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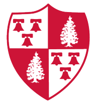

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Dynamic Genomic Evolution via Active LTR Transposable Elements in Maize

Taylor Isles

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Abstract: Long terminal repeats (LTR) retrotransposons, found across eukaryotes, are transposable elements which can copy and insert themselves into other loci within a genome. These transposable elements are similar to retroviruses in that they rely on reverse transcriptase to "copy and paste" themselves elsewhere in the genome. From the RNA transcript they are able to use reverse transcriptase to make another DNA copy of themselves. This initially gave them the moniker, selfish genes. However, in the decades after the discovery of reverse transcriptase and LTR retrotransposons, it became known that non-genic DNA could have other functions. LTR retrotransposons are sources of mutation, inserting themselves into and mutating genes within their host organism. However, LTR retrotransposons are prone to mutation themselves, quickly becoming inactive, incapable of transposition. LTR retrotransposons constitute approximately 75% of the total genomic sequence of maize. The vast majority of these LTR retrotransposons are completely inactive. While these inactive retrotransposons can be useful for gleaning information about an organism's evolutionary history, the active LTR retrotransposons are of more interest. They are capable of causing mutations in current maize crosses and maize lines. In this study we created a tool that is adept at filtering out the inactive LTR retrotransposons and finding the location and sequence of potentially active LTR retrotransposons. Building off the freely accessible tool for locating LTR's, known as "LtrDetector", we added additional functionality. In an initial filter, LtrDetector found over three million potential LTR retrotransposons across thirty publicly available maize lines. After adding restrictions for size, an intact primary binding site, polypurine tract, reverse transcriptase, RNase and integrase we narrowed down that large pool of candidates to just twenty-seven potentially active LTR retrotransposons.

Dynamic Genomic Evolution via Active LTR Transposable Elements in Maize

By Taylor Isles

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In Partial Fulfillment of the Requirements

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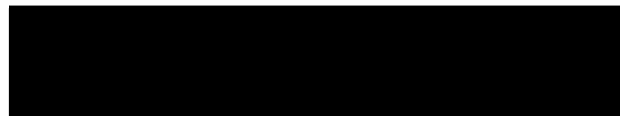

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DYNAMIC GENOMIC EVOLUTION VIA ACTIVE LTR TRANSPOSABLE ELEMENTS IN MAIZE

A THESIS

Submitted in partial fulfillment of the requirements

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By

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Montclair, NJ

2023

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INTRODUCTION:

LTR retrotransposons are transposable elements that can be found throughout the genomes of eukaryotes. In some maize lines they comprise up to 75% of the entire genome (Baucom, et al, 2009). In contrast, the two other classes of transposable retroelements made up just 1% of the maize genome (Baucom et al., 2009). In other eukaryotes it makes up a much lower but still significant portion of the genome, about 8% in humans (Cordaux and Batzer, 2009). It was initially thought that the genome was static. Genes and the large regions of "junk" between them were believed to be in fixed positions (Goodier and Kazazian, 2008). Today it is known that this is not the case. There are many mobile elements in the genomes of eukaryotes, and many have not yet been properly identified. The work of identification started in the 1940's when Barbara McClintock discovered what she called "Controlling elements". She found two distinct elements in maize, Ds (Disassociation)elements and Ac(Activator) elements (Goodier and Kazazian, 2008). Thus, beginning a long relationship between maize research and mobile element research. These transposable elements began to be sequenced in the eighties, and they were characterized by a retroviral-like sequence. Mount and Rubin (1985) discovered homology between transposons and the retroviral protein domains for gag protein, protease, reverse transcriptase, and integrase. Where they differed from retroviruses was in the lack of an envelope protein (Eickbush, Jamburuthugoda, 2008). Further experiments demonstrated that these elements replicated themselves through reverse transcription (Boeke et al., 1985). They were dubbed retrotransposons. These transposable elements or transposons are divided into two large groups, DNA transposons and retrotransposons. DNA transposons use a "cut and paste" mechanism where DNA is

removed from one location in the genome and relocated to another area (Goodier, Kazazian, 2008). Retrotransposons use a "copy and paste" system. The retrotransposons transcribes an RNA copy before that copy is reverse transcribed back into the genome as DNA (Finnegan, 2012). In this way retrotransposons can cause the genome to expand (Finnegan, 2012). Retrotransposons are found in bacteria, archaea and eukaryotes, implying an ancient origin (Beauregard et al., 2008). Retrotransposons are then grouped into two large families, extrachromosomally-primed (EP) retrotransposons and target-primed (TP) retrotransposons (Beauregard et al., 2008). EP retrotransposons are transcribed into an RNA template and then reverse transcriptase synthesizes cDNA from the RNA template (Beauregard et al., 2008). Integrase then allows access to the target site and the dsDNA is spliced back into the genome (Beauregard et al., 2008). The majority of these EP retrotransposons are LTR retrotransposons (Beauregard et al., 2008). LTR stands for long terminal repeats. They are defined by these two identical sequences at the 5' and 3' ends of the transposon. (Mount and Rubin, 1985) Within this group there are multiple different LTR retrotransposons, the most researched being Type I (Copia) and Type III (gypsy). These two types are differentiated by the order of their domains. Copia LTR's have integrase as the third domain in the retrotransposon, while Gypsy LTR's have the integrase domain last (Eikbush and Jamburuthugoda, 2008). The other family of retrotransposons are known as target-primed retrotransposons. This family is largely comprised of non-LTR retrotransposons but there are several exceptions (Beauregard et al., 2008). TP retrotransposons are different from EP retrotransposons in that the RNA transcript binds to a 3' hydroxyl group at the target site after endonuclease nicks a strand (Beauregard et al., 2008). To simplify, EP retrotransposons synthesize cDNA and then

integrates into the genome, while TP retrotransposons integrate first and then synthesize cDNA from the attached RNA transcript (Beauregard et al., 2008). Regardless of the mechanisms they use to transpose themselves these transposable elements have been shown as the cause of mutation in multiple different eukaryotes (Dooner et al., 2019). The genes and regulatory elements affected by these mobile elements vary based on where they insert themselves, as they can insert themselves in or near genes (Dooner et al., 2019). This is part of why retrotransposons are an important driver of evolutionary changes. For example, LTR retrotransposons and other transposable elements were shown to grow exponentially in the hominid genome shortly before major speciation events (Kim et al., 2004). However, not all LTR retrotransposons are capable of producing mutations. Most LTR retrotransposons are inactive. Older LTR retrotransposons are less capable of transposition than their younger counterparts (Jedlicka et al., 2020). LTR retrotransposition is not a perfect process, around one-third of all transpositions result in a “broken”, non-standard LTR retrotransposon, which goes a long way in explaining why older LTR retrotransposons become incapable of transposition (Dooner et al., 2019). In order to better understand transposons, they first must be found, sequenced, and annotated in order to better understand their effects on the genome. The innovations of the past two decades in bioinformatics and sequencing technology have been immensely helpful in this aspect (Dooner et al., 2019). It has become much simpler to sequence entire genomes rather than focusing on single genes. In this project, we developed a tool to locate LTR retrotransposons, making it easier to identify potentially active, young retrotransposons from among the many inactive ones. To do this we searched for the hallmarks of LTR retrotransposons, two identical LTR’s, a

primary binding site, a polypurine tract and the conserved domains for protease, reverse transcriptase, RNase and integrase (Goodier and Kazazian 2008). This bioinformatic tool read through 30 different publicly available maize lines from Maize GDB (Woodhouse, 2021), and filtered out any that did not match the typical LTR retrotransposon sequence. We hope that this tool greatly eases the process of identifying active LTR retrotransposons in not only the maize genome, but many different plant genomes. The tool is largely species agnostic, however, if applied to a very different organism, like a mammal or bacteria, the exact protein sequences searched for would need to be changed. In addition, we also discuss the ongoing work to grow maize crosses and search for novel active LTR retrotransposons.

METHODS:

To identify all the potential active LTR retrotransposons we employed the use of the program LtrDetector. This program looks for sets of identical long terminal repeats (Valencia and Girgis, 2019). Once this program was integrated, we focused on refining the search, as at this point we had over 100,000 candidate LTR's. Next, we had to add parameters in order to search for other components that are part of active. First, we added a filter looking for Polypurine Tracts, a stretch of multiple purines that is adjacent to the 3' LTR. Then a filter was added to look for the primary binding site. We used multiple different PBS logos to capture as many permutations of the PBS as possible. Then we generated amino acid logos for reverse transcriptase, RNase and GAG proteins. The program converted each LTR retrotransposon to its corresponding amino acid sequence and compared it to the generated logos to confirm that the desired domains were present.

The program confirmed the right and left LTR were identical. It checked for the presence of identical TSDs. It also checked for a match to the primary binding site logo. Finally checking for a polypurine tract upstream of the 3'LTR. To accomplish these tasks, the tool first loaded the indexed position of all retrotransposons in the sample set provided by the LTR detector. However, since the detector only provided the positions of the LTR in the genome and not the sequences themselves, the next step must be to pull and read the sequences present at these locations. To ensure each retrotransposon was unique, they were labeled according to the chromosome they are located on, as well as the starting and ending base pair index. For example, a retrotransposon located on the 3rd chromosome from the 10th base pair to the 25th would be labeled as "chr3:10-25". This labeling method allowed for the use of a HashMap, which sped up the process. The tool then proceeded to cut out the 5' and 3' LTR from each sequence and check whether they are identical. Subsequently, the tool examines the 20 base pairs upstream of the 3' LTR to determine the number of purines present. A purine content of more than 85% in the 20 base pair sample would indicate the presence of a polypurine tract. The tool also checked for the presence of a primer binding site immediately following the 5' LTR while ensuring that the target site duplications are present and identical. Only sequences that meet all the previous criteria were eligible for the next filter. Next, the tool converted each sequence into its six possible reading frame amino acid chains. Each chain is then checked for the presence of Reverse Transcriptase, RNase, and GAG proteins using a pattern identifier known as regex. Finally, the list of candidates was written to an output.fa file, which can be manually annotated and confirmed as active LTR retrotransposons.

Annotation

After the data collection tool went through the files on the high-performance computing cluster (HPC). The HPC runs on Linux and is comprised of 55 computing nodes, 24 GPU's, 1416 CPU cores, and 12.5TB of aggregate RAM. We manually annotated the transposons in order to verify that the tool was working. In order to annotate the LTR retrotransposons we performed the following steps. The Long Terminal Repeats are two identical sequences at the 5' and 3' end of LTR retrotransposons. They should be right next to the TSD's (target site duplications) and they should be not be more than 1000 base pairs. In this way we used what we knew about one element to find the other. LTR's are always directly next to TSD's, so I knew that the bases right next to it are part of the LTR. I took the first 10 or so bases that are right next to the 5' TSD and searched the document for copies (control+f or command+f), and I found the beginning of the 3' LTR this way. The 3' LTR ran from this sequence to the 3' TSD, which gives us the entire LTR, then by knowing the sequence of the 3' LTR, which means I could find the sequence of your 5' LTR and can highlight it as well. After that I found the Polypurine Tract. This is a site of purines (G's and A's) that should be no more than 2 base pairs from the 3' LTR. It should be 5-8 base pairs long. It could be a little longer but it's usually between 5-8 base pairs. Finally, I located the Primary Binding Site. The primary binding site is located right next to the 5' LTR, usually not more than a few base pairs away from the 5'LTR. There is only one primary binding site per transposon and we used logos from previous studies in order to search and identify the correct sequence.

In the logo below, the larger the number, the more likely that nucleotidecan be found there. In the below example, a primary binding site will always start with TGGTA and

will usually be followed by T, but can be followed by C. After identifying these regions that are within each LTR we needed to identify the domains inside each retrotransposon. I initially looked for gag, protease, RNAase H and integrase domains. To find these we used NCBI (https://www.ncbi.nlm.nih.gov/) and Uniprot's (https://www.uniprot.org/) conserved domain database. Within these databases we found the preexisting logos for the domains we were looking for. We also generated our own logos by feeding sequences identified by the conserved domain viewer (https://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi) on NCBI to the web app weblogo (https://weblogo.berkeley.edu/). This allowed us to confirm that the logos we selected were a match for the ones being used by the database to identify the domains in our sequences. Unfortunately, the gag logos that we generated and the logos used by the conserved domain database were very weak and were ultimately cut from our filter. The domain database noted that the gag domain logo was weak and not as strong as the other logos we were using. In order to find those other domains I entered each sequence from the first base pair after the PBS to the last base pair just before the PPT into the conserved domain viewer on NCBI (for this I kept the default settings). After the application was done processing the request it displayed our annotated sequence. This included domains mapped onto our sequence as well as their active sites, down to the nucleotide level. This permitted me find domains within our sequences manually. The viewer also provided links and logos for tagged domains allowing us to then incorporate NCBI's logos as well as start to develop our own using our annotated sequences.

RESULTS:

Bioinformatic Tool Filters Out Broken LTR's

LtrDetector initially detected 3,771,936 identical LTR's across 30 maize inbred lines. After filtering out the detected sequences that lacked a PBS, a PPT, two identical LTR's and were longer than 5,000 base pairs in length there were 1,792 detected LTR retrotransposons. The filter was not configured to search for conserved domains at this step. Table 1 displays the total number of detected LTR retrotransposons, the maize line in which they occurred and chromosome they can be found on. Most of the samples averaged between 30 to 45 detections. EP1, F7 and W22 are outliers with 297, 236 and 184 detections respectively. This consistency across multiple chromosomes is encouraging as a large difference between every maize line might imply that the quality of the genome sequencing was different between maize lines. A consistent number of LTR retrotransposon detections implies that the maize lines have undergone quality long read sequencing. PE0075 has only eight detected LTR retrotransposons. This is the lowest number of detections across the dataset and could be due to PE0075 having a lower quality genome sequencing. It also might imply PE0075 has a very low number of LTR retrotransposons. The LTR retrotransposons sampled from the 1,792 had all the identifiers we were looking for at this stage, indicating that our bioinformatic tool was performing correctly.

Table 1: 1,792 Potentially Active LTR Retrotransposons after First Filter

	chr1	chr2	chr3	chr4	chr5	chr6	chr7	chr8	chr9	chr10	**Total**
B73	6	6	2	5	3	3	4	1	3	5	38
B97	**5**	**6**	**3**	**2**	**8**	**5**	**3**	**4**	**2**	**2**	40
CML103	4	5	5	4	7	2	5	4	2	2	40
CML228	5	4	4	2	10	3	3	3	2	3	39
CML247	6	3	5	3	7	6	3	5	0	3	41
CML277	3	4	4	3	9	3	4	6	3	3	42
CML322	5	4	5	4	7	5	1	1	3	3	38
CML333	6	3	4	2	8	3	1	5	2	3	37
CML69	1	6	4	2	6	2	4	3	1	3	32
DK105	5	4	4	7	6	10	4	6	7	3	56
EP1	30	40	45	35	29	27	25	24	21	21	297
F7	27	22	31	27	23	24	22	21	19	20	236
HP301	1	10	2	3	3	3	4	4	1	5	36
Ia453	6	3	0	2	7	4	5	5	6	1	39
IL14H	5	5	1	5	5	2	6	5	7	3	44
K0326Y	4	6	2	7	4	4	7	6	2	3	45
Ki11	8	3	3	2	6	5	4	8	2	3	44
Ki3	7	3	4	2	8	4	3	5	1	4	41
Ky21	5	7	1	7	3	5	2	2	5	4	41
M162W	3	7	3	0	6	3	4	3	3	8	40
M37W	8	6	3	7	3	4	2	7	2	1	43
Mo18W	5	4	4	2	8	3	3	4	1	5	39
Ms71	10	6	8	0	4	3	3	4	3	5	46
NC350	3	4	6	0	5	5	2	10	3	0	38
NC358	7	4	4	3	5	7	9	4	3	5	51
Oh43	8	3	5	2	4	3	5	3	3	5	41
PE0075	0	1	1	2	0	1	1	0	2	0	8
Tx303	3	7	3	2	5	4	4	4	1	3	36
Tzi8	4	4	4	5	5	7	3	1	5	2	40
W22	20	25	22	19	20	13	15	25	19	6	184
											1792

Table 1 - LTR retrotransposons detected on 30 maize lines from MaizeGDB (https://www.maizegdb.org/) and the chromosome each is located on. At this stage the filter only selected sequences that were less than 5,000 base pairs with identical LTR's, a polypurine tract and a Primary Binding Site. The total number of retrotransposons that met these criteria across all Maize lines was 1792 detected LTR retrotransposons, narrowed from 3,771,936. The three maize lines with the greatest number of detected retrotransposons were EP1 (297 retrotransposons), F7 (236 retrotransposons) and W22(184 retrotransposons). PE0075 had the lowest with eight, making the range of detections eight to 297 with a mean of 59.73.

Table 2: LTR Retrotransposons Filtering for Conserved Domains

Maize Cross	Chr 1	Chr 2	Chr 3	Chr 4	Chr 5	Chr 6	Chr 7	Chr 8	Chr 9	Chr 10
B73				1	1					
B97									1	
CML103	1				1				1	
CML322			1		1					
CML333	1									
EP1				2			1			1
F7										1
HP301					1					
LA453					1				1	
IL14H					1				1	
K0326Y				1					1	
NC358	1				1					
Oh43					1					
PE0075				1						
Tx303									1	
Tzi8					1					

Table 2 – Active LTR retrotransposons detected by the bioinformatic tool after screening for Reverse Transcriptase, RNAase and Gag domains. The total number of detected LTR retrotransposons is twenty-seven. Maize lines that produced no hits were not included in the table.

Bioinformatic Tool Filters out Retrotransposons Lacking Desired Domains

After implementing filters for conserved sequences of domains only 27 LTR retrotransposons contained domains for reverse transcriptase, gag protein, and RNase. In order to filter the retrotransposons with the desired domains we generated logos from existing LTR retrotransposons on the NCBI database (Sayers et al., 2022). After finding LTR retrotransposons we used NCBI's domain database to identify the domains within these sequences, aligned them and used them to generate logos with the weblogo browser application (Crooks et al., 2004). The bioinformatic tool was then given pieces of these logos and filtered any sequence that did not contain them. In order to make the tool more expansive, multiple different sequences were added for reverse transcriptase and RNAase. As long as the tool found one of the sequences for reverse transcriptase it would

pass the filter. In this way we made sure we found as many permutations of active domains as possible. On Table 2, the 27 retrotransposons are listed with number, maize line and location within the genome. The filter did not find LTR retrotransposons in any of the other fourteen maize lines. After running the tool with filters for reverse transcriptase, RNase, and integrase it was decided that we would proceed without filtering for protease, as twenty-seven was a workable amount of retrotransposons for manual annotation.

Figure 1: Domain Logos

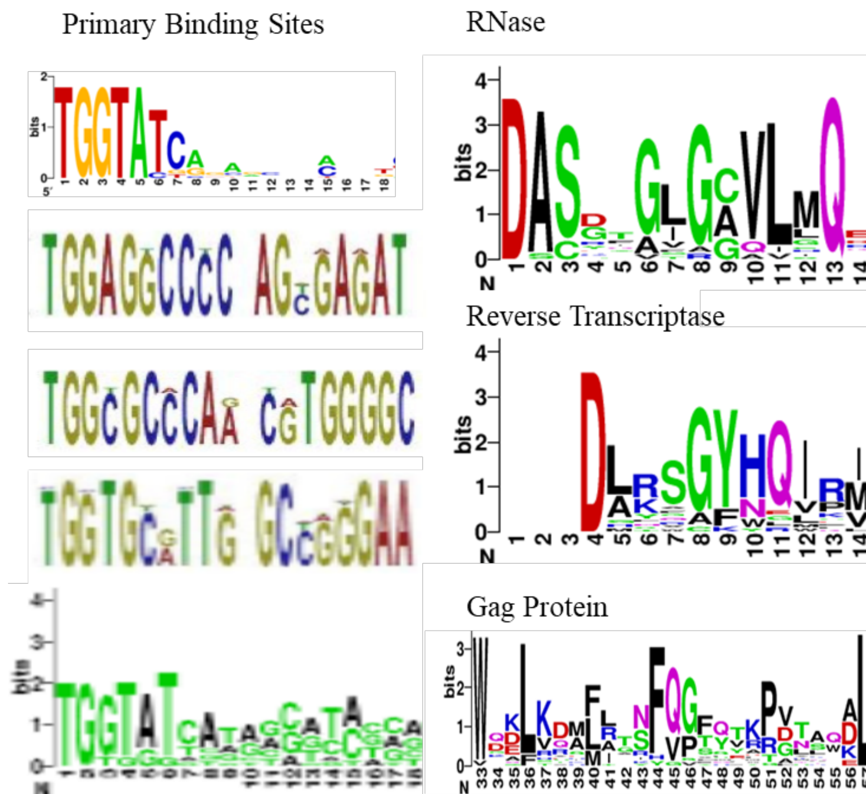

Figure 1 –The logos generated on weblogo.berkely.edu for the Primary Binding site of LTR retrotransposons, as well as the logos of RNase, reverse transcriptase and gag protein. The Gag protein had more variance than both RNase and Reverse Transcriptase, and was not annotated as it was difficult for our bioninformatic tool and NCBI's database to identify accurately in a sequence.

Table 3: LTR Retrotransposons and the Conserved Domains Found in Sequence

LTR Retrotransposons Conserved Domains				
LTR Retrotransposon	Protease	Reverse Transcriptase	Rnase	Integrase
B73 Ch4		X	X	X
B73 Chr 5		X	X	X
B97 Chr 9		X	X	X
CML103 Chr 1		X	X	X
CML103 Chr 5		X	X	X
CML103 Chr 9		X	X	
CML322 Chr 3	X	X	X	X
CML322 Chr 5		X	X	X
CML333 Chr 1				
EP1 Chr 4: 8015632-8020208	X	X	X	X
EP1 Chr 4: 258921835-258925715		X	X	X
EP1 Chr 7		X	X	X
EP1 Chr10		X	X	X
F7 Chr10		X	X	X
HPL301 Chr 5		X	X	X
LA453 Chr 5		X	X	X
LA453 Chr 9	X	X	X	X
IL14H Chr 5		X	X	X
IL14H Chr 9		X	X	X
K0326Y Chr 4		X	X	X
K0326Y Chr 9		X	X	
NC358 Chr 1	X	X	X	X
NC358 Chr 5		X	X	X
Oh43 Chr 5		X	X	X
PE0075 Chr 4		X	X	
Tx303 Chr 9	X	X	X	X
Tzi8 Chr 5		X	X	X

Table 3 - The Twenty-Seven LTR retrotransposons and their conserved domains. While not filtered for by the bioinformatic tool. Integrase was found in nearly all of sequences after the sequences were manually annotated.

Manual Annotation Confirms Presence of Complete LTR Retrotransposons

Within the annotated sequences almost all contained the requisite conserved domains. There were 27 total detected LTR retrotransposons. Twenty-six of them had Reverse Transcriptase and RNase and twenty-four of them had integrase. This was confirmed by checking against the logos of the conserved domain and pfam databases on NCBI and Uniprot. This shows that the bioinformatic tool was functioning correctly as most of LTR retrotransposons it found had the requested conserved domains. When selecting logos, we aimed to use active sites and the most highly conserved regions according to NCBI. We checked for protease manually in these twenty-seven sequences. Out of twenty-seven retrotransposons, six of these retrotransposons had a protease domain. They were located on chromosome 3 on maize line CML322, on chromosome 9 in maize line La453, on chromosome 1 in maize line NC358, on chromosome 9 in maize line Tx303, on chromosome 4 in maize line EP1 and on chromosome 4 in maize line B73. These six LTR retrotransposons show the least signs of degradation and mutation, making them the most likely to be active and capable of transposition. Given the order of the domains contained within the annotated sequences, (Figure 2) it is a type 3 LTR retrotransposon. Of note is that the incomplete LTR retrotransposons often repeated across maize lines. The sequences of the LTR retrotransposons found on chromosome 5 were extremely similar to one another. They had the same target site duplication CTCCA, the same three conserved domains, reverse transcriptase, RNase and integrase. The sequences on chromosome four and 9 often share repeating patterns as well.

Figure 2: CML322: Ch3 Annotated

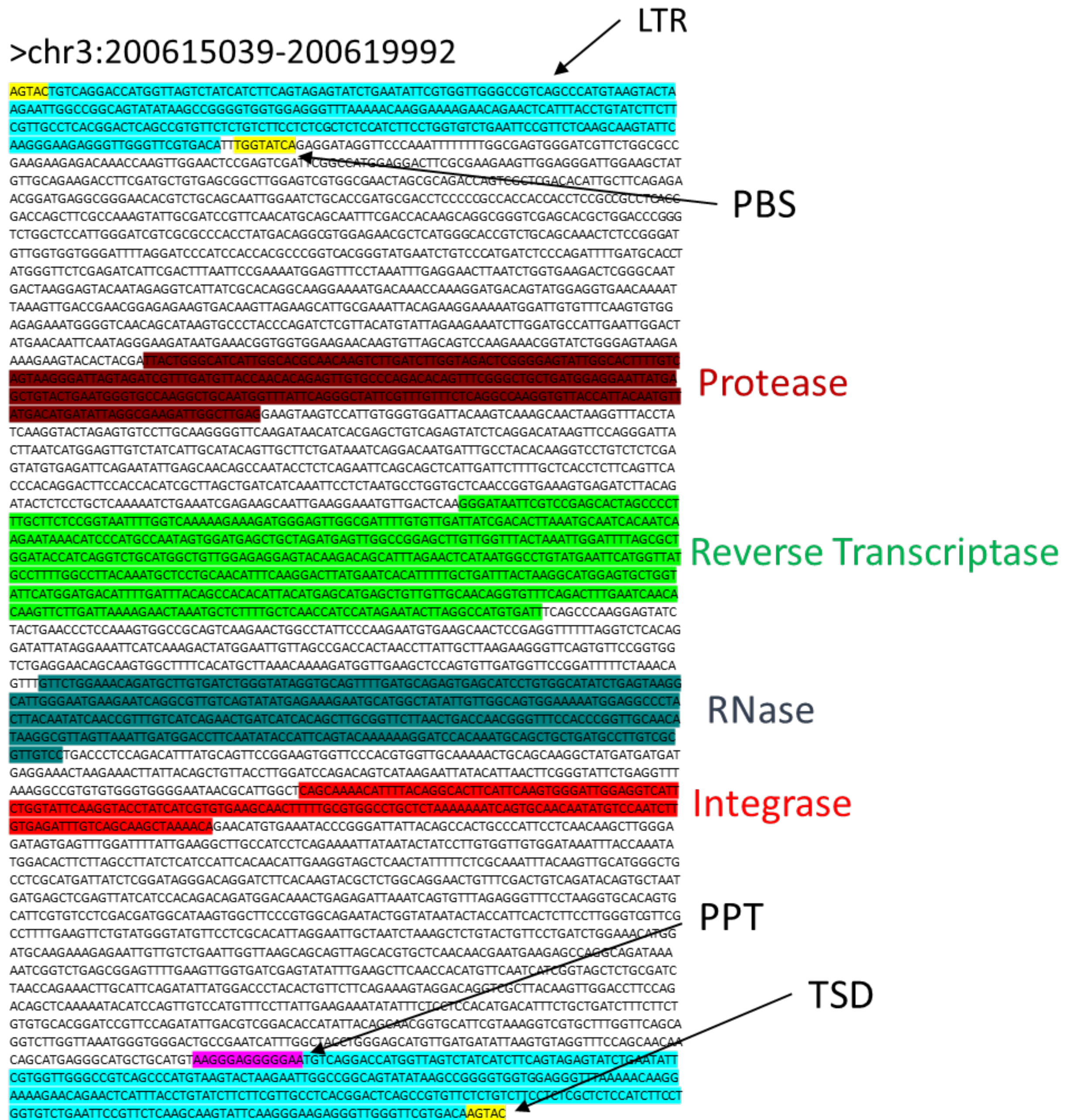

Figure 2 - An example of a fully annotated sequence pulled from the genome by the bioinformatics tool. This sequence has all the conserved domains requested. From top to bottom, in yellow – The First TSD, followed by the 5' LTR in sky blue. The primary binding site in yellow. Then after this the first filtered domain is reverse transcriptase, then RNase and integrase. Then is the PPT in purple. Finally the retrotransposon is We did not annotate gag due to the logo for gag being weakly conserved.

DISCUSSION:

LTR retrotransposons are retroviral-like transposable elements that are capable of driving mutation within eukaryotic genomes, especially plant genomes (Jedlicka et al., 2020). The active retrotransposons can be very low copy number and surrounded by inactive LTR retrotransposons, in repetitive regions, making finding them difficult (Dooner et al., 2019). Active LTR retrotransposons often adhere to a typical set of domains and features, two LTR's, a PBS, PPT and the conserved domains for gag, protease, reverse transcriptase, RNase and integrase (Goodier and Kazazian, 2008). The bioinformatic tool developed here will be useful in future projects due to its ability to detect domains analogous to those typical, functioning LTR retrotransposons. The tool was able to detect retrotransposons within the thirty publicly available maize lines. These maize lines were sequenced accurately enough to generate a consistent number of LTR retrotransposon detections. The one exception being PE0075, which had an abnormally low number of LTR retrotransposons. In addition to this the tool is capable of removing any LTR retrotransposons without the requisite conserved domains for reverse transcriptase, RNase and integrase. One thing that can be gleaned from a comparison between the results of the first filter and the results of the second filter is that the number of intact LTR's does not necessarily correlate with a high number of active LTR retrotransposons. Before the LTR retrotransposons without the conserved domains were filtered out, maize lines EP1, F7 and W22 had the highest numbers of LTR retrotransposons. In a previous stage of this project, it was anticipated that these lines would have higher than average numbers of active LTR retrotransposons after applying the second filter (Wiggington,

2022). This was not the case. EP1 has the highest number of detections in Table 3, with four, but F7 and W22 did not have a high frequency of detections. Maize line F7 had one detection and W22 had no detections. It's possible that maize line F7 and W22 have high levels of LTR retrotransposons, but average levels of transposition, meaning the majority of the LTR retrotransposons in these two maize lines are old and inactive. The other possibility is that our logos are too stringent, and that the conserved domains we are looking for has more functional permutations than exists in any of the publicly available databases. However, this is less likely since proteins like reverse transcriptase are highly conserved (Sundaravaradan et al., 2005).

The 21 sequences that did not have all of the conserved domains typical of an active LTR retrotransposon had interesting similarities to each other. All of the LTR retrotransposons on chromosome five had very similar sequences. They had the same three conserved domains, none of them had less, and none of them had protease. They also had the same TSD sequence, and PPT. While more analysis would have to be performed, these are likely the same retrotransposon represented across many different maize lines. The tool developed picked out the same sequence in nine of sixteen maize lines. It shows that the tool could be made more restrictive than it is currently to search for just a single LTR retrotransposon across multiple large genomes. The six annotated sequences found by the tool - and found to have the desired domains - are likely capable of transposition. However, one of them NC358 Chromosome 1 does not have identical TSD's. While the TSD's are not required for transposition, it is a signifier that the LTR retrotransposons have picked up mutations through ectopic recombination (Jedlicka, 2020). This means that it is likely older than the other five typical sequences and has begun to degrade. It

would be interesting to cross this maize line with a line that is known to have no LTR retrotransposon to see if something that is still largely intact is still capable of transposition. Regardless, all six of these maize lines are good candidates for future crosses as they are far more likely to have offspring with transpositions than other maize lines.

Conclusion: The bioinformatic tool developed for this project successfully identified LTR retrotransposons with the domains and features needed for transposition. Out of over three million LTR’s initially identified, just twenty-seven were pulled from the database as active LTR retrotransposons. Even the unrefined iteration reduced this number to just 1,792 likely active LTR retrotransposons. This tool can be of use in future experiments and data analysis to significantly cut time spent crossing and growing maize. Plants with little likelihood to contain active LTR retrotransposons can be ignored, and significant time and money saved. In the future further refinement of the tool will make it more accurate and variations could be made for other transposable elements. The tool can also work with other plant genomes, since the domain and structure of LTR retrotransposons are similar in plants kingdoms.

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APPENDIX A

Annotated LTR Retrotransposons

Legend:

TSD

Long Terminal Repeat

Primary Binding Site

Reverse Transcriptase

RNase

Integrase

Polypurine Tract

B97

>chr9:143627237-143631957

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>chr5:123190757-123194673

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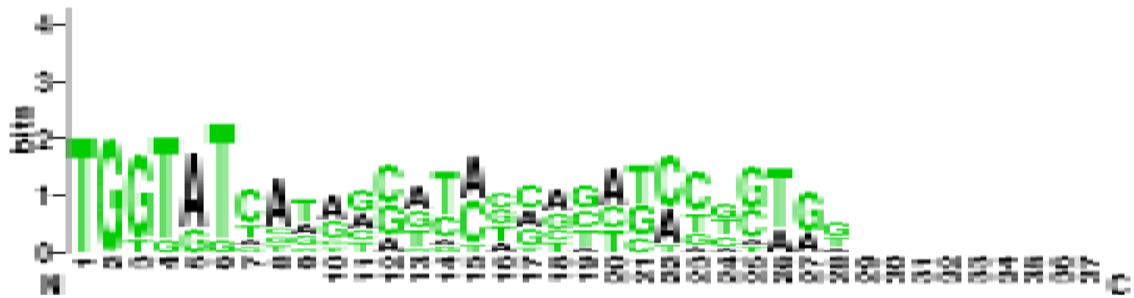
APPENDIX B

PBS Logos

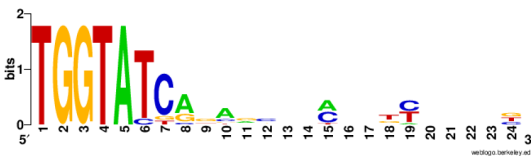


PBS Logo 5

PBS Logo 4

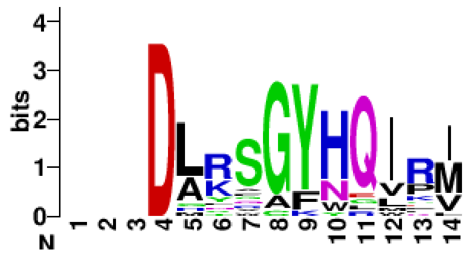
PBS Logo 3

PBS Logo 2

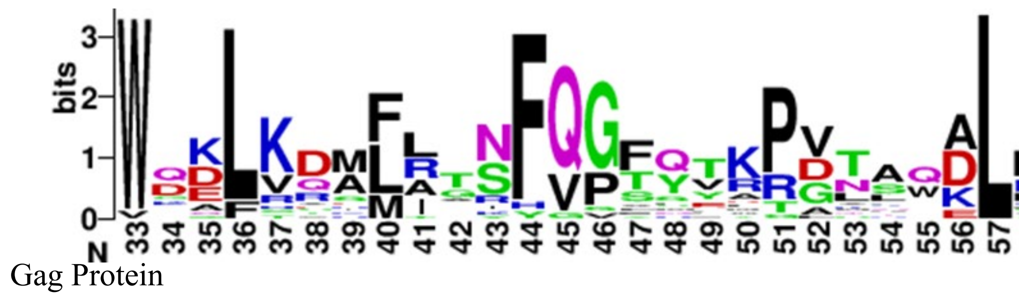


PBS Logo 1

RNase



Reverse Transcriptase



Gag Protein

APPENDIX C

```
import java.io.File;
import java.io.FileNotFoundException;
import java.io.FileReader;
import java.io.FileWriter;
import java.io.IOException;
import java.util.Arrays;
import java.util.HashMap;
import java.util.Scanner;
import java.util.regex.Matcher;
import java.util.regex.Pattern;

public class findRetrovirus_RNAse_GAG {
	static HashMap<String, String> codonTable = new HashMap<String, String>();
	static HashMap<String, String> origCandidates = new HashMap<String, String>();
	static HashMap<String, String[]> candidatesAmino = new HashMap<String, String[]>();
	static HashMap<String, String> candidates = new HashMap<String, String>();
	final static int NUM_RETRO_PATTERNS = 3;
	final static int NUM_RNA_PATTERNS = 2;
	final static int NUM_GAG_PATTERNS = 1;
//	final static int NUM_INT_PATTERNS = 1;

	public static void main(String[] args) throws IOException {
		initCodonToAminoMap();
		loadChrMapTEMP(args);
		Pattern[] retroPatterns = new Pattern[NUM_RETRO_PATTERNS];
		Matcher[] retroMatchers = new Matcher[NUM_RETRO_PATTERNS];
		Pattern[] RNAPatterns = new Pattern[NUM_RNA_PATTERNS];
		Matcher[] RNAMatchers = new Matcher[NUM_RNA_PATTERNS];
		Pattern[] GAGPatterns = new Pattern[NUM_GAG_PATTERNS];
		Matcher[] GAGMatchers = new Matcher[NUM_GAG_PATTERNS];
		retroPatterns[0] = Pattern.compile("NAPA");
		retroPatterns[1] = Pattern.compile("KTAF");
		retroPatterns[2] = Pattern.compile("M.FGL");
		RNAPatterns[0] = Pattern.compile("DAS.........Q");
```

```
		RNAPatterns[1] = Pattern.compile("D..SR");
		GAGPatterns[0] = Pattern.compile("............W.........................................L");
		for (String key : candidatesAmino.keySet()) {
			for (String aminoSeq : candidatesAmino.get(key)) {
				retroMatchers[0] = retroPatterns[0].matcher(aminoSeq);
				retroMatchers[1] = retroPatterns[1].matcher(aminoSeq);
				retroMatchers[2] = retroPatterns[2].matcher(aminoSeq);
				RNAMatchers[0] = RNAPatterns[0].matcher(aminoSeq);
				RNAMatchers[1] = RNAPatterns[1].matcher(aminoSeq);
				GAGMatchers[0] = GAGPatterns[0].matcher(aminoSeq);
				for (Matcher retroMatcher : retroMatchers)
					if (retroMatcher.find()) {
						for(Matcher RNAMatcher : RNAMatchers) {
							if(RNAMatcher.find()) {
								for(Matcher GAGMatcher: GAGMatchers)
{
									if(GAGMatcher.find()) {

	candidates.put(key, origCandidates.get(key));
									}
								}
							}
						}
					}
			}
		}
//		System.out.println(candidates.toString());
//		System.out.println(candidates.keySet().toString());
		writeNewCandidates(args);
	}

	private static void writeNewCandidates(String[] args) throws IOException {
		System.out.println(args[0]);
		String outputDirectory = args[0].replace("findPBS-sameleftright", "retrovirus-RNAase-GAG-CandidateLTRs-
");
		System.out.println(outputDirectory);
		File file = new File(outputDirectory);
		file.createNewFile();
		FileWriter writer = new FileWriter(file);
```

```
		for (String key : candidates.keySet())
			writer.write(key + "\n" + origCandidates.get(key) + "\n\n");

		writer.close();
	}

	public static void loadChrMapTEMP(String[] args) throws IOException {
		File chrs = new File(args[0]);
		Scanner fileReader = new Scanner(chrs);
		while (fileReader.hasNextLine()) {
			String name = fileReader.nextLine();
			String chr = fileReader.nextLine();
			fileReader.nextLine();
//			System.out.println(name + " -> " + chr);
			origCandidates.put(name, chr);
		}
		for (String key : origCandidates.keySet()) {
			candidatesAmino.put(key, convertBoth(origCandidates.get(key)));
//			System.out.println(key + " ---> \n" + Arrays.toString(convertBoth(candidates.get(key))));
		}
		fileReader.close();
	}

	public static void initCodonToAminoMap() {
		codonTable.put("TTT", "F");
		codonTable.put("ATT", "I");
		codonTable.put("GTT", "V");
		codonTable.put("TTC", "F");
		codonTable.put("CTC", "L");
		codonTable.put("ATC", "I");
		codonTable.put("GTC", "V");
		codonTable.put("TTA", "L");
		codonTable.put("CTA", "L");
		codonTable.put("ATA", "I");
		codonTable.put("GTA", "V");
		codonTable.put("TTG", "L");
		codonTable.put("CTG", "L");
		codonTable.put("ATG", "M");
```

```
codonTable.put("GTG", "V");
codonTable.put("TCT", "S");
codonTable.put("CCT", "P");
codonTable.put("ACT", "T");
codonTable.put("GCT", "A");
codonTable.put("TCC", "S");
codonTable.put("CCC", "P");
codonTable.put("ACC", "T");
codonTable.put("GCC", "A");
codonTable.put("TCA", "S");
codonTable.put("CCA", "P");
codonTable.put("ACA", "T");
codonTable.put("GCA", "A");
codonTable.put("TCG", "S");
codonTable.put("CCG", "P");
codonTable.put("ACG", "T");
codonTable.put("GCG", "A");
codonTable.put("TAT", "Y");
codonTable.put("CAT", "H");
codonTable.put("AAT", "N");
codonTable.put("GAT", "D");
codonTable.put("TAC", "Y");
codonTable.put("CAC", "H");
codonTable.put("AAC", "N");
codonTable.put("GAC", "D");
codonTable.put("CAA", "Q");
codonTable.put("AAA", "K");
codonTable.put("GAA", "E");
codonTable.put("CAG", "Q");
codonTable.put("AAG", "K");
codonTable.put("GAG", "E");
codonTable.put("TGT", "C");
codonTable.put("CGT", "R");
codonTable.put("AGT", "S");
codonTable.put("GGT", "G");
codonTable.put("TGC", "C");
codonTable.put("CGC", "R");
codonTable.put("AGC", "S");
```

```
		codonTable.put("GGC", "G");
		codonTable.put("CGA", "R");
		codonTable.put("AGA", "R");
		codonTable.put("GGA", "G");
		codonTable.put("TGG", "W");
		codonTable.put("CGG", "R");
		codonTable.put("AGG", "R");
		codonTable.put("GGG", "G");
		codonTable.put("CTT", "L");
		codonTable.put("TAA", "-");
		codonTable.put("TAG", "-");
		codonTable.put("TGA", "-");
	}

	public static String codonToAmino(String codon, boolean print) {
		if (print) {
//			System.out.println(codon + "->" + codonTable.get(codon));
//			String reversecodon = new StringBuilder(codon).reverse().toString();
//			System.out.println(reversecodon + "-->" + codonTable.get(reversecodon));
		}
		return codonTable.get(codon);
	}

	public static String codonToAmino(String codon) {
		return codonTable.get(codon);
	}

	public static String[] convertBoth(String codonSeq) {
		String[] out = new String[6];
		String genestrand1 = codonSeq;
		String genestrand2 = codonSeq.replace('A', 'H').replace('T', 'A').replace('H', 'T').replace('C', 'H')
				.replace('G', 'C').replace('H', 'G');
		String[] first = codonSeqToAminoSeq(genestrand1);
		String[] second = codonSeqToAminoSeqAntiPair(genestrand2);
		return new String[] { first[0], first[1], first[2], second[0], second[1], second[2] };
	}

	public static String[] codonSeqToAminoSeq(String codonSeq) {
```

```
        String aminoSeqF1 = "";
        String aminoSeqF2 = "";
        String aminoSeqF3 = "";
        for (int i = 0; i + 2 < codonSeq.length(); i += 3) {
            aminoSeqF1 += codonToAmino(codonSeq.substring(i, i + 3));
            if (i + 3 < codonSeq.length())
                aminoSeqF2 += codonToAmino(codonSeq.substring(i + 1, i + 4));
            if (i + 4 < codonSeq.length())
                aminoSeqF3 += codonToAmino(codonSeq.substring(i + 2, i + 5));
        }
        return new String[] { aminoSeqF1, aminoSeqF2, aminoSeqF3 };
    }

    public static String[] codonSeqToAminoSeqAntiPair(String codonSeq) {
        String aminoSeqF4 = "";
        String aminoSeqF5 = "";
        String aminoSeqF6 = "";
        codonSeq = new StringBuilder(codonSeq).reverse().toString();
        for (int i = 0; i + 2 < codonSeq.length(); i += 3) {
            aminoSeqF4 += codonToAmino(codonSeq.substring(i, i + 3));
            if (i + 3 < codonSeq.length())
                aminoSeqF5 += codonToAmino(codonSeq.substring(i + 1, i + 4));
            if (i + 4 < codonSeq.length())
                aminoSeqF6 += codonToAmino(codonSeq.substring(i + 2, i + 5));
        }

        return new String[] {aminoSeqF4, aminoSeqF5, aminoSeqF6};
    }
}
```