualifies them as separate lineages or species is an ongoing debate. Lacking any known sexual stage in *F. oxysporum*, inferences on this matter rely solely on studying the genetic makeup of many isolated FOSC individuals. One important locus that has received little prior attention in *F. oxysporum* is the mating type locus. Mating type is to fungi what sex determination is to plants and animals. In sexually reproducing populations there is pressure for these idiomorphs to remain conserved, meaning this locus offers a unique view of phylogeny in the FOSC as well as the likelihood of a sexual stage. In this thesis, the multitude of lineages in the FOSC are investigated at the mating type 1 idiomorph, mating type 2 idiomorph, a small concordant fragment of the mating type 2 idiomorph, and the flanking regions of the mating type locus. A bioinformatics approach is used to generate phylogenetic trees of these genetic sequences. These are then used to draw conclusions about the delineation of the FOSC and the fecundity of this fungus.

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Chapter 1

Introduction

The genus Fusarium encompasses a group of filamentous ascomycotan fungi that are pathogenic on a wide range of plant hosts. Included in this genus is the species *Fusarium oxysporum*. *F. oxysporum* is notable for its role as the causal agent of wilt diseases in multiple hosts, including bananas where it leads to the devastating Panama Disease. In addition to its diversity as a disease, *F. oxysporum* is also characterized by a multiplicity of distinguishable genetic clades (O'Donnell et al., 1998) (Achari et al., 2020). These clades, or lineages, make up what is known as the *Fusarium oxysporum* species complex (FOSC). Lineage designations are based on multi-loci phylogenetic analyses which compare the genetic differences of many different FOSC isolates. Pathogenicity within a given host between FOSC lineages has previously been linked to the presence of virulence genes and entire accessory chromosomes (Ma et al., 2013). These genes are able to mobilize among members of the FOSC, and Fusarium as a whole, thus making it difficult to track the evolutionary paths taken by otherwise similar fungi. Additionally, *F. oxysporum* has no known sexual stage, making it difficult to distinguish between what are separate clonal populations in the FOSC and what may be considered separate species. Of particular interest is lineage 5 in the FOSC, which has been considered a separate species referred to as *F. foetens* (Schroers et al., 2004). Refer to Appendix A for more information on lineage sorting in the FOSC. What *F. oxysproum* does have are the genes necessary for a sexual stage, situated in the so-called Mating Type locus (MAT1 types). Sex in ascomycotan fungi (AKA mating type) is typically determined by mating type idiomorphs, which are sequences present at the same location in a genome that encode for completely unrelated proteins. These idiomorphs experience pressure to remain conserved in mating populations due to their importance in the sexual stage of the species. In other words, the genetic sequence within these idiomorphs does not change as quickly as in other genes so long as the fungus is still entering its sexual stage. This gives a unique advantage to using MAT1 type in phylogenetic studies, as it can give an idea of

which specimen are within a mating population and whether they are sexually reproducing at all. MAT1 type in the FOSC is broken down into mating type 1 (MAT1_1) and mating type 2 (MAT1_2).

In this paper, the MAT1 type locus and its flanking sequence regions in the FOSC are investigated for resolution of previously published lineages as well as evidence of sexual recombination. Five lineages are recognized within the FOSC with several sublineages (1, 2A – 2G, 3A – 3G, 4, and 5 [recognized as *Fusarium foetens*]). A bioinformatics approach is taken to compare MAT1_1 and MAT1_2 regions, and their flanks, between lineages in a search for fungal fecundity.

Chapter 2

Methods

Bioinformatics

During the course of this thesis, multiple bioinformatic programs were employed. Sequence analyses, alignments, and extractions were handled through the desktop version of Geneious Prime. Tree building was performed through the IQ-TREE web server (CIBIV, Austria). Subsequently, trees were rooted and designed for easier viewing on FigTree. Each program was run on its respective default settings.

Sequence Collection and Identification

Lineage and outgroup representative isolate sequences were identified from an unpublished data set, courtesy of David Geiser and Ningxiao Li, for both MAT1 types. Accession numbers from the data set were used to download full sequences available online from the NCBI database. Isolate sequences were then uploaded to Geneious Prime for subsequent analysis.

MAT1 Locus Searching

To find the MAT1_1 and MAT1_2 locus in corresponding isolate sequences, each sequence was first set up as a local BLAST server. Known MAT1_1 (4017 base pairs) and MAT1_2 (3851 bp) sequences from Yun et al. (2000) were then searched against each sequence BLAST database. As a result, the contigs or scaffolds (DNA segments) bearing the MAT1_1 or MAT1_2 idiomorph, from MAT1_1 or MAT1_2 isolates respectively, were picked out by the Geneious Prime software. Each contig or scaffold was labeled for its individual corresponding lineage, mating type, and isolate sequence name.

MAT1_1 and MAT1_2 Alignment and Tree Building

MAT1_1 and MAT1_2 contigs were mapped to their related known sequences using the 'Map to Reference' feature of Geneious Prime. This lined up each sequence at the MAT1_1 or MAT1_2 locus. The corresponding MAT1 locus sequences were then extracted to create a list of sequences consisting solely of the locus with no flanking regions. This list was then subjected to the Geneious Prime default MUSCLE alignment tool to create an alignment of the sequences. Separate mapping, extraction, and alignment were performed for each MAT1 locus. Both alignments were then exported as FASTA files and uploaded to the IQ-TREE web server for default tree building (1000 Ultrafast bootstrap alignments). Completed trees were downloaded and opened with FigTree to prepare the figures for better viewing.

MAT1_2Frag Alignment and Tree Building

During the course of MAT1 locus searching, a 345 bp fragment of the MAT1_2 idiomorph (MAT1_2Frag) was discovered roughly 270 bp upstream of the MAT1_1 locus in all analyzed isolates. This fragment was subjected to the same BLAST search, mapping, extraction, alignment, and tree building as the MAT1_1 and MAT1_2 loci. The presence of this fragment in both MAT1 types allowed for a single analysis including both MAT1_1 and MAT1_2 individuals rather than separate analyses for both types. Therefore, the tree produced contains all MAT1_1 and MAT1_2 isolates, allowing for a unique comparison.

MAT1 Locus Flanking Region Analysis

As part of this thesis, the regions of sequence flanking the FOSC MAT1 idiomorphs were also subjected to alignment and tree building. MAT1_1 and MAT1_2 individuals were aligned with the Geneious Prime Mauve whole genome alignment tool. This alignment was performed separately for each

lineage but could not be performed in lineages with only a MAT1_1 or MAT1_2 representative. Next, 3000 bp sequences were extracted from both flanking regions for both MAT1 idiomorphs. Due to the inverted nature of the MAT1 idiomorphs, the downstream flank of MAT1_2 / upstream flank of MAT1_1 will be referred to as the 'L' flank (Left) and the upstream flank of MAT1_2 / downstream flank of MAT 1_1 will be referred to as the 'R' flank (Right). Flanking regions for Mauve aligned sequence were extracted from the Mauve alignment. Sequences from lineages with only a MAT1_1 or MAT1_2 representative were extracted directly from the L and R flanks in unaligned contigs. L and R extractions were taken from both MAT1_1 and MAT1_2 individuals. Extractions were then mapped to a reference sequence to align them. Separate mappings were performed for the L and R flanks (Lineage1 L and R flanks used as references for mapping, respectively). A second extraction was performed to produce a list of sequences of exact length and alignment. These extractions were 1352 bp for the R flank and 2864 bp for the L flank. The extractions were then subjected to MUSCLE alignment, exported as FASTA files, and submitted to IQ-TREE to produce separate L flank and R flank trees.

Refer to Appendix B for further information on the regions used for MAT1_1, MAT1_2, MAT1_2Frag, and 'L' and 'R' flanks anyalyses in this thesis.

Chapter 3

Results

Lineage Representative Assignment

Representatives chosen for each lineage can be found in Table 1. Not every lineage had a sequence available for both MAT1 loci, and MAT1_2 received greater coverage than MAT1_1. Lineage and MAT1 type combinations without a representative isolate are designated N/A. Lineage 5 and *F. foetens* are synonymous.

Table 1: Isolates assigned as lineage representatives for each mating type.

Lineage/Species	MAT1_1 Representative	MAT1_2 Representative
1	VPRI42181	RBG5831
2A	N/A	RBG5714
2B	N/A	Focb_160527
2C	Fo63	RBG6505
2D	koae_44	physalis_B01
2E	RBG7070	Fon002
2F	Lag_3_1	VPRI17796
2G	lagenariae_01_03008	lilii_Fol39
3A	N/A	VPRI31638
3B	RBG6477	N/A
3C	VPRI42176	N/A
3D	lycopersici_R1_IPO1530_B1	melonis_26406
3E	N/A	FoBulbTu58
3F	Foa133	matthiolae_PHW726

3G	VPRI32288	FoC_125
4	Fo65_endo	N/A
5 (*F. foetens*)	N/A	NRRL38302
F. commune	betae O-1122	NRRL28387

Phylogenetic Analysis of MAT1 Loci at Lineage Level

The trees resulting from each region investigated in this thesis vary in lineage representation. The availability of isolates at both MAT1 types for each lineage is mostly responsible for this, however there are other reasons for these differences as well. Notably, some representative isolates had small flanking regions due to the size of the MAT1 containing contig or scaffold. This made it impossible to map these flanking regions along with other related sequences, and thus they could not be incorporated in the resulting tree. The trees for MAT1_1 and MAT1_2 locus only alignments contain exclusively their respective isolates, however the other three trees include as many of the chosen isolates as would align. Each tree uses *F. commune* as the outgroup, which is the most genetically distant individual in a tree used as a reference for the differences between the isolates of interest. Branch length equates to the genetic change between individuals on the tree. A longer branch means more genetic difference, whereas a shorter branch signifies less. Each branch on the trees also has a corresponding SH-aLRT % support value and an ultrafast bootstrap % support value in the form of SH-aLRT % support / Ultrafast bootstrap % support. For example, a branch with the value 80.5/90.5 has SH-aLRT % support of 80.5 % and ultrafast bootstrap support of 90.5% (Trifinopoulos et al., 2016). These values indicate the likelihood that the clade evaluation is true and are presented in green text for ease of identification. For further viewing ease, MAT1_1 individuals are presented in black text and MAT1_2 isolates are given in red text.

Figure 1 shows the phylogenetic relationship between lineages at the MAT1_1 locus. In this tree, most lineage 2s and 3s are grouping together with a high degree of support. The exceptions to this are lineages 2C and 3G, which are shown as grouping with lineages 4 and 1 respectively. This also gets a high support value from IQ-TREE. The 3s show a greater divergence than is seen within the 2s. The tree in fact indicates that 2F and 2G are identical with a high amount of support.

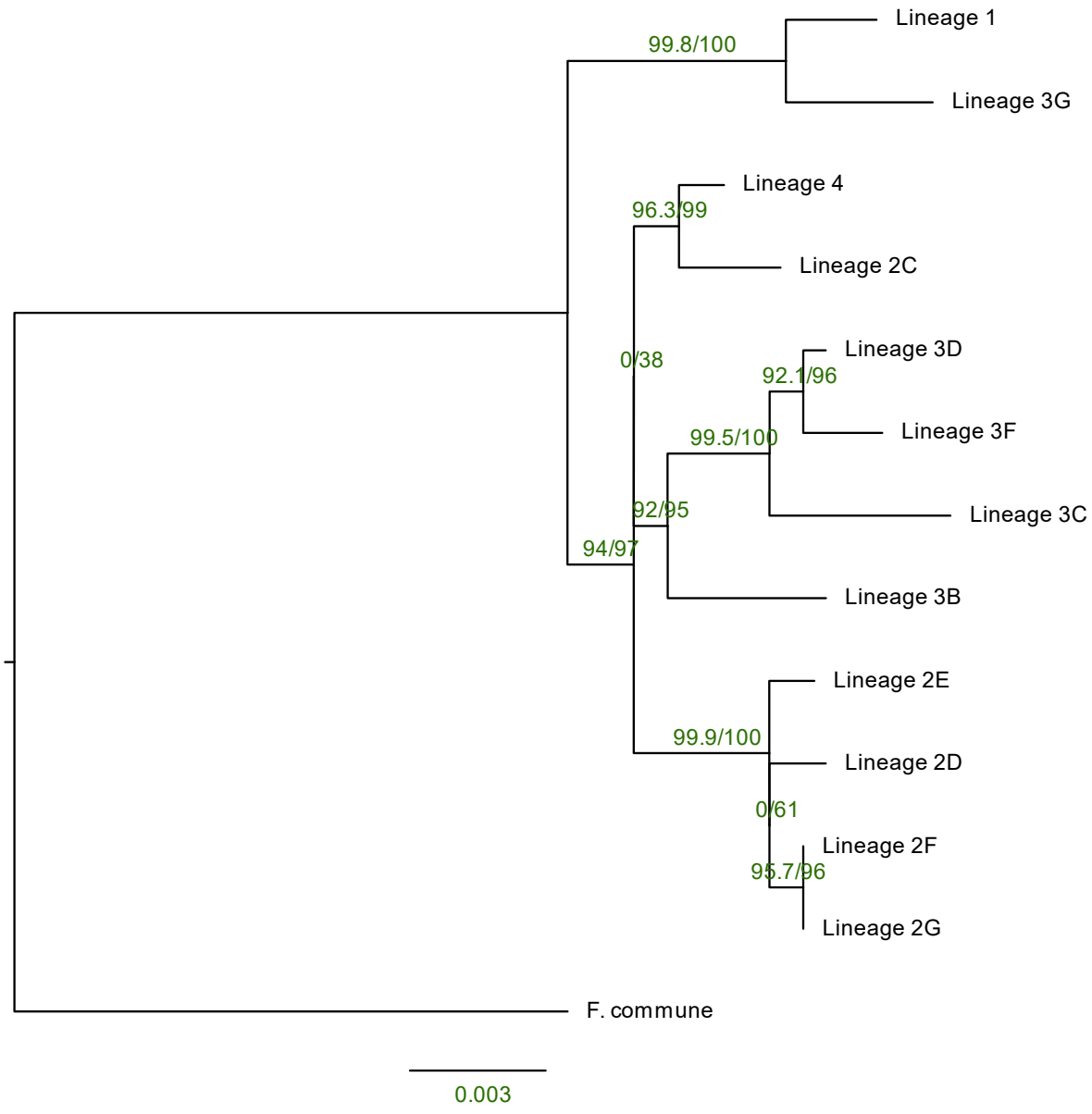


Figure 1: Phylogeny of lineages for MAT1_1.

Figure 2 shows the phylogenetic relationship between lineages at MAT1_2 and covers a greater diversity of lineages. The 2s and 3s completely resolve together in this tree with a large amount of support for this distinction. Lineage 1 shows up within the group of lineage 3s, however it receives a significantly longer branch and lower support values. More diversity can be seen within the 2s in this tree, however 2F and 2G are still determined to be identical. Figure 2 includes lineage 5 (*F. foetens*) which resolves apart from all other lineages, appearing more like the *F. commune* outgroup in the tree than any of the other lineages.

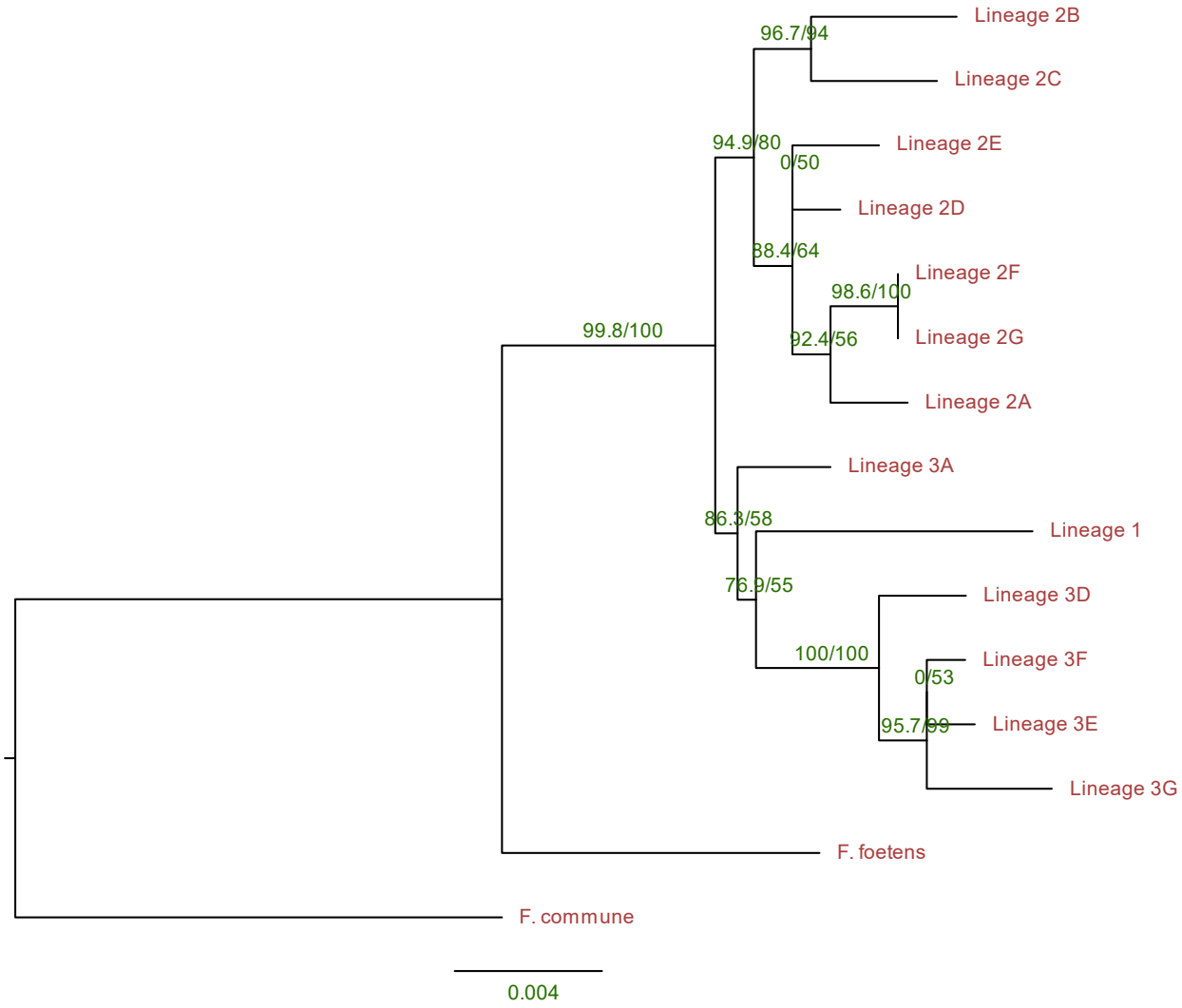


Figure 2: Phylogeny of lineages for MAT1_2.

Figure 3 shows the phylogeny for the MAT1_2Frag found in both the MAT1_2 locus and upstream of the MAT1_1 locus. This tree includes both MAT1 types for this reason and is based on a much smaller sequence than any of the other trees. Isolate sorting in this tree seems to be more based on MAT1 type than lineage, however within each group there is some tendency for 2s and 3s to stick together. Few of the branches receive strong support in this tree, however the branches for *F. foetens* and lineage 1 receive distinct support for their placements. Within the MAT1_2 isolates there is greater diversity (branch lengths) than within the MAT1_1 isolates. Notable exceptions are the 3G and 1 MAT1_1 isolates having the greatest divergence and the 2F and 2G MAT1_2 isolates remaining identical.

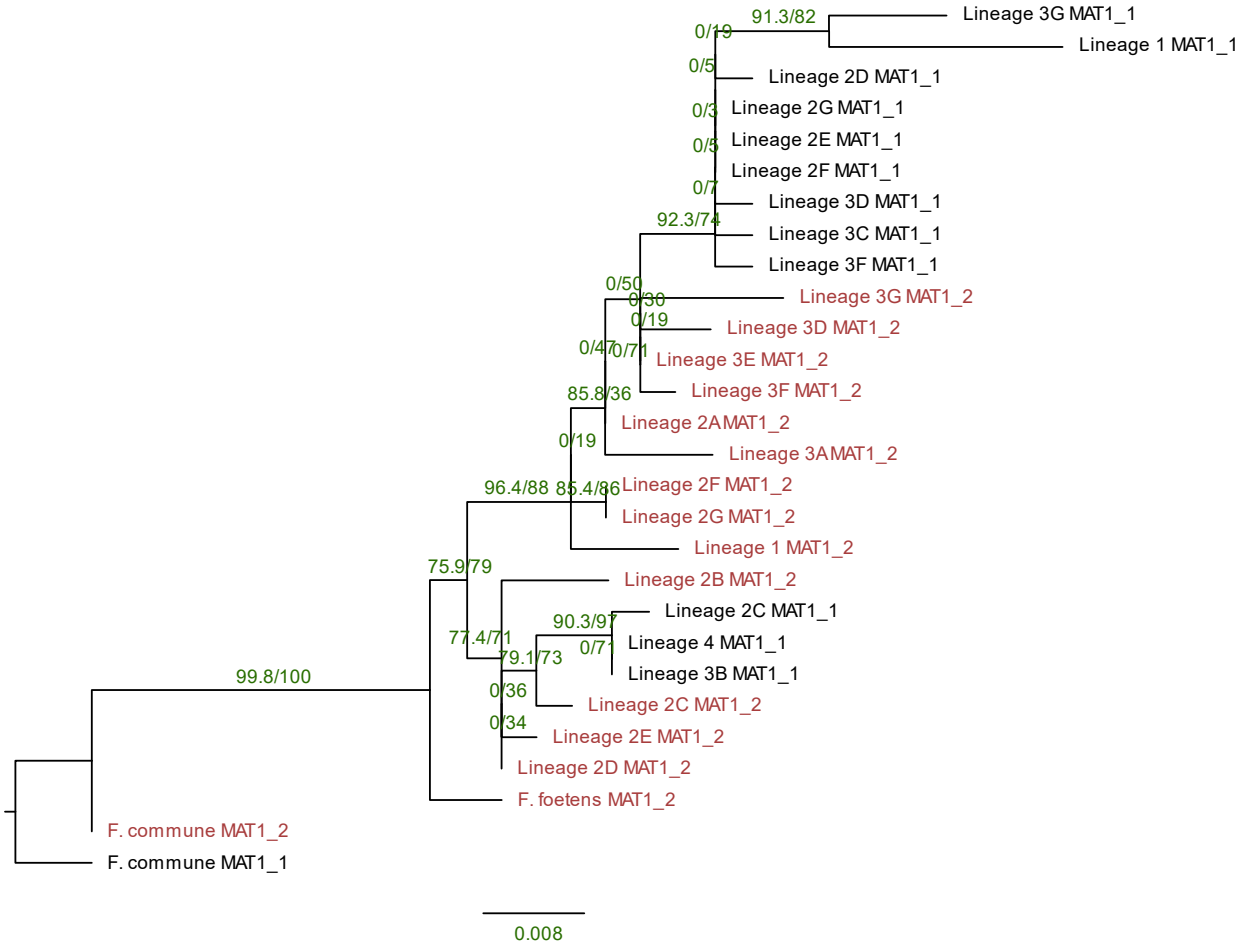


Figure 3: Phylogeny of lineages for MAT1_2Frag.

Figure 4 is showing the phylogeny at the R flanking region of both MAT1 type isolates for each lineage. This flank sequence was the second shortest of the sequences investigated in this paper. In half of

the cases where MAT1_1 and MAT1_2 representatives were available, we can see them resolving as a pair for their lineage. Exceptions to this are 2G, 2F, 3D, and 3F, which show greater similarity to other isolates than to their corresponding MAT1 type pair. *F. foetens*, lineage1, and lineage 4 all resolve outside of the 2s and 3s, with *F. foetens* receiving an especially long branch. Many of the branches in this tree receive low or no support from IQ-TREE.

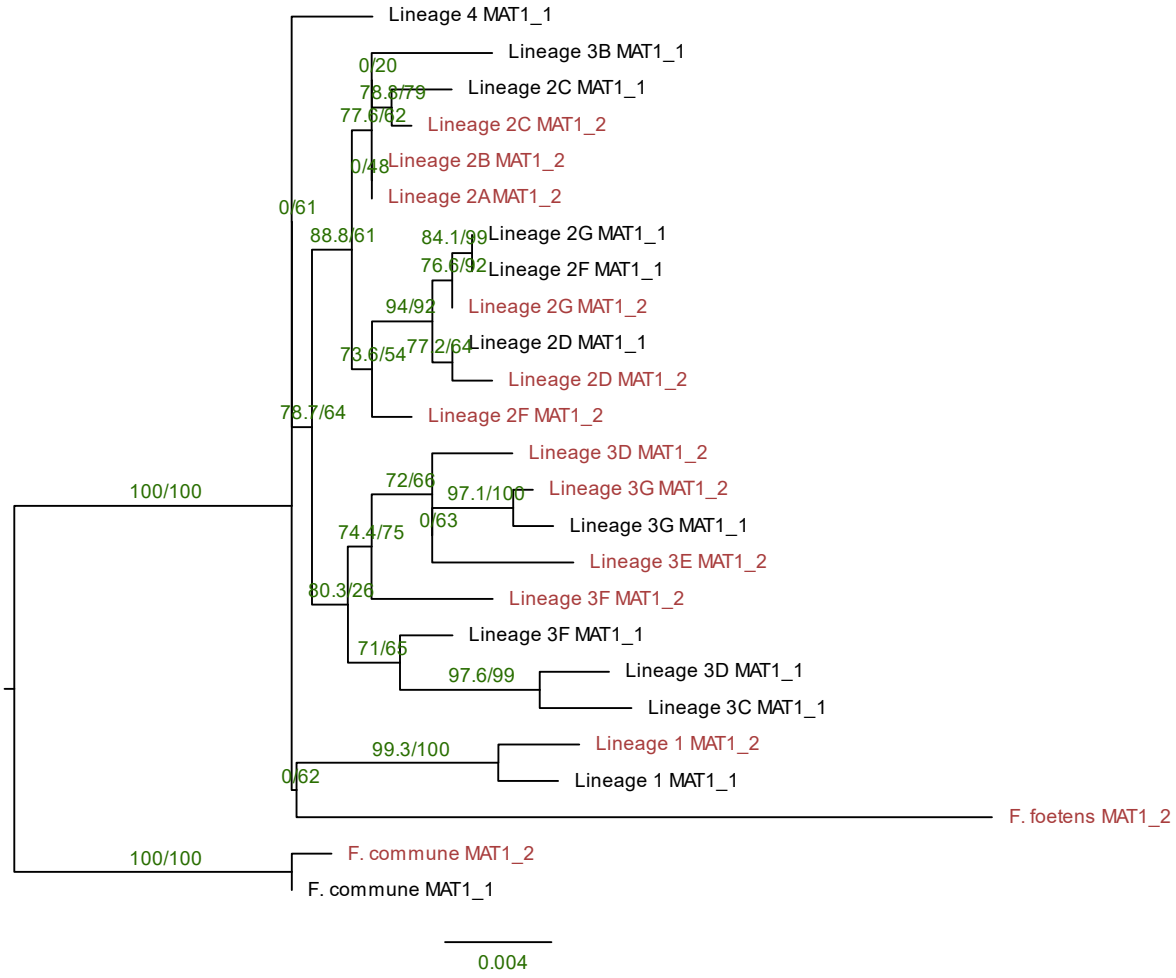


Figure 4: Phylogeny of lineages at R flanking region of the MAT1 locus.

Figure 5 contains the phylogeny for the L flanking region of MAT1 type locus. This flanking sequence was significantly longer than the R flanking region sequence. Few of the lineages resolve as MAT1 type pairs, although the 2s and 3s are generally grouped together. Exceptions to this are 2A, 3A, and 3B. In fact, 3A shows up as more dissimilar than any other lineage within the FOSC. Branch support

varies greatly, however more support is given here than in the other two trees that include both MAT1 types.

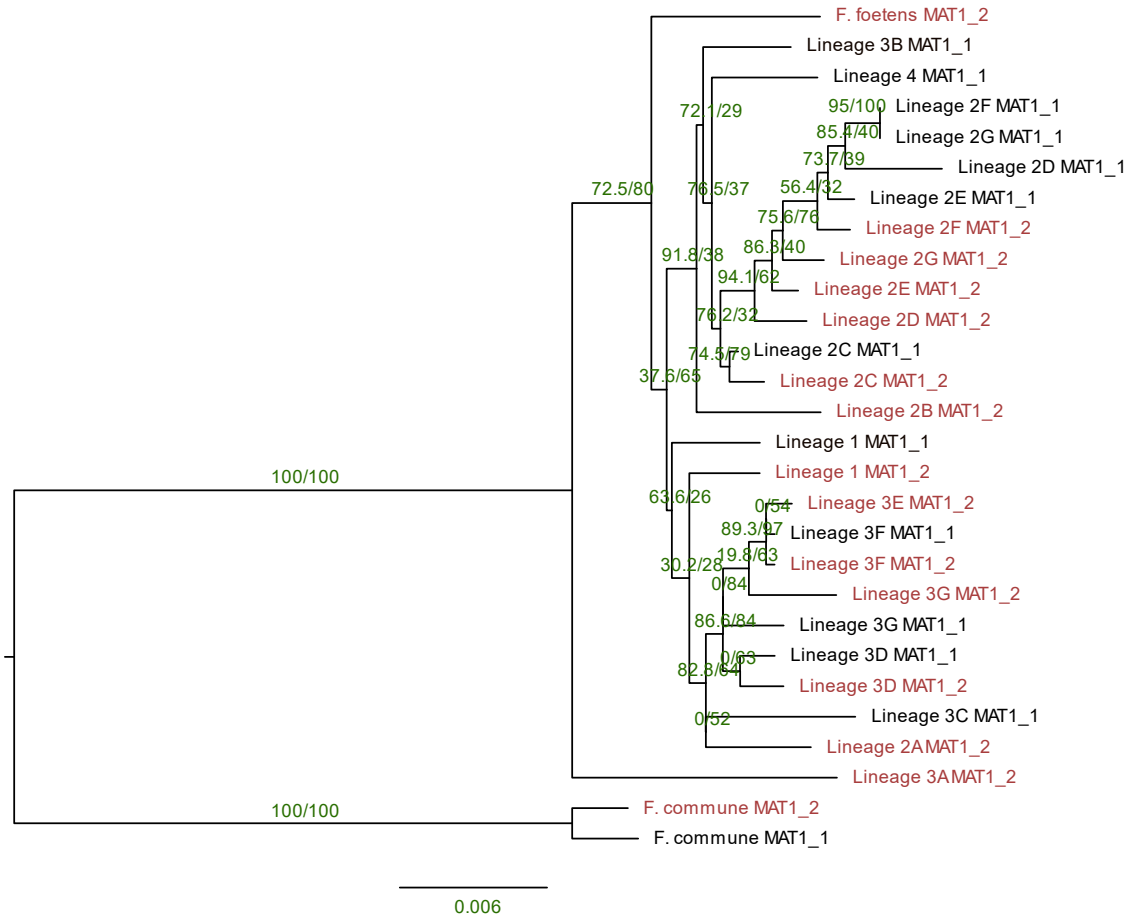


Figure 5: Phylogeny of lineages at L flanking region of the MAT1 locus.

Chapter 4

Discussion

Lineage Representative Assignment

Table 1 shows that there is a significant gap in the amount of representation covered by this thesis. The lack of complete MAT1_1 and MAT1_2 coverage for each lineage limits the scope of this study by excluding comparisons of some lineages between all trees. Additionally, the overall scarcity of chromosome level assemblies in *F. oxysporum* limits the degree to which MAT1 locus flanking regions can be investigated.

MAT1_1 and MAT1_2 Phylogenies

The MAT1 type specific trees had the greatest support for the resolution of branches of any of the trees. This is a product of the larger sequences covered by the alignments for these trees. In both trees the lineages 2s and 3s are resolving as separate groups, as would be expected for these related lineages. This grouping indicates that the MAT1 idiomorphs are retaining their identities more in closely related lineages of *F. oxysporum*. This would be the case if there was evolutionary pressure from a sexual cycle selecting for conservation of the MAT1 type idiomorphs. The exceptions to this grouping are 2C and 3G in the MAT1_1 tree, which resolve as being paired with lineage 4 and 1 respectively. This is most likely a result of 2C and 3G diverging from other 2s and 3s rather than these lineages being more closely related to 4 and 1. Interestingly, 2F and 2G MAT1 loci show up as identical in these trees, implying there has been no divergence between these two lineages. This could also suggest that one of the two representative isolates is belonging to the other's lineage, however flanking region analysis shows there is splitting off

of the 2F and 2G isolates outside of the MAT1 idiomorphs. Lineages 1 and 4 do not resolve on their own in either of these trees, however they do have large branch lengths indicating a greater divergence from the lineages they branch off from. *F. foetens* is distinct and appears as though it is an outgroup.

MAT1_2Frag Phylogeny

The fragment of MAT1_2 found also in the sequence upstream from the MAT1_1 locus provides an opportunity to observe evolution acting on a rearrangement in the MAT1 idiomorphs of Fusarium. Unfortunately, the small size of this region means percent support for tree resolution is low and little can be strongly inferred. Important to note from this tree is the trend of MAT1_1 and MAT1_2 isolates to pair with others of the same MAT1 type, despite lineage. This suggests that the MAT1_2Frag has evolved differently between the two MAT1 types. In MAT1_2 isolates, the MAT1_2Frag would be crucial as a part of the entire MAT1_2 idiomorph. However, in MAT1_1 individuals, the sequence would not be under as much selective pressure. Therefore it would not need to operate properly or to match the evolutionary patterns of the rest of the related lineage's genomes. The MAT1_2Frag does not seem to sort as well at the lineage level. This is likely due to the short length of the sequence and the inclusion of both MAT1 types in the same analysis. Interestingly, this fragment sequence was also found in the *F. commune* outgroup, implying the rearrangement may be common among other species in the genus Fusarium.

MAT1 Flanking Regions

The analyses of regions flanking either side of the MAT1 idiomorphs can be used to develop a benchmark of divergence between lineages. By comparing these regions with the MAT1 type loci, the relative conservation of the MAT1 sequences can be extrapolated. Again, short sequence lengths used for

the L and R flank alignments contribute to low branch support values and therefore low support for inferences made from these trees. In both trees, like lineages nicely sort together. The exceptions to this are 2A and 3B in the L flank tree and 3B in the R flank tree. Additionally, both MAT1 types for a lineage, where they are available, tend to resolve close together. This is expected as the regions outside of the MAT1 idiomorphs should be very similar within lineages despite the MAT1 types of the isolates used. Lineages 1, 4, and *F. foetens* sort within the 2s and 3s in the L flank tree and outside the 2s and 3s in the R flank tree. The expectation for these lineages is that they would resolve solely outside of the other lineages. It may be that the L flank, because of the concordant MAT1_2Frag present in both MAT1 types, experiences separate evolutionary pressures than the R flank. Consequently, 1, 4, and 5 appear more akin to some lineage 2s and 3s than other 2s and 3s do. The 2s and 3s are also showing variance in the amount they diverge from other 2s and 3s in either flanking region. In the L flank, 3s appear to have diverged from each other much more than the 2s, with several 2s appearing nearly identical to each other. Conversely, the 2s show a greater amount of separation from each other in the R flank whereas the 3s are resolving with less divergence. It is likely that these flanking regions are under diverse selective pressures unique to either group of lineages. An interesting juxtaposition demonstrated by these trees are the identical nature of the 2F and 2G MAT1_1 flanking regions in comparison to the divergence of the MAT1_2 flanking regions. Considering that both 2F and 2G MAT1 loci resolve as identical in the MAT1_1 and MAT1_2 loci trees, there is an expectation they would do the same in the flanking region trees. As this is not the case, there must be some evolutionary pressure acting on MAT1_2 flanking regions to change or MAT1_1 flanking regions to remain the same. This gives an example of how a sequence that is crucial, or was recently crucial, to a species' survival like the MAT1 idiomorph may remain unchanged even as neighboring sequences start to diverge.

Chapter 5

Conclusions

This thesis offers new inferences about the conservation of the MAT1 locus in *F. oxysporum* and about the potential necessity of a sexual stage in the FOSC. Sexual recombination in this species has also been suggested by analyses of the mitochondrial genome of FOSC individuals (Brankovics et al., 2017). Lineages in the MAT1_1 and MAT1_2 trees typically resolve near their phylogenetic sister lineages, a result expected if MAT1 type sequences were unique to the identity of each evolving population. Exceptions to this found in either tree are likely the result divergence of a lineage away from its sister lineages rather than a similarity of this lineage to a more distant phylogeny. The divergent tendency of the MAT1_2Frag along MAT1 type boundaries suggests that there are different selective pressures on sequences within and without the MAT1 regions. A nearly identical sequence found in these two positions varies distinctly and as a result is implied to be conserved in one and relaxed in the other. Lastly, analysis of the MAT1 locus flanking regions gives an idea of to what extent the MAT1_1 and MAT1_2 idiomorphs are conserved when compared to the neighboring genome. As an example, lineages 2F and 2G, which appear as identical at both MAT1 idiomorphs, begin to diverge from each other when compared at their flanking regions. There is reason to conclude that the mating type idiomorphs in *F. oxysporum* are specially conserved by this species when compared to genes that control less crucial functions. Considering the evidence in this thesis, MAT1 idiomorphs have evolved in accordance with the constraint of maintaining sexual viability among closely related groups. Additionally, the limited degree of divergence between lineages in any of these trees, when compared to an outgroup, suggests that the FOSC covers a single species, rather than a phylogeny of closely related species. A caveat to the research performed here is the incomplete picture of the FOSC given by the limited amount of lineage/MAT1 type representatives found. Not every lineage can be examined in full, meaning inferences cannot be expanded to the entire species complex. Furthermore, the sampling of *F. oxysporum* has traditionally focused on the

agronomic systems in which this fungus causes disease, therefore excluding a huge amount of diversity available in natural ecosystems. Future research on mating type in *F. oxysporum* should include a wider array of isolates, including multiple individuals to represent each lineage and mating type combination. Larger flanking sequences should also be used to form a stronger baseline against which the conservation of the MAT1 idiomorphs can be compared.

Appendix A

41-Gene Phylogenetic FOSC Tree

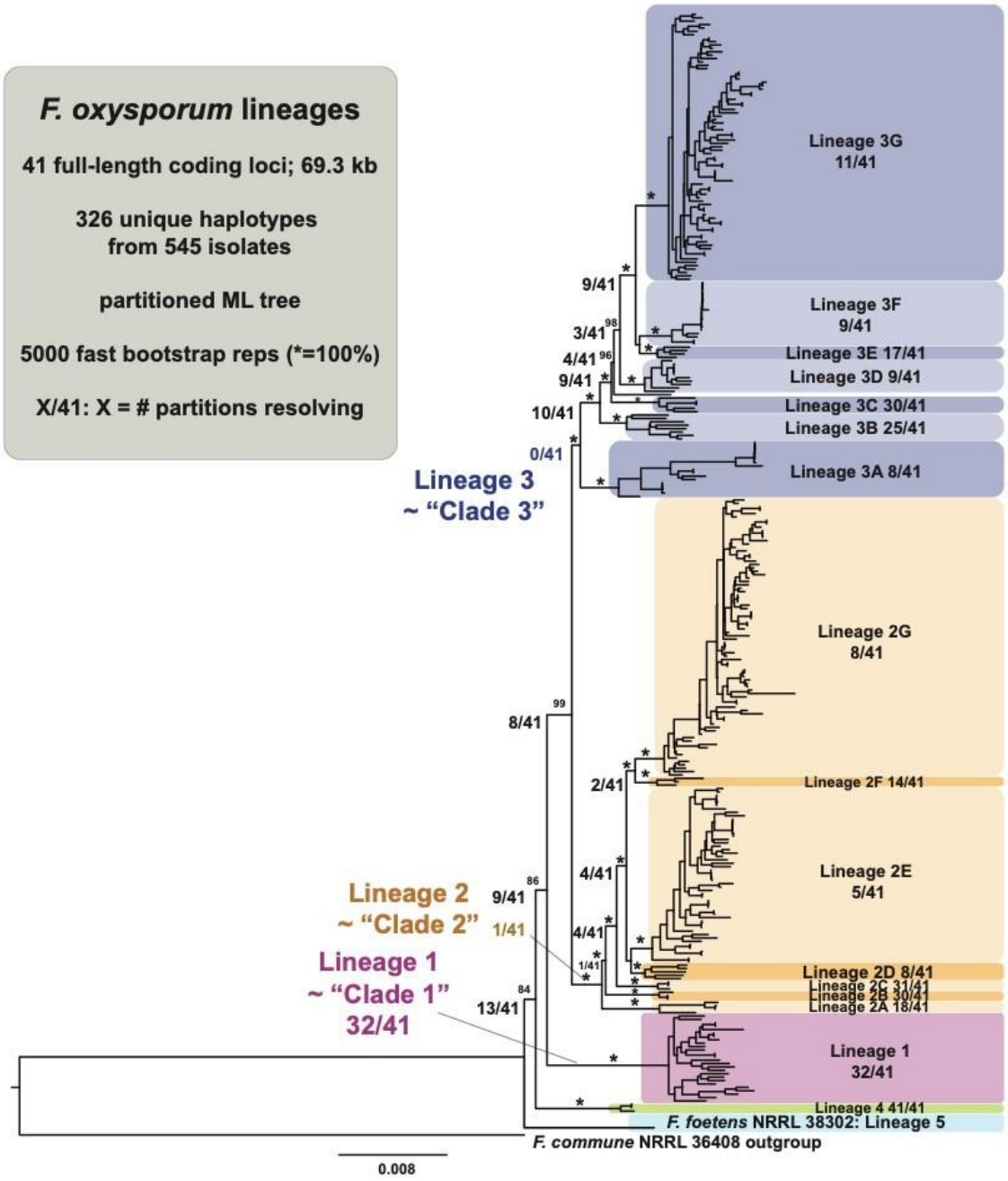
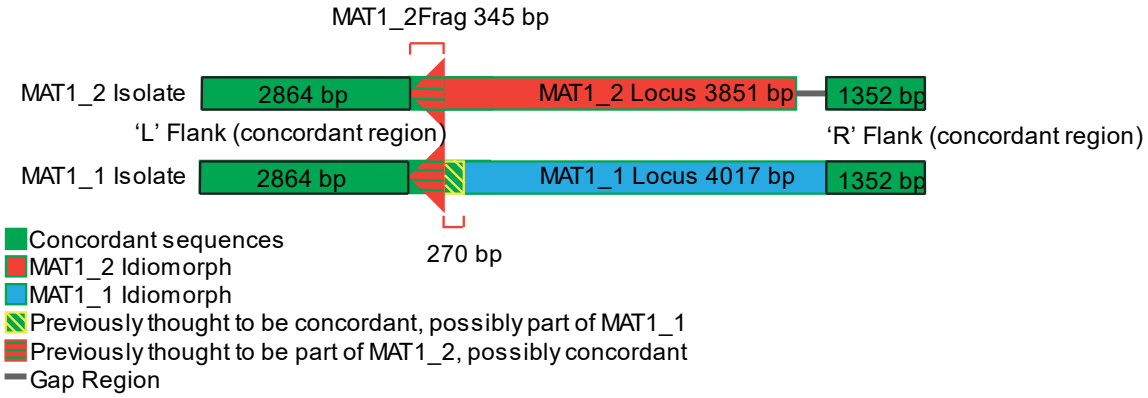


Image courtesy of David Geiser

Appendix B

Depiction of MAT1_1, MAT1_2, and Flanking Regions



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ACADEMIC VITA

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Education :

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Minors in Plant Pathology and Chemistry Senior

Relevant coursework includes Cell and Organelle Biology, Microbes and Plants, Genetics, Plant Virology, Fungal Biology, Principles of IPM, and Post-Harvest Crop Physiology.

Experience :

- Research Assistant in Penn State Fusarium Research Center (Summer 2022 to Current)
  - Prepared various culture media for isolation, propagation, and long-term storage of fungal isolates.
  - Isolated microbes from environmental samples for study on *Fusarium xyrophilum*.
  - Transferred and expanded cultures of *Fusarium* for use in genetic studies.
  - Extracted and analyzed DNA with PCR, gel electrophoresis, and nanodrop techniques for later sequencing.
  - Investigated large pool of fungal genetics with genomics software to build and support senior honors thesis.
- Summer Research Fellow in Virginia Tech Department of Biochemistry (Summer 2021)
  - Developed procedural outline to test hypothesis and extract relevant data.
  - Formulated essential oil dilutions to match wild plant aromatic profiles.
  - Designed plan for collection of valuable specimens, collected specimen.
  - Processed over 500 samples.
- GIS Analyst at Warren City Municipal Office (Summer and Winter 2020)
  - Processed data collection and applied it in online GIS mapping solutions.
  - Collected information in both field and office settings.
  - Coordinated with other municipal departments in prioritizing and designing maps for future use.
  - Gained ARCGIS and QGIS software experience.
  - Analyzed data trends in finalized maps.

Skills :

- Proficient with QIAGEN CLC Main Workbench, Geneious Prime, Adobe Illustrator, FigTree Microsoft Excel, RSudio, QGIS, and ARCGIS.
- Trained in PCR techniques, DNA extraction, gel electrophoresis, culture preparation, autoclave use, Nanodrop, NMR/IR analysis, Gas Chromatography/Mass Spectrometry, and sterile agar plating.