

1 **Global multi-environment resistance QTL for foliar late blight resistance in tetraploid**
2 **potato with tropical adaptation**

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20 **Short running title:** Late blight resistance in tetraploid potato

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26

27 **Abstract** (single paragraph of max 250 words):

28 The identification of environmentally stable and globally predictable resistance to potato late
29 blight is challenged by the crop's clonal and polyploid nature and the pathogen's rapid
30 evolution. Genome-wide analysis (GWA) of multi-environment trials can add precision to
31 breeding for complex traits. A diversity panel of tetraploid potato germplasm bred for multiple
32 resistance and quality traits was genotyped by genotyping by sequencing (GBS) and
33 phenotyped for late blight resistance in a trait observation network spanning three continents
34 addressed by the International Potato Center's (CIP's) breeding program. The aims of this
35 study were to (i) identify QTL underlying resistance in and across environments and (ii)
36 develop prediction models to support the global deployment and use of promising resistance
37 sources in local breeding and variety development programs. Health-indexed *in vitro* plants of
38 380 clones and varieties were distributed from CIP headquarters in Peru to China and Ethiopia
39 and tuber seed was produced centrally in each country. Phenotypes were recorded as rAUDPC
40 following field exposure to local isolates of *Phytophthora infestans*. Stringent filtering for
41 individual read depth >60 resulted in 3,239 tetraploid SNPs. Meanwhile, 55,748 diploid SNPs
42 were identified using diploidized data and individual read depth >17. The kinship matrix was
43 utilized to obtain BLUP and identify best performing germplasm in each and all environments.
44 Genotypes with high levels of resistance in all environments were identified from the B3,

- 45 LBHT and B3-LTVR populations. GWA identified stable QTL for late blight resistance in
46 chromosome 9 and environment specific QTL in chromosomes 3, 5, 6 and 10.

47 **Introduction**

48 Potato genetic resources comprise a polyploid series consisting of a tremendously diverse
49 germplasm of wild relatives and cultivated landraces (Spooner 2014; Ovchinnikova et al.,
50 2011). However, most commercially cultivated potato varieties are tetraploid ($2n=4x=48$) with
51 the genome consisting mostly of *Solanum tuberosum* Group *tuberosum* with some
52 introgressions from a few wild species and cultivated landraces (Bradshaw et al., 2006;
53 reviewed by Bethke et al., 2017; reviewed by Gaiero et al., 2018). Tetraploid potato is a highly
54 heterozygous, outcrossing autopolyploid, crop which complicates genetic analysis. Most of the
55 early genetic mapping studies utilized bi-parental populations at the simpler, diploid level
56 ($2n=2x=24$) and several disease resistance loci were identified in the genome of potato this
57 way (reviewed by Gebhardt and Valkonen 2001). However, this approach does not permit the
58 assessment of large gene pools or multi-allelic interactions that influence traits in polyploids.
59 Significant progress has recently been made in the development of algorithms and software for
60 genotype calling, linkage and QTL analysis in polyploid species. SNP arrays have been
61 developed for potato: 8K SolCAP (Hamilton et al., 2011) and the 20K SolSTW arrays (Vos et
62 al., 2015). These were developed using North American and European potato germplasm,
63 respectively, and are not consequently the best options for genotyping CIP germplasm since it
64 contains more introgressions from the native South American gene pool. According to our
65 previous experience, less than 50% of the SNPs on the 8K SolCAP array were informative in
66 a test sample of CIP germplasm (Lindqvist-Kreuze et al., 2014). Genotyping by sequencing
67 (GBS) has been applied to tetraploid potato (Uitdewilligen et al., 2013, Sverrisdottir et al.,
68 2017); and variant calling from short read sequencing data considering allele dosage is now
69 possible using several different tools, such as GATK, Freebayes, or SAMtools to name a few
70 (Clevenger et al., 2015). However, reliable dosage calling in the heterozygous individuals
71 depends on the read depth in the SNP loci. It was recently demonstrated in autopolyploid

72 blueberry, that a read depth of 61 was adequate to reliably call the allele dosage, while only 17
73 reads were needed to reliably classify simplex tetraploids as heterozygous with 95% accuracy
74 (Matias et al., 2019). The identification of QTL in autopolyploids is facilitated by new tools,
75 such as called GWASpoly that considers allele dosage effects (Rosyara et al., 2016). Together,
76 these advances make genomic analysis of tetraploid potato more informative and applicable to
77 evolutionary and breeding studies.

78

79 The goal of CIP potato breeding program is to develop resilient, high yielding, healthy and
80 early maturing varieties for small-holder farming systems in the developing world. We are
81 targeting farming systems that usually function with minimum input of pesticides and therefore
82 a high level of disease resistance is an indispensable trait. To this end, CIP's potato breeding
83 program has developed breeding populations selected for high levels of resistance to late blight
84 caused by the oomycete *Phytophthora infestans*, and resistance to Potato Virus Y (PVY), Potato
85 Virus X (PVX) and Potato Leaf Roll Virus (PLRV). Previous studies have identified genomic
86 regions in CIP's breeding germplasm explaining resistance to late blight focusing on
87 phenotypic data collected from field trials in Peru or using local pathogen strains in greenhouse
88 conditions (Li et al., 2010; Lindqvist-Kreuze et al., 2014, Jiang Rui et al., 2018). Performance
89 information has been sporadically published about CIP's bred materials in the target regions
90 where they have been distributed to (Muhinyuza et al., 2015; Hirut et al., 2017b) but to our
91 knowledge no genetic analysis has been published identifying resistance QTL for resistance in
92 CIP germplasm tested in environments outside Peru.

93

94 The overall goal of this research was to collect data on the foliar late blight resistance of CIP's
95 advanced tetraploid potato clones in Ethiopia and China to inform breeding decisions. To
96 systematically evaluate CIP's breeding materials in diverse target environments we established

97 a trait observation network (TON) of collaborators and assembled a diversity panel that
98 consists of representative advanced clones (including elite materials) from each of CIP's
99 breeding populations. This so-called TON panel was then distributed from Peru to China and
100 Ethiopia, where it was included in a series of trait evaluation experiments by national research
101 and CIP institutions. The specific aims of this study were to (i) identify QTL underlying
102 resistance in and across environments and (ii) develop prediction models to support the global
103 deployment and use of promising resistance sources in local breeding and variety development
104 programs.

105 We report the genotyping, estimation of linkage disequilibrium and population structure of the
106 TON panel and identification of QTL for late blight resistance via genome wide association
107 (GWA). In addition, we present a case for genomics assisted breeding for foliar late blight
108 resistance and show how the use of genomics and pedigree information can be used to select
109 best bet clones for breeding and variety development in diverse target environments.

110

111 **Materials and methods**

112

113 **Germplasm**

114 The TON panel used in this study consisted of 380 genotypes representing seven CIP breeding
115 populations as well as a group of varieties with variable origins (Table 1.). 'Population A' was
116 developed at 1980-1990 with emphasis on late blight resistance. Sources of late blight
117 resistance were improved materials with *S. demissum*-derived resistance from breeding
118 programs around the world, native Andean cultivars *S. tuberosum* groups *andigena*, *phureja*
119 and *stenotomun*, wild species *S. acaule* and *S. bulbocastanum*. 'Population B3' genotypes were
120 derived from 'Population A' with emphasis on increasing frequencies and levels of quantitative
121 resistance to late blight. The 'B1 population' is derived from *S. tuberosum* group *andigena*.

122 The ‘LTVR population’ is characterized mainly for its resistance to the most important virus
123 diseases (PVY, PVX and PLRV), short crop duration, and adaptation to warm environments.
124 The ‘LB-HT’ population combines late blight resistance from the ‘B3 population’ and heat
125 tolerance from North American and European bred varieties and the LTVR population. ‘B3-
126 LTVR’ population contains hybrid genotypes originating from crosses between ‘B3’ and
127 ‘LTVR populations’. The ‘pre-Bred’ population has genotypes that have LB resistance
128 introduced from wild *Solanum* species into the tetraploid background of ‘B3’ or ‘LTVR’. The
129 varieties group consists of a group of potato varieties or key breeding lines: ‘Desiree’,
130 ‘Atlantic’, ‘Spunta’, ‘Granola’, ‘Yungay’, ‘Tomas Condemayta’, ‘DTO-33’, ‘Kufri Yoti’, and
131 ‘Chucmarina’. CIP numbers and the parentage of the 380 genotypes are given in the
132 Supplementary Table S1.

133

134 **Environments**

135 The field sites in Ethiopia and China are important potato production areas, while in the field
136 site in Peru, potato is not the main crop (Table 2). The late blight pathogen populations have
137 been described in each location. In Peru and Ethiopia only the A1 mating type has been
138 identified and different clonal lineages are present that frequently contain virulence to most of
139 the known *S. demissum* *R* genes (Lindqvist-Kreuze et al.; 2019 Mihretu et al., 2019). In contrast
140 in Southern China A2 mating type has been found dominating (Chen et al., 2017).

141

142 **Field trials**

143 Standard protocols at CIP were utilized for planning and conducting the field trials (Bonierbale,
144 2007). The statistical designs in each trial are shown Table 2. Uniform tuber seed was produced
145 centrally in each country following the introduction of *in vitro* plants or mini-tubers from CIP
146 facilities in Peru or Kenya.

147 Late blight resistance was evaluated under endemic disease pressure. The disease level in the
148 plots was recorded as ‘percent leaf area infected’ at 7-day intervals until susceptible controls
149 reached 100% infection. These values were used to calculate the area under the disease progress
150 curve (AUDPC) and relative AUDPC (rAUDPC). The data was collected and processed using
151 the HiDAP field book system (<https://research.cip.cgiar.org/gtdms/hidap/>).

152

153 **Statistical analysis of phenotypic data**

154 From the weekly observations of the disease incidence in the plots, the AUDPC was calculated
155 and the estimated means (BLUEs) were transformed to the relative AUDPC (rAUDPC) to
156 facilitate the comparisons among the different locations. The best linear unbiased predictor
157 (BLUP) and best linear unbiased estimator (BLUE) and values as well as ranked predictors
158 were calculated using ASREML package.

159

160 **Genotyping, variant calling and filtering for association analysis**

161 In total 380 potato clones were genotyped. Library construction and genotyping by genotyping
162 by sequencing (GBS) was outsourced to the Genomics Facility at Cornell University in 2015.
163 The DNA was digested with EcoT221 restriction enzyme and the libraries were 48x
164 multiplexed for sequencing. The diploid calling was by the service provider using the Tassel
165 pipeline (Bradbury et al., 2007). The resulting Variant Call Format (VCF) file was processed
166 with Bcftools (<https://samtools.github.io/bcftools/>) to filter the variants for minimum read
167 depth (RD) of 17, minimum genotype quality (GQ) of 30, and minor allele frequency (MAF)
168 0.03. The SNPs that didn’t pass these criteria were changed to missing call, and finally only
169 the SNP sites that contained less than 30% missing data were selected.

170

171 For polyploid calling the raw FASTQ files were processed with Stacks (Catchen et al., 2013)
172 to remove the barcodes and with TrimGalore <https://github.com/FelixKrueger/TrimGalore> to
173 trim the ends of reads. The reads were aligned to the reference genome version *S.*
174 *tuberosum_448_v4.03* (Sharma et al., 2013) using BWA (Li and Durbin, 2009) and the
175 resulting SAM files were converted to BAM files using Samtools (Li et al., 2009). The variants
176 were called using GATK HaplotypeCaller option (Poplin et al., 2017), disabling the duplicate
177 read filter (this is recommended for GBS data) and joint genotyping using the -ERC GVCF
178 mode. From the VCF files SNP calls were filtered using Bcftools for minimum RD of 61,
179 minimum GQ of 30 and MAF of 0.03. The samples that didn't pass these criteria were changed
180 to missing call, and finally only the SNP sites that contained less than 30% missing data were
181 included in the analysis.

182

183 **Analysis of the Population sub-structuring**

184 Population sub-structuring with tetraploid data was done using PolyRAD (Clark et al., 2019).
185 Only variants in pairwise LD under 0.1 were previously filtered (LD pruning). The diploid
186 dataset was analyzed using SNPrelate (Zheng et al., 2012) using the subset of bi-allelic SNPs,
187 filtering for LD (0.2) MAF (<0.03) and missingness (<0.3).

188

189 **GWA**

190 Marker trait associations were modelled for all the trials independently and using the diploid
191 and the tetraploid marker sets with the GWASpoly package (Rosyara et al., 2016). For the
192 tetraploid dataset *general*, *additive*, *simplex dominant* (1-dom) and *duplex dominant* (2-dom)
193 models were used while for the diploid dataset *diplo-general*, *diplo-additive*, and the *simplex*
194 *dominant* (1-dom) model were used. The parameters used for the GWAS modelling function
195 *GWASpoly* in R were the following: no fixed effects, 4 principal components were included

196 as covariates, a minimum MAF of 0.03 and a maximum genotype frequency (after applying
197 dominance relations) equal to 0.95 were set, and P3D approximation was used. To detect
198 statistical significance, the Bonferroni correction method was used, ensuring the genome-wide
199 type I error is not greater than 0.05. Manhattan plots were generated to display significant SNP
200 in the different genetic models. In addition, Q-Q plots were used to evaluate the goodness of
201 fit of the genetic model and the quality of the phenotypic data.

202 The genomic positions of the resulting SNPs associated with plausible QTL for pathogen
203 resistance in relation to other loci, known genes and QTL, were determined using the *S.*
204 *tuberosum* Group Phureja DM1-3 516R44 (v4.03) pseudomolecule browser
205 (<http://solanaceae.plantbiology.msu.edu/>) available from the Potato Genome Sequence
206 Consortium (PGSC). To obtain an approximate of the physical location of markers for
207 pathogen resistance present in literature, the position in cM was obtained from the GABI
208 Primary Database (<https://www.gabipd.org/projects/Pomamo/>) and then “translated” to an
209 approximate physical position in Mbp using information provided in Sharma et al. (2013) that
210 integrates the potato genome and physical and genetic maps.

211

212 **Results and discussion**

213

214 **Population structure**

215 The tetraploid dataset included a total of 305,345 SNPs after the GATK variant calling, while
216 the diploidized dataset after Tassel pipeline had a SNP count of 312,727. After filtering these
217 datasets, the Principal component analyses based on 23,804 diploid SNPs and 182,435
218 tetraploid variants identified no strong population sub-structuring (Figure 1 for the tetraploid
219 data, Figure S1 for the diploid data) in the diversity panel which makes it an ideal genotype set
220 for GWA. Only population ‘B1’ separates from the rest most likely because the genetic

221 background of the ‘B1’ population is *S. tuberosum* group *andigena*, while the rest are mostly
222 group tuberosum type. ‘LB-HT’ shares alleles with the ‘B3’ population, as expected since these
223 clones are hybrids with B3 clones in their pedigrees. ‘B3’ and ‘LTVR’ population clones are
224 also mostly separated with a few exceptions of clones that may have been mislabelled. ‘B3-
225 LTVR’, which is a hybrid between the two populations and this can be clearly seen in the PCA
226 plot as well. Not surprisingly, Population ‘A’ is intermingled within population ‘B3’ since the
227 ancestors of the ‘B3’ clones were selected clones of the ‘A’ population.

228

229 **SNP sets for GWA**

230 After applying filtering parameters tailored for GWA to all variants in both datasets, the
231 numbers of SNPs were reduced to 3,239 tetraploid SNPs and 55,748 diploid SNPs. The DP
232 thresholds were based on the Matias et al. 2019. The study points out, that assuming the GBS
233 method entails 0.5% allelic error, a minimal RD of 17 is necessary in order to classify simplex
234 tetraploid calls as heterozygous with a 95% accuracy. To annotate the allele dosage with the
235 same accuracy, a much higher RD of 61 is needed. Both sets of filtered SNPs were used in the
236 GWAS to identify trait-linked QTL.

237

238 **Linkage disequilibrium**

239 LD decay was estimated using the tetraploid marker set. A spline was fitted on the 90th
240 percentile of the squared correlation coefficient between the alleles in a pair of markers (r^2)
241 and the physical distance between these pairs of markers on the “short” distance of up to 10
242 Mb (Figure 2A) and “long” distance up to 80 Mb (Figure 2B) over all chromosomes. The
243 intersection of a defined significance threshold of $r^2=0.1$ and the fitted spline allowed us to
244 estimate the short distance vs long distance LD decay. On the short distance the threshold is
245 reached at 2Mb, while on the long distance it is reached at 5.5Mb. Considering the short

246 distance LD-decay estimate of $r^2_{1/2\max, 90}$, which was suggested as the most consistent estimator
247 for LD decay in potato by Vos et al (2017), we obtain the $r^2_{1/2\max, 90}$ value of 0.55 Mb. This $r^2_{1/2\max, 90}$
248 value is equivalent in Vos (2017) data for recent European potato varieties (0.6 Mb)
249 and a bit lower than the study of Sharma et al., (2018) where the $r^2_{1/2\max, 90}$ value was 0.91 Mb.
250 The average r^2 for the short distance in our dataset was 0.091, which is a bit lower than the
251 average r^2 (0.19-0.22) reported for the European varieties (Vos et al., 2017), indicating that
252 there were probably more founder haplotypes in our diversity panel than in the European
253 pooled varieties. The LD decay estimated was moderate, and comparable to the LD decay
254 found in the European potato germplasm. Estimates based on the average r^2 of the markers
255 along the short distance suggest that high diversity is retained in the germplasm and that tens
256 of thousands of markers would be needed to cover the entire tetraploid genome.

257

258 **Late blight resistance**

259 There was a high number of genotypes with rAUDPC values comparable to the resistant control
260 genotype which is released as a variety called Chucmarina in Peru and as Belete in Ethiopia
261 (Figure 3). Notably, most of the genotypes tested in China were more resistant than the local
262 variety C-88 that has been popular because of its good late blight resistance.

263 In this research project over 300 advanced tetraploid clones from CIP were shared with
264 partners, but due to various reasons not all were evaluated in all environments. The genotypes
265 can only be internationally distributed as *in vitro* plants with a health certificate. After receiving
266 the plants, there needs to be at least two rounds of multiplication involving either cuttings or
267 tubers to obtain seed for the replicated trials. However, the performance of all genotyped clones
268 and their pedigree parents could be estimated in all environments by incorporating the marker
269 data into the mixed model.

270 The GGE biplot for predicted values (BLUP) and marker-based kinship matrix shows the
271 performance of the genotypes and some of their parents in all environments (Figure 4). The
272 most resistant genotypes belong to the B3 and B3-HT populations, while only a few from the
273 LTVR and B3-LTVR had high level of resistance. From this figure, we evidenced that some
274 genotypes' resistance to late blight is environment specific, nevertheless several genotypes
275 show stable resistance across environments. The correlations among environments were high
276 (Figure 5). Particularly the environment in Peru is highly correlated with all the other
277 environments suggesting that resistant clones selected in Peru will also likely have good
278 resistance in these other environments.

279 CIP's breeding strategy defined in the 1990s focused on improving the quantitative resistance
280 in the B3 population by phenotypic recurrent selection under endemic pressure from the "new
281 population" of *P. infestans* in the Peruvian Andes supplemented by progeny tests to identify
282 parents with good general combining ability and eliminate those resulting in segregation for
283 hypersensitive response against the test isolates. The pathogen population in this area is
284 dominated by the A1 mating type and EC-1 clonal lineage, which is highly aggressive and
285 complex in its virulence (Lindqvist-Kreuze et al., 2019). Despite the differences in the
286 pathogen populations in terms of the mating type and clonal lineages among the countries it
287 seems that phenotypic selection for late blight resistance in Peru was largely successful and
288 results transferable across the three environments tested here.

289

290 **QTL for late blight resistance**

291 Several SNPs were significantly associated with late blight resistance in the field trials with a
292 total of 16 markers tagging possible QTL (Table 3 and Table 4). In the tetraploid data, 6
293 markers for late blight resistance were found in chromosomes III, V and IX while in the diploid
294 dataset 14 markers on chromosomes 0, III, V, VI, IX and X were associated with the resistance

295 phenotype. Populations of *P. infestans* are diverse and there is a trend of increasing diversity
296 in potato-growing regions worldwide (Cooke and Lees, 2004). Taking this into account, the
297 markers on chromosome IX could indicate a QTL for broad resistance not specific to regional
298 late blight strains, because the QTL was observed in data from trials in Peru and China, while
299 markers associated to the QTL on chromosomes III, V and VI were found with the data of
300 unique locations (Table 3 and Table 4). For example, the neighbouring SNPs on chromosome
301 III, could be indicating a QTL particularly responsible for resistance against late blight strains
302 specific to Holeta, Ethiopia. On the other hand, the marker on chromosome X found in the
303 diploidized data could indicate a QTL for broad resistance having been observed in data
304 collected in Peru as well as in China (Table 4). The highest number of SNPs associated to late
305 blight resistance in the GWAS were mapped between 59 and 61.2 Mbp of chromosome IX. All
306 mapped to the end of the long arm of the chromosome, in a region that had been previously
307 associated with late blight resistance in Peru (Lindqvist-Kreuze et al., 2014). Additionally, the
308 markers were within or surrounding the segment between 59.3 and 61.0 Mbp that forms a large
309 cluster of putative resistance genes. For example, the locus PGSC0003DMG400020587
310 encodes a homolog of *Rpi-vnt1* (Mosquera et al., 2015), a major gene for resistance to *P.*
311 *infestans* that has been previously cloned and characterized in the wild potato species *Solanum*
312 *venturii* (Pel et al., 2009; Foster et al., 2009).

313 A few markers for late blight resistance QTL have been found in the past on chromosome III.
314 These include a QTL tagged between the markers GP25 and CP6 (Gebhardt and Valkonen,
315 2001) which can be located near the locus PGSC0003DMB000000154 or approx. between 42
316 and 51 Mbp in the Phureja DM1-3 genome. The SNPs 3_45458723, 3_45458753 and
317 3_45458754 found in the diploidized dataset mapped close to this QTL. These markers are
318 located within a WREBP-2 protein / transcription factor IIIA gene
319 (PGSC0003DMG400009082). Marker 3_3319097 is localized within a gene encoding an iron

320 binding oxidoreductase (PGSC0003DMG40002252) that is located near an already known
321 QTL tagged with marker T6135 (Gebhardt and Valkonen, 2001).

322 Several late blight resistance genes originated from *Solanum demissum* have been already
323 mapped to specific positions of the genome. These include *R1* in chromosome V, *R3*, *R6* and
324 *R7*, all in the distal segment of chromosome XI and *R2* in chromosome IV. Also, the genes
325 *Rber* and *Rblc* belonging to other *Solanum* groups have been mapped to chromosomes X and
326 VIII, respectively. These genes show resistance to contemporary races of *Phytophthora*
327 *infestans*. Additionally, promising QTL are thought to be located on chromosomes III, IV, V
328 and VI (Gebhardt and Valkonen 2001). The region with *R1* and QTL for late blight resistance
329 in chromosome V is flanked by the markers GP21 and GP179 approximately between 2 and 5
330 Mbp in the DM genome containing the SNPs 5_4260524 and 5_5572873 in the tetraploid and
331 the diploid dataset, respectively (Table 3, 4). The SNP 10_51544544 found on chromosome X
332 in the diploid dataset and associated with resistance in three experiments (Table 4), is mapped
333 to a region associated with late blight resistance conferred by gene *Rber*, tagged by the marker
334 TG63 is located approximately at 52 Mbp in the DM genome.

335 The SNP 6_45694949 found on chromosome VI, mapped to a physical position around 45.7
336 Mbp, is located near a gene and two flanking QTL that have been recently associated with
337 quantitative late blight resistance. Álvarez et al. (2017) used association mapping to identify
338 SNPs in genes from a set of candidate genes in *Solanum tuberosum* group Phureja associated
339 with quantitative resistance. The gene expresses a stem 28 kDa glycoprotein and is located
340 around 49.1 Mbp between the Ib6a and Pin6b – lb6b QTL. The favourable allele of this SNP
341 has a significant effect on the resistance in Yunnan in 2015 and 2016, and an additive effect
342 since the individuals homozygous for the favourable allele are more resistant than the
343 heterozygous individuals (Figure 6).

344

345 The 48x plex multiplexing of the samples during the sequencing and stringent filtering for
346 minimum read depth in all samples yielded relatively few SNP (less than 4K), which is too few
347 considering the level of LD decay-based estimate of 10s of thousands SNP to fully cover the
348 genome. Therefore, the GWA was done using both tetraploid and the diploidized data. Three of
349 the markers (9_58779951, 9_59967523, 9_60067335) map in chromosome 9 in the same
350 chromosome region previously found associated with late blight resistance in Peru (Lindqvist-
351 Kreuze et al., 2014; Li et al., 2010). These markers are physically separated in the DM genome
352 by 1.3Mb, which fits the estimate for the LD decay in these potato genotypes. In the QTL
353 dPI09c reported by Li et al. (2010) the R8 gene originating from *Solanum demissum* was
354 recently identified (Jian Rui et al., 2018). The QTL dPI09c interval in potato DM1-3 516 R44
355 (Potato Genome Sequencing Consortium, 2011) begins at 60615044 bp, hence over 600Mbp
356 away from the nearest GBS marker (9_60067335) we identified in the current research. In our
357 tetraploid GBS marker set there are no SNP mapping in the dPI09c interval possibly because
358 of the low sequencing depth and the complexity of the region that consists of several RXLR
359 type resistance genes (Jiang Rui et al., 2018). In the diploid marker set, however, four markers
360 (9_60067335, 9_61106174, 9_61108928, 9_61261167) that map in the QTL dPI09c interval
361 were identified.

362

363 **Conclusions**

364

365

366 **Acknowledgements**

367

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373 bioinformatic analysis and to Janet Higgins at EI for the bioinformatics support.

374

375 **Contributions:**

376 Designed experiments and obtained funding: HLK, MB

377 Implemented field trials and collected data: MG, XL, JQ, GW, BH, ZP, QS, KN, IS

378 Analyzed and interpreted data: HLK, DG, BDB, PU

379 Bioinformatics: HLK, JDV, DG

380 Statistics: BDB

381 Wrote the manuscript: HLK, PU, MB

382

383

384

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533 **Table 1.** Contribution of CIP breeding populations to the TON diversity panel

534

Breeding population	Genotypes evaluated	main breeding objective
A	13	late blight resistance
B1	11	late blight resistance
B3	100	late blight resistance
B3-HT	37	late blight resistance, heat tolerance
B3-LTVR	25	Hybrid population combining late blight resistance, heat tolerance, virus resistance
LTVR	186	virus resistance, heat tolerance, drought tolerance, salinity tolerance
PREBRED	2	late blight resistance
VARIETY	6	varied
Grand Total	380	

535

536

537 **Table 2.** Description of the phenotypic evaluations involving the TON panel clones.

Country	Location	Year	number of genotypes evaluated (statistical design)	checks
Peru	Pasco, Oxapampa 10.5853°S, 75.4053°W	2014	241 (RCBD)	Chucmarina Unica Tomas Desiree
China	Yunnan, Kunming 24.8801°N, 102.8329°E	2015	306 (RCBD)	Chucmarina C-88
		2016	336 (RCBD)	Unica Desiree
Ethiopia	Oromia, Holetta 9.0633°N, 38.4902°E	2017	60 (RCBD)	Belete Gudene Unica
		2016	128 (Augmented)	Gudene Belete Unica Tomas

538

539

540 **Table 3.** Markers tagging QTL for late blight resistance with the general, additive and 1-
541 dominance models of GWASpoly and tetraploid SNP.

Marker (chromosome followed by position)	Ref	Alt	Trait	Model	Threshold	Score	Effect
0_36073482	G	A	Oxa2014	general	4.71	8.64	NA
				additive	4.78	8.64	-0.18
				1-dom-alt	4.71	8.64	-0.18
			Yun2015	general	4.74	20.21	NA
				additive	4.78	20.21	-0.29
				1-dom-alt	4.71	20.21	-0.29
			Yun2016	general	4.75	19.37	NA
				additive	4.78	19.37	-0.25
				1-dom-alt	4.71	19.37	-0.25
3_3319097	A	T	Hol2017	general	4.49	5.83	NA
				1-dom-alt	4.71	6.05	0.43
5_4260524	A	T	Yun2016	1-dom-alt	4.71	5.01	0.14
9_58779951	G	A	Oxa2014	additive	4.78	4.84	-0.11
				1-dom-alt	4.71	5.52	-0.13
				Yun2015	general	4.74	4.94
			Yun2015	1-dom-alt	4.71	5.92	-0.14
				Yun2016	1-dom-alt	4.71	4.77
9_59967523	A	T	Yun2015	general	4.74	7.3	NA
				additive	4.78	6.94	-0.14
				1-dom-alt	4.71	8.18	-0.17
			Yun2016	general	4.75	7.76	NA
				additive	4.78	8.29	-0.13
				1-dom-alt	4.71	8.38	-0.15
9_60067335	A	G	Hol2016	1-dom-alt	4.71	4.81	-0.22
			Oxa2014	general	4.71	11.11	NA
				additive	4.78	11.64	-0.2
				1-dom-alt	4.71	12.1	-0.21
			Yun2015	general	4.74	19.39	NA
				additive	4.78	18.99	-0.26
				1-dom-alt	4.71	20.31	-0.28
			Yun2016	general	4.75	16.53	NA
				additive	4.78	17.26	-0.22
1-dom-alt	4.71	17.59		-0.23			

542

543

544 **Table 4.** Markers tagging QTL for late blight resistance with the diplo-general, diplo-additive
545 and 1-dominance models of GWASpoly and diploid SNP.

546

Marker (chromosome followed by position)	Ref	Alt	Trait	Model	Threshold	Score	Effect
0_36073482	G	A	Oxa2014	diplo-general	6	10.27	NA
				diplo-additive	6.03	10.27	-0.2

				1-dom-alt	6.02	10.27	-0.2
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.31
				1-dom-alt	6.02	25.69	-0.31
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.27
				1-dom-alt	6.02	25.69	-0.27
3_45458723	A	C	Hol2017	diplo-general	5.94	25.69	NA
				diplo-additive	6.02	25.69	0.47
				1-dom-alt	6.02	25.69	0.47
3_45458753	G	A	Hol2017	diplo-additive	6.02	25.69	0.47
				1-diplo-alt	6.02	25.69	0.47
3_45458754	A	T	Hol2017	diplo-additive	6.02	25.69	0.47
				1-diplo-alt	6.02	25.69	0.47
5_5572873	G	A	Oxa2014	diplo-additive	6.03	25.69	0.17
				1-diplo-alt	6.02	25.69	0.17
6_45694949	G	A	Yun2015	diplo-general	6.01	25.69	NA
				1-dom-alt	6.02	25.69	-0.15
			Yun2016	diplo-general	6.02	25.69	NA
				1-dom-alt	6.02	25.69	-0.13
9_58779951	G	A	Oxa2014	diplo-general	6	25.69	NA
				diplo-additive	6.03	25.69	-0.17
				1-dom-alt	6.02	25.69	-0.17
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.18
				1-dom-alt	6.02	25.69	-0.18
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.15
				1-dom-alt	6.02	25.69	-0.15
9_59967523	A	T	Oxa2014	diplo-general	6	25.69	NA
				diplo-additive	6.03	25.69	-0.14
				1-dom-alt	6.02	25.69	-0.14
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.21
				1-dom-alt	6.02	25.69	-0.21
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.19
				1-dom-alt	6.02	25.69	-0.19
9_59997331	T	C	Oxa2014	diplo-general	6	25.69	NA
				diplo-additive	6.03	25.69	-0.17
				1-dom-alt	6.02	25.69	-0.17
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.25
				1-dom-alt	6.02	25.69	-0.25
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.21
				1-dom-alt	6.02	25.69	-0.21
9_60067335	A	G	Oxa2014	diplo-general	6	25.69	NA
				diplo-additive	6.03	25.69	-0.23
				1-dom-alt	6.02	25.69	-0.23
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.32
				1-dom-alt	6.02	25.69	-0.32
			Yun2016	diplo-general	6.02	25.69	NA

				diplo-additive	6.03	25.69	-0.26
				1-dom-alt	6.02	25.69	-0.26
9_61106174	C	T	Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.14
				1-dom-alt	6.02	25.69	-0.14
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.14
				1-dom-alt	6.02	25.69	-0.14
9_61108928	T	G	Oxa2014	diplo-additive	6.03	25.69	-0.12
				1-dom-alt	6.02	25.69	-0.12
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.17
				1-dom-alt	6.02	25.69	-0.17
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.14
				1-dom-alt	6.02	25.69	-0.14
			9_61261167	A	C	Oxa2014	diplo-general
diplo-additive	6.03	25.69					-0.21
1-dom-alt	6.02	25.69					-0.23
Yun2015	diplo-general	6.01				25.69	NA
	diplo-additive	6.03				25.69	-0.3
	1-dom-alt	6.02				25.69	-0.32
Yun2016	diplo-general	6.02				25.69	NA
	diplo-additive	6.03				25.69	-0.25
	1-dom-alt	6.02				25.69	-0.26
10_51544544	A	G	Oxa2014	diplo-general	6	25.69	NA
				diplo-additive	6.03	25.69	-0.22
				1-dom-alt	6.02	25.69	-0.22
			Yun2015	diplo-general	6.01	25.69	NA
				diplo-additive	6.03	25.69	-0.3
				1-dom-alt	6.02	25.69	-0.3
			Yun2016	diplo-general	6.02	25.69	NA
				diplo-additive	6.03	25.69	-0.27
				1-dom-alt	6.02	25.69	-0.27

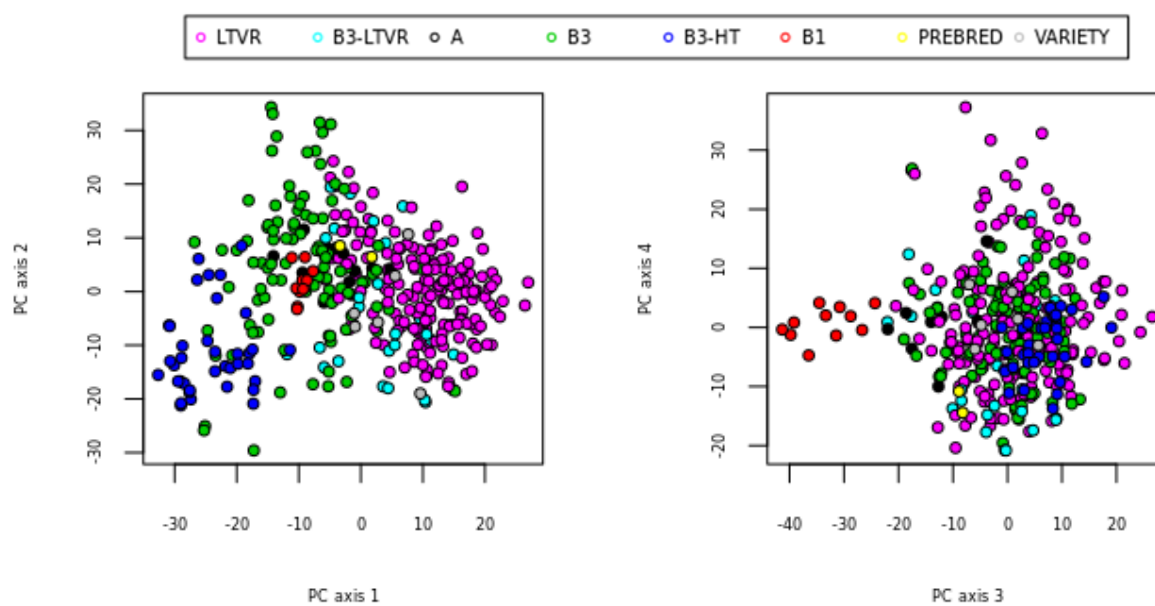
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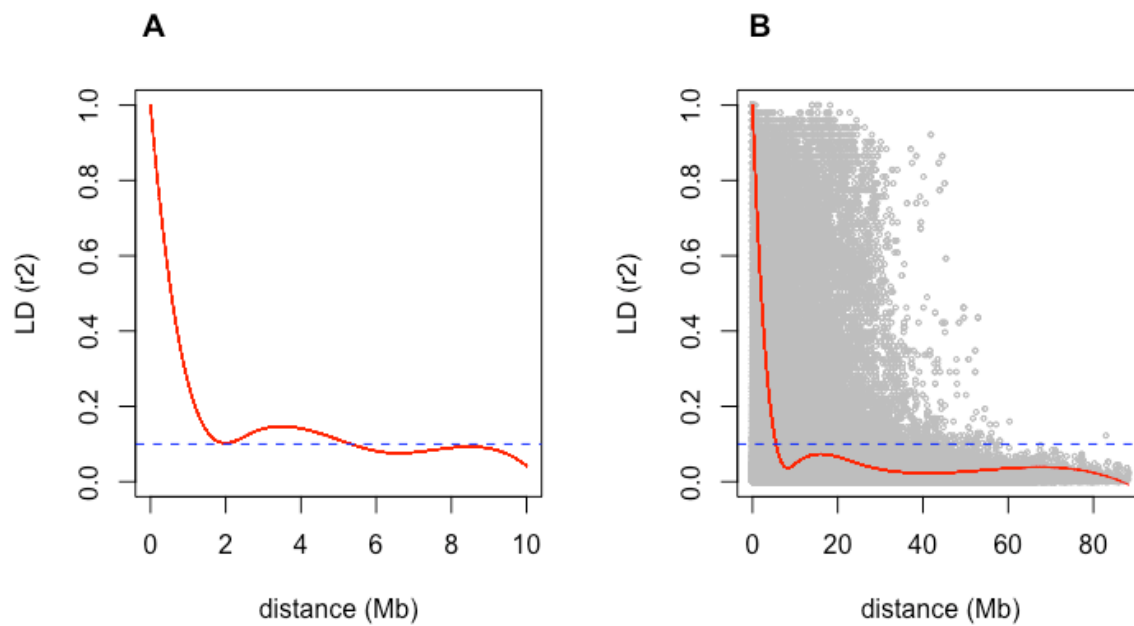
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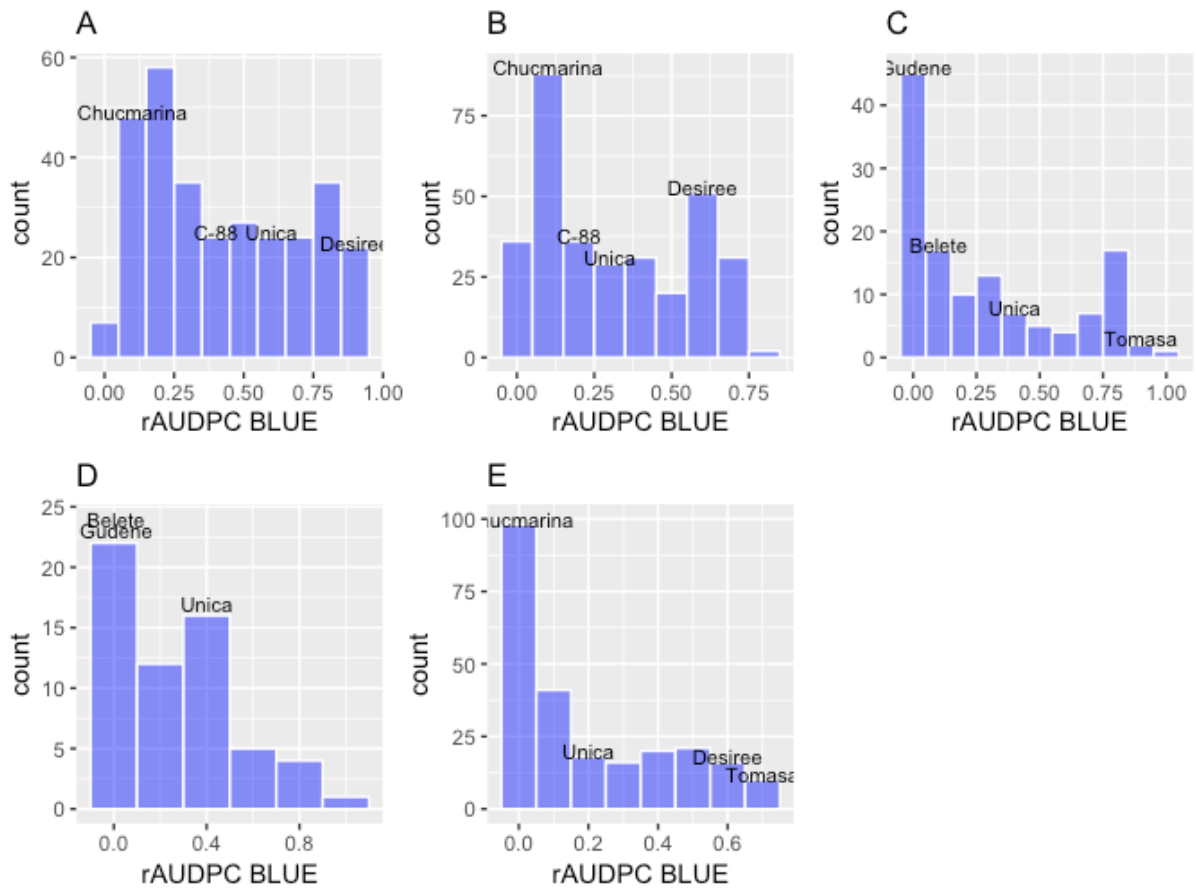


552 **Figure 1.** Population sub-structuring based on polyRAD estimation of genotype probabilities

553

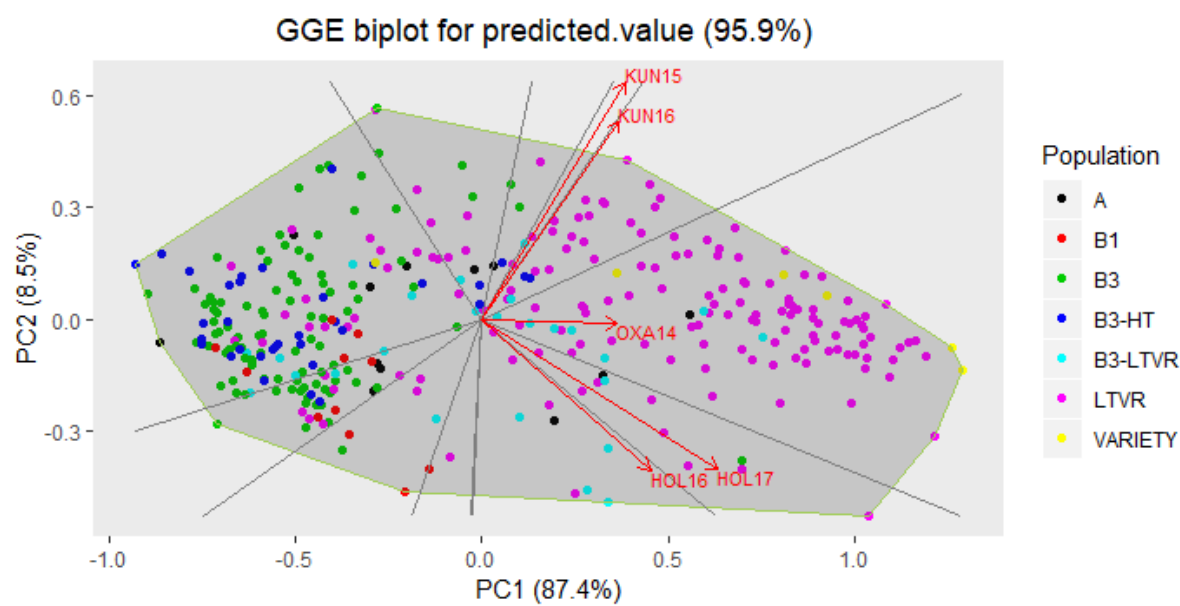


554 **Figure 2.** Linkage disequilibrium (LD) estimated in the TON panel based on Pearson
555 correlation coefficient (r^2) plotted against the physical map distance (Mb) between pairs of
556 SNP.



557 **Figure 3.** Histograms of rAUDPC values in Kunming, China in 2015(A) and in 2016 (B),
558 Holeta, Ethiopia in 2016 (C) and 2017 (D), and Oxapampa, Peru at 2014 (E). The control
559 genotypes (checks) in each trial are indicated in the plots based on their rAUDPC value.

560



561

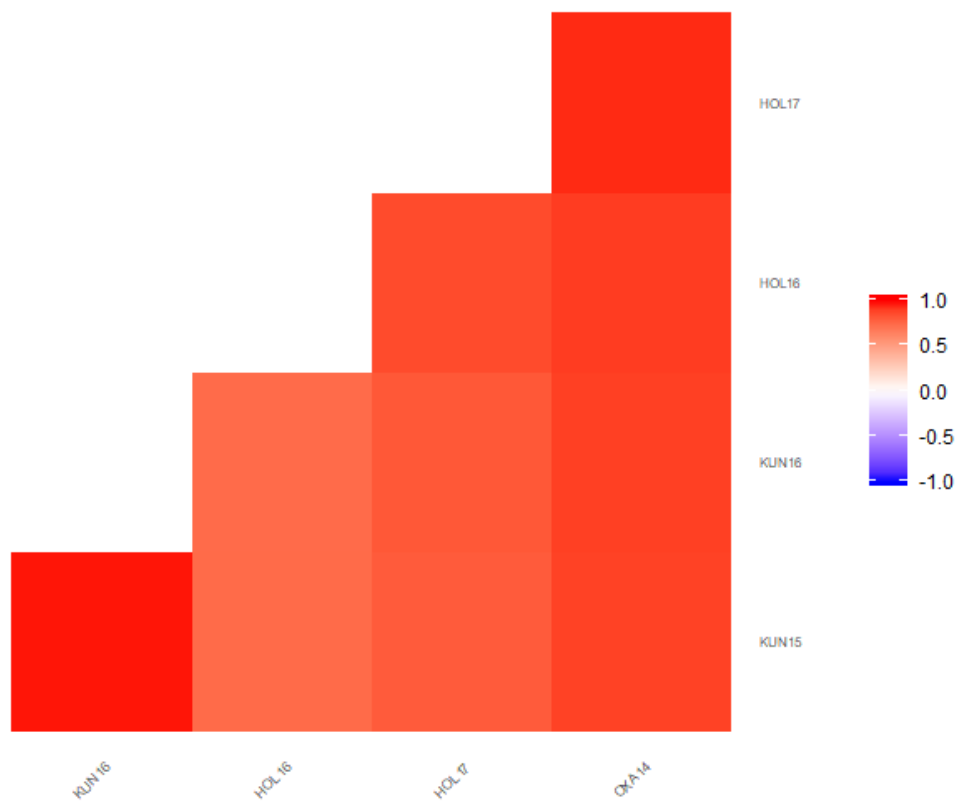
562 **Figure 4.** GGE biplot for predicted performance (based on BLUP and genetic kinship matrix)

563 of the test genotypes and their parents in Kunming 2015 (KUN15) and 2016 (KUN16),

564 Oxapampa 2014 (OXA14), Holetta 2016 (HOL16) and 2017 (HOL17).

565

Correlations of environments for predicted.value



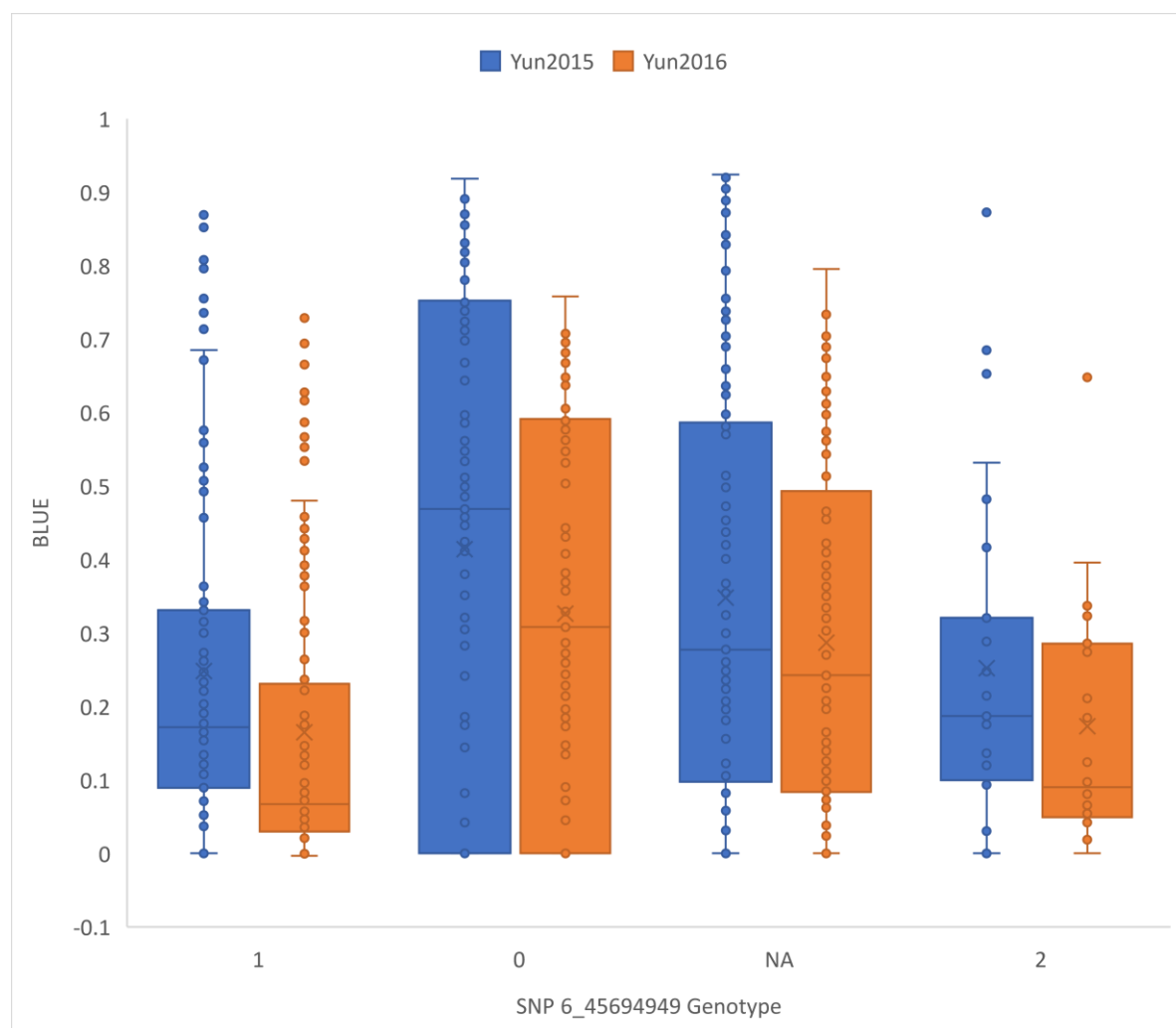
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568

569 **Figure 5.** Heat-plot on the correlations among the different trials.

570



571

572 **Figure 6.** Boxplot for BLUE value distribution in the different genotype classes for the SNP
573 6_45694949 found in the diploidized dataset. “0” and “2” stand for homozygous for the
574 reference and alternative alleles respectively. “1” indicates heterozygote and “NA”, missing
575 genotype. Lower values indicate a higher resistance.

576

577 **Table S1.** Population denominations, and parentage of the potato genotypes evaluated in this
 578 study.
 579

population	CIP code	female parent	male parent
A	CIP384866.5	376724.1=(85LB70.5)	BULK PRECOZ
A	CIP381379.12	378356.895	PRECOZ BULK
A	CIP381381.9	378493.915	PRECOZ BULK
A	CIP381381.13	378493.915	PRECOZ BULK
A	CIP381403.16	378507.833	BULK
A	CIP381178.14	378943.565	PHY BULK
A	CIP384321.3	380479.15	BULK 3
A	CIP391691.96	381381.9	LB-CUZ.1
A	CIP387224.11	382121.25	676008=(I-1039)
A	CIP374080.5	801013=(MEX 72 =I-1058)	700764=(Casa Blanca EE-2010)
A	CIP380011.12	GRETA	SEEDLINGS 79 BULK
A	CIP380496.6	INDIA-1058 B	XY BULK
A	CIP377744.1	M-1266-14 MEX	374035.1
B1	CIP399053.15	395230.1	395322.11
B1	CIP399067.22	395257.2	395271.6
B1	CIP399075.32	395266.2=(B1C4046.2)	395282.3=(B1C4062.3)
B1	CIP399075.7	395266.2=(B1C4046.2)	395282.3=(B1C4062.3)
B1	CIP399078.11	395266.3=(B1C4046.3)	395260.8=(B1C4040.8)
B1	CIP399048.24	395272.2	395257.6
B1	CIP399079.22	395274.1	395257.6
B1	CIP399085.17	395296.2=(B1C4076.2)	395256.1=(B1C4036.1)
B1	CIP399085.30	395296.2=(B1C4076.2)	395256.1=(B1C4036.1)
B1	CIP399083.4	395296.2=(B1C4076.2)	395247.1=(B1C4027.1)
B1	CIP399085.23	395296.2=(B1C4076.2)	395256.1=(B1C4036.1)

B3	CIP389746.2	381379.9	386614.16=(XY.16)
B3	CIP393220.54	381400.22	387170.9
B3	CIP387164.4	382171.1	575049=(CEW-69-1)
B3	CIP391046.14	386209.1	387338.3
B3	CIP391047.34	386209.1	387338.3
B3	CIP393228.67	386209.1	387170.9
B3	CIP391002.6	386209.1	386206.4
B3	CIP393227.66	386209.1	381400.22
B3	CIP391583.25	386209.15	387170.9
B3	CIP392617.54	387002.11	387170.9
B3	CIP393248.55	387002.11	386614.16=(XY.16)
B3	CIP393242.50	387002.11	381400.22
B3	CIP391580.30	387002.2	387214.9
B3	CIP393079.4	387004.13	390357.4
B3	CIP393079.24	387004.13	390357.4
B3	CIP391004.18	387004.4	386206.4
B3	CIP393284.39	387015.12	387170.9
B3	CIP393073.179	387015.13	389746.2
B3	CIP393073.197	387015.13	389746.2
B3	CIP393280.82	387015.3	386316.14=(XY.14)
B3	CIP393280.64	387015.3	386316.14=(XY.14)
B3	CIP393280.57	387015.3	386316.14=(XY.14)
B3	CIP391011.17	387041.12	386206.4
B3	CIP391585.179	387132.2	387170.9
B3	CIP391585.5	387132.2	387170.9
B3	CIP392633.64	387132.2	387334.5
B3	CIP392634.49	387136.14	387170.9
B3	CIP392634.52	387136.14	387170.9
B3	CIP392637.10	387143.22	387170.9

B3	CIP392637.27	387143.22	387170.9
B3	CIP392639.34	387143.22	387334.5
B3	CIP393339.242	387164.4	SANI IMILLA
B3	CIP393371.157	387170.16	389746.2
B3	CIP393371.58	387170.16	389746.2
B3	CIP393371.164	387170.16	389746.2
B3	CIP393371.159	387170.16	389746.2
B3	CIP391058.175	387170.16	387338.3
B3	CIP393349.68	387170.6	387338.3
B3	CIP392650.12	387181.7	387170.9
B3	CIP393382.44	387205.5	387338.3
B3	CIP393385.47	387231.7	387170.9
B3	CIP393385.39	387231.7	387170.9
B3	CIP393399.7	387303.71	387338.3
B3	CIP393075.54	387315.27	389746.2
B3	CIP393083.2	387315.27	390357.4
B3	CIP393084.31	387326.27	390357.4
B3	CIP392657.171	387341.1	387170.9
B3	CIP392657.8	387341.1	387170.9
B3	CIP393077.159	387348.2	389746.2
B3	CIP391065.81	387348.2	387338.3
B3	CIP393077.54	387348.2	389746.2
B3	CIP393085.5	387348.2	390357.4
B3	CIP391065.69	387348.2	387338.3
B3	CIP396008.104	391002.15	393382.64
B3	CIP396004.263	391002.6	393382.64
B3	CIP396004.225	391002.6	393382.64
B3	CIP396004.337	391002.6	393382.64
B3	CIP396012.266	391004.1	393280.58

B3	CIP396009.240	391004.4	393280.58
B3	CIP396009.258	391004.4	393280.58
B3	CIP395037.107	391004.4	391679.12
B3	CIP396018.241	391046.14	393280.58
B3	CIP396023.109	391047.34	393280.57
B3	CIP396244.12	391580.3	392633.1
B3	CIP395077.12	391586.109	393053.6
B3	CIP395109.29	391589.26	393079.4
B3	CIP395109.34	391589.26	393079.4
B3	CIP395112.19	391686.15	393079.4
B3	CIP395112.32	391686.15	393079.4
B3	CIP395112.6	391686.15	393079.4
B3	CIP395112.36	391686.15	393079.4
B3	CIP395111.13	391686.5	393079.4
B3	CIP396027.205	392633.23	393382.64
B3	CIP396026.101	392633.4	393280.64
B3	CIP396026.103	392633.4	393280.64
B3	CIP395084.9	392633.6	393053.6
B3	CIP396031.119	392633.64	393382.64
B3	CIP396031.108	392633.64	393382.64
B3	CIP396241.4	392634.52	392626.9
B3	CIP396033.102	392639.53	393382.64
B3	CIP395169.17	392652.8	391679.12
B3	CIP396034.268	393042.5	393280.64
B3	CIP396034.103	393042.5	393280.64
B3	CIP395123.6	393046.7	393079.4
B3	CIP396036.201	393077.51	393382.64
B3	CIP396038.101	393077.54	393280.64
B3	CIP396037.215	393077.54	393382.64

B3	CIP396038.107	393077.54	393280.64
B3	CIP396038.105	393077.54	393280.64
B3	CIP395015.6	393083.2	391679.12
B3	CIP395017.14	393085.13	392639.8
B3	CIP395017.229	393085.13	392639.8
B3	CIP395017.242	393085.13	392639.8
B3	CIP395017.227	393085.13	392639.8
B3	CIP395011.2	393085.5	392639.8
B3	CIP395096.2	393085.5	393053.6
B3	CIP396240.2	393371.58	391679.12
B3	CIP396240.23	393371.58	391679.12
B3	CIP396043.226	393401.55	393280.57
B3	CIP396046.105	TXY.4	393280.64
B3-HT	CIP398180.612	392657.171	392633.64
B3-HT	CIP398180.289	392657.171	392633.64
B3-HT	CIP398180.292	392657.171	392633.64
B3-HT	CIP398180.253	392657.171	392633.64
B3-HT	CIP398180.144	392657.171	392633.64
B3-HT	CIP398193.650	393077.54	392633.64
B3-HT	CIP398192.213	393077.54	392633.54
B3-HT	CIP398190.735	393077.54	392639.2
B3-HT	CIP398190.112	393077.54	392639.2
B3-HT	CIP398192.41	393077.54	392633.54
B3-HT	CIP398192.592	393077.54	392633.54
B3-HT	CIP398190.571	393077.54	392639.2
B3-HT	CIP398190.615	393077.54	392639.2
B3-HT	CIP398190.404	393077.54	392639.2
B3-HT	CIP398190.530	393077.54	392639.2
B3-HT	CIP398193.553	393077.54	392633.64

B3-HT	CIP398193.158	393077.54	392633.64
B3-HT	CIP398190.605	393077.54	392639.2
B3-HT	CIP398192.553	393077.54	392633.54
B3-HT	CIP398190.200	393077.54	392639.2
B3-HT	CIP398190.523	393077.54	392639.2
B3-HT	CIP398201.510	393242.5	392633.64
B3-HT	CIP398203.509	393280.82	392633.64
B3-HT	CIP398098.65	393371.58	392639.31
B3-HT	CIP398208.58	393371.58	392633.64
B3-HT	CIP398208.33	393371.58	392633.64
B3-HT	CIP398098.205	393371.58	392639.31
B3-HT	CIP398208.219	393371.58	392633.64
B3-HT	CIP398208.670	393371.58	392633.64
B3-HT	CIP398098.231	393371.58	392639.31
B3-HT	CIP398098.203	393371.58	392639.31
B3-HT	CIP398098.570	393371.58	392639.31
B3-HT	CIP398208.704	393371.58	392633.64
B3-HT	CIP398098.119	393371.58	392639.31
B3-HT	CIP398208.29	393371.58	392633.64
B3-HT	CIP398208.505	393371.58	392633.64
B3-HT	CIP398208.620	393371.58	392633.64
B3-LTVR	CIP301056.54	385205.5	393613.2=(TXY.2)
B3-LTVR	CIP301037.85	387205.5	702853=(LOP-868)
B3-LTVR	CIP301045.74	387205.5	391207.2=(LR93.050)
B3-LTVR	CIP301024.14	388615.22=(C91.640)	387170.9
B3-LTVR	CIP301024.95	388615.22=(C91.640)	387170.9
B3-LTVR	CIP301026.23	389746.2	BOGNA
B3-LTVR	CIP301041.26	389746.2	LOP-886
B3-LTVR	CIP301055.53	389746.2	393617.1=(TXY.11)

B3-LTVR	CIP301023.15	391180.6=(C90.266)	387170.9
B3-LTVR	CIP301044.36	392025.7=(LR93.221)	LOP-886
B3-LTVR	CIP396063.1	392633.1	TXY.12
B3-LTVR	CIP396063.16	392633.1	TXY.12
B3-LTVR	CIP396180.22	392633.6	393615.6=(TXY.6)
B3-LTVR	CIP396268.9	392639.34	393613.2=(TXY.2)
B3-LTVR	CIP396272.18	392639.34	TXY.12
B3-LTVR	CIP396268.1	392639.34	393613.2=(TXY.2)
B3-LTVR	CIP396272.21	392639.34	TXY.12
B3-LTVR	CIP396272.12	392639.34	TXY.12
B3-LTVR	CIP396272.2	392639.34	TXY.12
B3-LTVR	CIP396272.37	392639.34	TXY.12
B3-LTVR	CIP396273.48	393220.54	TXY.12
B3-LTVR	CIP396269.16	393371.58	393613.2=(TXY.2)
B3-LTVR	CIP396269.14	393371.58	393613.2=(TXY.2)
B3-LTVR	CIP301029.18	C97.255	C95.397
B3-LTVR	CIP301040.63	UNICA	702853=(LOP-868)
LTVR	CIP394899.5	28.68	C90.205
LTVR	CIP394898.13	28.68	BWH-87.344R
LTVR	CIP385558.2	32) 2	NT 91.002
LTVR	CIP394901.2	34.73	393617.1=(TXY.11)
LTVR	CIP394900.1	34.73	BWH-87.344R
LTVR	CIP392285.72	36.14	382157.3
LTVR	CIP379706.27	377257.1=(LT-1)	PVX + PVY BULK
LTVR	CIP388676.1	378015.18	PVY-BK
LTVR	CIP385561.124	38) 8	ML 91.007
LTVR	CIP391180.6	385305.1=(XY.9)	378017.2=(LT-7)
LTVR	CIP388972.22	386316.1=(XY.20)	377964.5

LTVR	CIP397079.6	386768.10=(MARIA TAMBEÃ'A)	392820.1=(C93.154)
LTVR	CIP397079.26	386768.10=(MARIA TAMBEÃ'A)	392820.1=(C93.154)
LTVR	CIP392797.22	387521.3	APHRODITE
LTVR	CIP303381.30	388611.22=(C91.612)	676008=(I-1039)
LTVR	CIP395434.1	388611.22=(C91.612)	N93.067
LTVR	CIP394600.52	388611.22=(C91.612)	388972.22=(C89.315)
LTVR	CIP395192.1	388611.22=(C91.612)	C92.044
LTVR	CIP395195.7	388611.22=(C91.612)	C92.167
LTVR	CIP397044.25	388611.22=(C91.612)	391180.6=(C90.266)
LTVR	CIP395193.6	388611.22=(C91.612)	C92.030
LTVR	CIP303381.106	388611.22=(C91.612)	676008=(I-1039)
LTVR	CIP397197.9	388615.22=(C91.640)	388972.22
LTVR	CIP304345.102	388615.22=(C91.640)	676008=(I-1039)
LTVR	CIP395432.51	388615.22=(C91.640)	C92.030
LTVR	CIP397039.53	388615.22=(C91.640)	388972.22=(C89.315)
LTVR	CIP395436.8	388615.22=(C91.640)	388615.22=(C91.640)
LTVR	CIP397039.51	388615.22=(C91.640)	388972.22=(C89.315)
LTVR	CIP392759.1	388676.1=(Y84.027)	PENTLAND CROWN
LTVR	CIP397006.18	389468.3=(92.119)	88.052
LTVR	CIP397067.2	390663.8=(C91.628)	392820.1=(C93.154)
LTVR	CIP300101.11	390674.33=(95.303)	387170.9
LTVR	CIP397065.2	391180.6=(C90.266)	392820.1=(C93.154)
LTVR	CIP397065.28	391180.6=(C90.266)	392820.1=(C93.154)
LTVR	CIP399101.1	391213.1	388972.22
LTVR	CIP300066.11	391382.18=(95.108)	392820.1=(C93.154)
LTVR	CIP300065.4	391382.18=(95.108)	387170.9
LTVR	CIP397098.12	391533.1=(LR93.060)	391207.2=(LR93.050)

LTVR	CIP397012.20	391846.5=(LR93.309)	88.052
LTVR	CIP397012.22	391846.5=(LR93.309)	88.052
LTVR	CIP397078.12	391846.5=(LR93.309)	392820.1=(C93.154)
LTVR	CIP393617.1	391896.15=(DXY.15)	DXY.33
LTVR	CIP393613.2	391896.15=(DXY.15)	391894.7=(DXY.7)
LTVR	CIP396311.1	391925.2	C92.030
LTVR	CIP397036.7	392011.1=(LR93.160)	392745.7=(92.187)
LTVR	CIP397077.16	392025.7=(LR93.221)	392820.1=(C93.154)
LTVR	CIP397014.2	392739.4=(92.062)	88.108
LTVR	CIP397060.19	392739.4=(92.062)	392820.1=(C93.154)
LTVR	CIP397196.8	392797.22	388611.22=(C91.612)
LTVR	CIP397196.3	392797.22	388611.22=(C91.612)
LTVR	CIP397069.11	392797.22=(C92.140)	392820.1=(C93.154)
LTVR	CIP397069.5	392797.22=(C92.140)	392820.1=(C93.154)
LTVR	CIP304347.6	392820.1=(C93.154)	676008=(I-1039)
LTVR	CIP397099.4	392822.3=(LR93.073)	391207.2=(LR93.050)
LTVR	CIP397099.6	392822.3=(LR93.073)	391207.2=(LR93.050)
LTVR	CIP397073.15	392823.4=(LR93.120)	392820.1=(C93.154)
LTVR	CIP397073.7	392823.4=(LR93.120)	392820.1=(C93.154)
LTVR	CIP397100.9	392823.4=(LR93.120)	391207.2=(LR93.050)
LTVR	CIP397073.16	392823.4=(LR93.120)	392820.1=(C93.154)
LTVR	CIP304366.46	392823.4=(LR93.120)	676008=(I-1039)
LTVR	CIP397035.26	392823.4=(LR93.120)	92.187
LTVR	CIP300048.12	392973.48=(95.048)	392820.1=(C93.154)
LTVR	CIP300046.22	392973.48=(95.048)	393613.2=(TXY.2)
LTVR	CIP300099.22	393533.2=(95.302)	392820.1=(C93.154)
LTVR	CIP300063.9	393536.13=(95.103)	392820.1=(C93.154)
LTVR	CIP300063.4	393536.13=(95.103)	392820.1=(C93.154)
LTVR	CIP396285.1	393617.1=(TXY.11)	104.12 LB

LTVR	CIP395448.1	393617.1=(TXY.11)	BWH-87.344R
LTVR	CIP385499.11	65-ZA-5	377964.5
LTVR	CIP391919.3	69.4 (1043) BW	-
LTVR	CIP392780.1	703364=(SEDAFIN)	YY.3
LTVR	CIP389468.3	720087=(SERRANA)	388216.1=(YY.5)
LTVR	CIP390478.9	720087=(SERRANA)	386287.1=(XY.4)
LTVR	CIP390663.8	720087=(SERRANA)	386316.14=(XY.14)
LTVR	CIP388611.22	720091=(MEX-32)	385305.1=(XY.9)
LTVR	CIP394904.20	720118.1=(37-35A)	C90.205
LTVR	CIP302498.70	720139=(YAGANA-INIA)	391180.6=(C90.266)
LTVR	CIP302499.30	720139=(YAGANA-INIA)	392820.1=(C93.154)
LTVR	CIP394611.112	780280=(PW-88-6203)	676008=(I-1039)
LTVR	CIP304383.41	800824=(RED PONTIAC)	92.187
LTVR	CIP304383.80	800824=(RED PONTIAC)	92.187
LTVR	CIP391724.1	800959=(GRANOLA)	386316.1=(XY.20)
LTVR	CIP391207.2	800959=(GRANOLA)	385305.1=(XY.9)
LTVR	CIP392739.4	86001	386614.16=(XY.16)
LTVR	CIP392740.4	87055	386614.16=(XY.16)
LTVR	CIP397054.3	87059	392820.1=(C93.154)
LTVR	CIP397055.2	88052	392820.1=(C93.154)
LTVR	CIP392745.7	88078	386316.1=(XY.20)
LTVR	CIP397029.21	92.118	92.187
LTVR	CIP397016.7	92.119	88.108
LTVR	CIP397030.31	93.003	92.187
LTVR	CIP300054.29	95.059	392820.1=(C93.154)
LTVR	CIP300056.33	95.071	387170.9
LTVR	CIP300055.32	95.071	393613.2=(TXY.2)
LTVR	CIP300072.1	95.139	392820.1=(C93.154)
LTVR	CIP300137.31	95.187	387170.9

LTVR	CIP300093.14	95.206	392820.1=(C93.154)
LTVR	CIP388615.22	B-71-240.2	386614.16=(XY.16)
LTVR	CIP392781.1	B71-74-49.12	385280.1=(XY.13)
LTVR	CIP394034.65	B79.638.1	676008=(I-1039)
LTVR	CIP394034.7	B79.638.1	676008=(I-1039)
LTVR	CIP394881.8	B84-606.5	386287.1=(XY.4)
LTVR	CIP393536.13	BEROLINA	386287.1=(XY.4)
LTVR	CIP394895.7	BWH-87.230R	C90.205
LTVR	CIP391930.1	BWH-87.338	SELF
LTVR	CIP395438.1	BWH-87.344R	393617.1=(TXY.11)
LTVR	CIP395445.16	BWH-87.415	391894.7=(DXY.7)
LTVR	CIP394906.6	BWH-87.420	C90.205
LTVR	CIP395446.1	BWH-87.446R	393613.2=(TXY.2)
LTVR	CIP395186.6	C91.902	C92.032
LTVR	CIP395197.5	C91.921	BK-RKN-3
LTVR	CIP398014.2	C91.923	N93.107
LTVR	CIP395194.9	C93.059	C93.030
LTVR	CIP304350.78	CHIEFTAIN	392820.1=(C93.154)
LTVR	CIP304350.95	CHIEFTAIN	392820.1=(C93.154)
LTVR	CIP304350.100	CHIEFTAIN	392820.1=(C93.154)
LTVR	CIP304349.8	CHIEFTAIN	92.187
LTVR	CIP304350.18	CHIEFTAIN	392820.1=(C93.154)
LTVR	CIP304351.109	CHIEFTAIN	676008=(I-1039)
LTVR	CIP304351.31	CHIEFTAIN	676008=(I-1039)
LTVR	CIP304350.118	CHIEFTAIN	392820.1=(C93.154)
LTVR	CIP393615.6	DXY.33	391896.15=(DXY.15)
LTVR	CIP395196.4	ES-92.005	BK-RKN-1
LTVR	CIP391533.1	G-7445	385280.1=(XY.13)
LTVR	CIP394579.36	KONDOR	393615.6=(TXY.6)

LTVR	CIP392973.48	KRASA	385280.1=(XY.13)
LTVR	CIP392025.7	LINEA 21	386614.16=(XY.16)
LTVR	CIP392032.2	LOTOS	385280.1=(XY.13)
LTVR	CIP392822.3	MARIELA	YY.1
LTVR	CIP302428.20	MARIELA	392745.7=(92.187)
LTVR	CIP391382.18	MARIELA	386287.1=(XY.4)
LTVR	CIP304369.22	MARIELA	676008=(I-1039)
LTVR	CIP300135.14	MARIVA	392820.1=(C93.154)
LTVR	CIP300135.3	MARIVA	392820.1=(C93.154)
LTVR	CIP304371.67	MONALISA	92.187
LTVR	CIP392820.1	MONALISA	388216.1=(YY.5)
LTVR	CIP304371.20	MONALISA	92.187
LTVR	CIP304371.58	MONALISA	92.187
LTVR	CIP392821.1	PW-31	385280.1=(XY.13)
LTVR	CIP390637.1	PW-31	385305.1=(XY.9)
LTVR	CIP393708.31	PW-31	391895.10=(DXY.10)
LTVR	CIP304387.39	REINHORT	92.187
LTVR	CIP304387.92	REINHORT	92.187
LTVR	CIP304387.17	REINHORT	92.187
LTVR	CIP304394.56	SHEPODY	391207.2=(LR93.050)
LTVR	CIP304399.5	SNOWDEN	92.187
LTVR	CIP304399.15	SNOWDEN	92.187
LTVR	CIP391931.1	SR-17.50	SELF
LTVR	CIP302476.108	TITIA	392745.7=(92.187)
LTVR	CIP394613.139	TXY.4	676008=(I-1039)
LTVR	CIP394613.32	TXY.4	676008=(I-1039)
LTVR	CIP394614.117	TXY.8	676008=(I-1039)
LTVR	CIP394638.3	TXY.8	TITIA
LTVR	CIP396287.5	TXY.8	387170.9

LTVR	CIP304405.47	WA.018	676008=(I-1039)
LTVR	CIP304405.42	WA.018	676008=(I-1039)
LTVR	CIP304406.31	WA.077	676008=(I-1039)
LTVR	CIP394223.9	XY.13	C-282LM87B
LTVR	CIP394223.19	XY.13	C-282LM87B
LTVR	CIP302476.19	TITIA	392745.7=(92.187)
LTVR	CIP304330.34	391382.18=(95.108)	676008=(I-1039)
LTVR	CIP304345.47	388615.22=(C91.640)	676008=(I-1039)
LTVR	CIP304349.110	CHIEFTAIN	92.187
LTVR	CIP304349.4	CHIEFTAIN	92.187
LTVR	CIP304351.15	CHIEFTAIN	676008=(I-1039)
LTVR	CIP304351.9	CHIEFTAIN	676008=(I-1039)
LTVR	CIP309003.11	388611.22	304387.17
LTVR	CIP309017.101	395438.1	801088
LTVR	CIP309024.1	397036.7	392820.1
LTVR	CIP309026.72	397036.7	801088
LTVR	CIP309028.32	397036.7	801152
LTVR	CIP309062.106	303381.106	302499.24
LTVR	CIP309064.42	303381.30	392797.22
LTVR	CIP309064.76	303381.30	392797.22
LTVR	CIP309074.123	304330.34	392745.7
LTVR	CIP309078.56	304330.34	304356.32
LTVR	CIP309088.120	304347.6	302499.24
LTVR	CIP309093.50	304349.25	392820.1
LTVR	CIP309103.85	304349.8	801152
LTVR	CIP309128.87	304368.46	304356.32
LTVR	CIP309129.11	304368.46	304371.19
LTVR	CIP309131.16	304387.31	392820.1
LTVR	CIP309137.95	800258	396311.1

LTVR	CIP380389.1	BL-1.2	MURILLO III-80
LTVR	CIP720043	NARANJA	(KATAHDIN x MANTARO)
LTVR	CIP720088	MPI 61.375/23	B 25.65=(Atleet x Huinkul MAG)
PREBRED	CIP694474.16	4x-84.1	2x-5.26
PREBRED	CIP694474.33	4x-84.1	2x-5.26
VARIETY-Tomasa	CIP720072	(B 606.37 X KATAHDIN)	(RENACIMIENTO x YANA IMILLA)
VARIETY-Kufri Jyoti	CIP800258	3069D (4)	2814A (1)
VARIETY-Atlantic	CIP800827	800823=(WAUSEON)	B-5141.6
VARIETY-Spunta	CIP800923	BEA	USDA X 96.56
VARIETY-Desiree	CIP800048	URGENTA	DEPESCHE
VARIETY-DTO-33	CIP800174	WISC 639	W5295.7

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