LUCIANA APARECIDA MIGUEL

GENETIC ANALYSIS OF QUANTITATIVE TRAITS IN POTATO BREEDING: PARTITIONING ADDITIVE AND NON-ADDITIVE EFFECTS FOR OPTIMIZING CLONAL AND PARENTAL SELECTION

LAVRAS – MG
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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Genética e Melhoramento de Plantas, área de concentração em Melhoramento Genético de Plantas, para a obtenção do título de Doutor.

Prof. Dr. Tiago de Souza Marçal
Orientador

Prof. Dr. Welison Andrade Pereira
Coorientador

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APROVADA em 23 de abril de 2025.
Dra. Flávia Maria de Avelar Gonçalves UFLA
Dr. Mário Henrique Murad Leite Andrade UM
Dr. Pedro Crescêncio de Souza Carneiro UFV
Dr. Vinícius Quintão Carneiro UFLA
Dr. Tiago de Souza Marçal UFLA

Prof. Dr. Tiago de Souza Marçal
Orientador

Prof. Dr. Welison Andrade Pereira
Coorientador

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Deus, com toda a minha gratidão e meu amor, por ter me ajudado em todos os momentos, principalmente nos difíceis que considerei impossíveis...
Ofereço

Aos meus pais e amigos por todo apoio e carinho durante toda essa trajetória. Por todo amor e atenção nessa etapa.
Dedico

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RESUMO

Solanum tuberosum L. é uma das principais culturas alimentares do mundo, desempenhando papel essencial na segurança alimentar global devido ao seu alto valor nutricional, versatilidade e adaptabilidade em diferentes ambientes. No entanto, a produtividade da cultura ainda está aquém do seu potencial, principalmente devido à ocorrência de doenças bacterianas severas como a podridão mole, causada por bactérias dos gêneros *Pectobacterium* e *Dickeya*. Essas doenças são de difícil controle, ocasionam perdas econômicas expressivas tanto em campo quanto no armazenamento, e não respondem eficientemente a métodos químicos de manejo, exigindo estratégias alternativas, como o melhoramento genético. Considerando a natureza quantitativa e complexa de caracteres como a produtividade de tubérculos (TTY), teor de matéria seca (SG) e resistência à podridão mole, torna-se fundamental a utilização de abordagens genéticas robustas que permitam entender a arquitetura desses caracteres. A partição da variância genética em componentes aditivos e não aditivos permite otimizar estratégias de seleção clonal e parental, especialmente em espécies autotetraploides como a batata, que apresenta alta heterozigosidade. Modelos mistos, como o modelo animal proposto por Oakey et al. (2007), oferecem ferramentas eficazes para estimar tais efeitos com base em informações de pedigree. Ness contexto, o objetivo do primeiro artigo foi investigar as implicações da integração de efeitos genéticos aditivos e não aditivos em um modelo linear misto, com ênfase na partição da variância genotípica e na estimativa da precisão seletiva para pais e clones em estágios iniciais de um programa de melhoramento de batata tetraploide, para uso direto ou para cruzamento. Já o segundo artigo teve por objetivo dissecar os efeitos genéticos em componentes aditivos e não aditivos para os caracteres TTY, SG e resistência à podridão mole; realizar a seleção simultânea de clones e genitores com base em múltiplas características e avaliar a eficiência da inclusão dos efeitos não aditivos em modelos mistos aplicados ao melhoramento de batata tetraploide. O primeiro artigo forneceu análises de duas populações (POP1 e POP2), enquanto que para o segundo foi utilizado apenas uma população. Foram testados cinco modelos no artigo um (M1, M2wE, M2pE, M3wE e M3pE) e três no artigo dois (M1, M2 e M3). Os resultados mostraram que os efeitos não aditivos foram mais relevantes para TTY, indicando maior potencial de ganho por meio da seleção clonal. Para SG, predominaram os efeitos aditivos, sugerindo maior estabilidade genética e eficiência tanto na seleção de clones quanto na escolha de genitores. Observou-se, ainda, correlação negativa entre SG e a severidade da podridão mole, demonstrando que clones com maior teor de matéria seca apresentaram menor diâmetro de lesão, sugerindo maior resistência à doença sem comprometer a produtividade. Este estudo reforça a importância da modelagem genética detalhada para aprimorar a seleção precoce em programas de melhoramento de batata, contribuindo para o desenvolvimento de cultivares mais produtivas e resistentes às principais doenças bacterianas da cultura.

Palavras chaves: *Solanum tuberosum* L.; *Pectobacterium* spp. e *Dickeya* spp.; produtividade total de tubérculos; gravidade específica.

ABSTRACT

Solanum tuberosum L. is one of the world's main food crops, playing an essential role in global food security due to its high nutritional value, versatility and adaptability to different environments. However, crop productivity is still below its potential, mainly due to the occurrence of severe bacterial diseases such as soft rot, caused by bacteria of the genera *Pectobacterium* spp. and *Dickeya*. spp. These diseases are difficult to control, cause significant economic losses both in the field and in storage, and do not respond efficiently to chemical management methods, requiring alternative strategies, such as genetic improvement. Considering the quantitative and complex nature of traits such as tuber yield (TTY), dry matter content (SG) and resistance to soft rot, it is essential to use robust genetic approaches that allow understanding the architecture of these traits. Partitioning genetic variance into additive and non-additive components allows optimizing clonal and parental selection strategies, especially in autotetraploid species such as potato, which presents high heterozygosity. Mixed models, such as the animal model proposed by Oakey et al. (2007), offer effective tools for estimating such effects based on pedigree information. In this context, the objective of the first article was to investigate the implications of integrating additive and non-additive genetic effects in a linear mixed model, with emphasis on the partitioning of genotypic variance and the estimation of selective precision for parents and clones in early stages of a tetraploid potato breeding program, for direct use or for crossing. The second article aimed to dissect the genetic effects into additive and non-additive components for the traits TTY, SG and resistance to soft rot; to perform simultaneous selection of clones and parents based on multiple traits; and to evaluate the efficiency of including non-additive effects in mixed models applied to tetraploid potato breeding. The first article provided analyses of two populations (POP1 and POP2), while the second used only one population. Five models were tested in article one (M1, M2wE, M2pE, M3wE and M3pE) and three in article two (M1, M2 and M3). The results showed that non-additive effects were more relevant for TTY, indicating greater potential for gain through clonal selection. For SG, additive effects predominated, suggesting greater genetic stability and efficiency in both clone selection and parental selection. A negative correlation was also observed between SG and soft rot severity, demonstrating that clones with higher dry matter content had smaller lesion diameter, suggesting greater resistance to the disease without compromising productivity. This study reinforces the importance of detailed genetic modeling to improve early selection in potato breeding programs, contributing to the development of more productive cultivars that are resistant to the main bacterial diseases of the crop.

Key words: *Solanum tuberosum* L.; *Pectobacterium* spp.; and *Dickeya* spp.; total tuber productivity; specific gravity.

INDICADORES DE IMPACTO

Este trabalho gerou impactos significativos em diferentes dimensões, tecnológica, produtiva e educacional, ao propor uma abordagem inovadora e acessível para o melhoramento genético da batata (*Solanum tuberosum* L.). A partir da partição de efeitos genéticos aditivos e não aditivos, foi possível otimizar a seleção clonal e parental de genótipos superiores quanto à produtividade de tubérculos, teor de matéria seca e resistência à podridão mole, uma das doenças bacterianas mais severas que afetam a cultura. A utilização de modelos lineares mistos com base em pedigree, aliada à análise fatorial, resultou em uma metodologia eficiente, de baixo custo e aplicável em fases iniciais de programas de melhoramento, mesmo na ausência de genotipagem molecular. Essa ferramenta permite ganhos genéticos mais precisos e maior acurácia seletiva, tornando-se uma alternativa viável para instituições públicas ou cooperativas com recursos limitados. Os resultados encontrados têm aplicabilidade direta no desenvolvimento de cultivares com maior potencial agronômico e estabilidade, o que pode aumentar a produtividade, reduzir perdas no armazenamento e minimizar o uso de defensivos agrícolas, refletindo positivamente na sustentabilidade da cadeia produtiva. O trabalho também possui caráter extensionista. Foram diretamente envolvidos estudantes de graduação, pós-graduação, técnicos e docentes da Universidade Federal de Lavras (UFLA), totalizando ao menos 12 participantes ativos. Além disso, durante as fases experimentais, houve interação com outras instituições e troca de experiências, favorecendo a disseminação do conhecimento técnico-científico e a aproximação entre universidade e setor produtivo. Isso reforça o compromisso social do trabalho e sua contribuição para a formação de recursos humanos qualificados e sensibilizados com a realidade do campo. O território impactado inclui o Sul de Minas Gerais, região estratégica na produção de batata no Brasil, mas os conhecimentos gerados podem ser aplicados em outros contextos produtivos nacionais. O público beneficiado abrange produtores de batata, empresas de melhoramento, estudantes, técnicos agrícolas e instituições de pesquisa. Os impactos do trabalho se enquadram em diversas áreas da Política Nacional de Extensão Universitária, com destaque para Tecnologia e Produção, pela aplicação de métodos de seleção avançados; Educação, pela formação de estudantes e transferência de conhecimento; Meio Ambiente, por promover práticas menos dependentes de insumos químicos; e Trabalho, ao fortalecer a base técnica e produtiva da agricultura familiar.

IMPACT INDICATORS

This work generated significant impacts in different dimensions, technological, productive and educational, by proposing an innovative and accessible approach for the genetic improvement of potatoes (*Solanum tuberosum* L.). Based on the partition of additive and non-additive genetic effects, it was possible to optimize the clonal and parental selection of superior genotypes in terms of tuber productivity, dry matter content, and resistance to soft rot, one of the most severe bacterial diseases affecting the crop. The use of mixed linear models based on pedigree, combined with factor analysis, resulted in an efficient, low-cost methodology that can be applied in the initial phases of breeding programs, even in the absence of molecular genotyping. This tool allows for more precise genetic gains and greater selective accuracy, making it a viable alternative for public institutions or cooperatives with limited resources. The results found have direct applicability in the development of cultivars with greater agronomic potential and stability, which can increase productivity, reduce storage losses, and minimize the use of agricultural pesticides, positively reflecting on the sustainability of the production chain. The work also has an extensionist nature. Undergraduate and graduate students, technicians, and professors from the Federal University of Lavras (UFLA) were directly involved, totaling at least 12 active participants. In addition, during the experimental phases, there was interaction with other institutions and an exchange of experiences, favoring the dissemination of technical-scientific knowledge and the rapprochement between the university and the productive sector. This reinforces the social commitment of the work and its contribution to the formation of qualified human resources who are aware of the reality of the field. The impacted territory includes the South of Minas Gerais, a strategic region for potato production in Brazil, but the knowledge generated can be applied in other national production contexts. The target audience includes potato producers, breeding companies, students, agricultural technicians and research institutions. The impacts of the work fit into several areas of the National Policy for University Extension, with emphasis on Technology and Production, through the application of advanced selection methods; Education, through the training of students and the transfer of knowledge; Environment, by promoting practices that are less dependent on chemical inputs; and Work, by strengthening the technical and productive base of family farming.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

The potato (*Solanum tuberosum* L.) is the third most consumed food crop in the world, behind only rice and wheat. With great edaphoclimatic adaptability, this tuberous species has a wide geographic distribution and plays a crucial role in the food security of several countries (Devaux et al., 2021; FAO, 2024). Due to its high production capacity, the potato is considered a strategic crop for facing global food challenges, especially in the face of climate change and the growing population demand for food. Brazil occupies a prominent position in Latin America as one of the largest potato producers, and the crop is essential for the agriculture of small and medium-sized producers. The state of Minas Gerais leads national production, with a production of approximately 1.3 million tons in 2023. Between 2015 and 2023, there was a 10.8% increase in productivity (FAO, 2023), the result of technological advances and improvements in management and breeding practices. Despite this, the average potato yield is still below its genetic potential, estimated at more than 60 t/ha under ideal conditions. Productivity is strongly affected by factors such as soil quality, water availability, nutritional management and, mainly, by the incidence of pests and diseases.

Among the phytosanitary problems that compromise the yield and quality of tubers, bacterial diseases are notorious for their wide distribution, difficulty in controlling and potential to cause severe losses both in the field and during storage. The most important are blackleg and soft rot, caused by species of the genera *Pectobacterium* spp. and *Dickeya* spp., both belonging to the complex of pathogens known as “soft rot Enterobacteriaceae” (SRE).

Blackleg is characterized by necrotic lesions on the lenticels, dark coloration and a waterlogged appearance on the surface of the tubers, and is often confused with physiological damage. Soft rot is a destructive disease that affects the parenchymal tissues of tubers and stems, resulting in watery rot with a characteristic foul odor (Czajkowski et al., 2011; Charkowski, 2018). In both cases, the bacteria penetrate through wounds or natural openings and multiply rapidly in conditions of high humidity and moderate temperatures, making prevention and control extremely difficult.

Chemical control of these diseases is ineffective, and management depends mainly on the use of healthy seeds, hygienic practices in the storage and handling of tubers, and the use of more tolerant varieties. However, genetic variability for resistance to these bacteria is still limited, and the plant's defense mechanisms remain poorly understood. Inheritance studies reveal that resistance to soft rot is influenced by multiple genes with additive and non-additive effects, and is considered a quantitative trait with a complex genetic architecture. Although

some QTLs have already been identified, they still explain only a small fraction of the phenotypic variability, making their direct application in breeding programs difficult (Charkowski et al., 2020).

In parallel with disease resistance, potato breeding seeks to meet the growing demand for high productivity, adequate dry matter contents, and technological quality. Tuber productivity, for example, is a trait of high agronomic and economic relevance, but it is difficult to directly select, as it presents quantitative inheritance and is strongly influenced by the environment. Furthermore, its phenotypic value is composed of multiple genetic, additive, dominant and epistatic effects, in addition to genotype x environment (G×E) interactions.

Another crucial trait is the specific gravity of tubers, which is directly associated with dry matter content. This trait influences industrial yield in the processing of potatoes for frying, chips and frozen sticks. Varieties with higher specific gravity are preferred by the industry, as they result in crispier products, less soggy and with less oil absorption (Assis, 2007). However, there are challenges in simultaneously selecting for high productivity, specific gravity and disease resistance, since these traits can be negatively correlated.

Despite the advancement of genotyping techniques, the high cost of genomic selection still limits its large-scale application, especially in the early stages of breeding. As an alternative, the use of statistical models based on phenotypic and pedigree data has shown promise for estimating the components of genetic variance more accurately. In this context, Oakey et al. (2006) proposed the partitioning of genotypic effects into additive and non-additive components. This approach simultaneously considers the effects of dominance and kinship structure, allowing the capture of different sources of genetic variability and providing more realistic estimates of the genetic value of individuals. It is especially relevant in species such as potatoes, which present autotetraploid inheritance and a high level of heterozygosity.

The methodology proposed by Oakey and collaborators stands out for its applicability in clonally reproduced crops or those with complex inheritance systems. The application of this type of model allows not only a more effective selection of parents with high additive value, but also the identification of superior clones, whose performance results from the combination of additive and non-additive effects, which is fundamental in clonal selection.

By considering these different components of genetic variance, genetic improvement gains in precision, allowing more informed decisions both in the choice of crosses and in the selection of individuals in advanced phases of the program. This approach is also particularly

useful for traits with low heritability or complex environmental expression, such as productivity, dry matter content (specific gravity) and resistance to soft rot.

In addition, multivariate strategies can be employed to simultaneously consider several traits of interest and their interrelationships, increasing the efficiency of selection in segregating populations (Rocha et al., 2018). This approach allows the construction of selection indices or the identification of linear combinations between traits, which is particularly useful in crops with complex genetic architecture such as potatoes.

Therefore, the studies presented in this thesis have as their central objective the dissection of the additive and non-additive genetic effects of quantitative traits in potato breeding, with a special focus on tuber productivity, specific gravity and resistance to soft rot. By integrating detailed phenotypic data with robust statistical models, we seek to optimize clonal selection and the choice of parents, contributing to the development of more productive cultivars, adapted and tolerant to the main bacterial diseases that affect the crop.

SEGUNDA PARTE – ARTIGOS

ARTIGO 1- GENETIC INSIGHTS INTO NON-ADDITIVE EFFECTS IN TETRAPLOID POTATO BREEDING

Redigido seguindo as normas do periódico Euphytica.

Luciana Aparecida Miguel[1*], Rafaela Pereira Carvalho[1], Roberto Henrique de Lima Ribeiro[1], Mayra Alejandra Rincón Rueda[1], Ivan David Briceño-Pinzón[1], Lucimara Cruz de Souza[1], Vinicius Samuel Martins[1], Leticia Novais Padua[1], José Airton Rodrigues Nunes- 0000-0002-6260-7890[1], Pedro Crescêncio de Souza Carneiro[2], Mário Henrique Murad Leite Andrade[3], Márcio Fernando Ribeiro Resende Jr[4], Lincoln Zotarelli[4], Tiago de Souza Marçal[1*]

[1] Department of Biology, Federal University of Lavras, Lavras, MG, Brazil

[2] Department of Biology, Federal University of Viçosa, Viçosa, MG, Brazil

[3] School of Food and Agriculture, University of Maine, Orono, ME, United States

[4] Department of Horticultural Sciences, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, United States

[*] Corresponding authors: luciana.apamiguel@gmail.com https://orcid.org/0000-0002-5720-6267; tiago.marcal@ufla.br https://orcid.org/0000-0002-4262-9611

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Abstract
Despite the continuous growth of the global potato yield over the last 60 years, it still falls significantly short of its potential. Achieving this potential requires an efficient framework to dissect genotypic effects into additive and non-additive genetic components, enabling accurate selection of parents and clones in the early stages of potato breeding. The objective of this study was to investigate the implications of integrating additive and non-additive genetic effects into a mixed linear model, with an emphasis on genotypic variance partitioning and the estimation of selective accuracy for parents and clones in early stages of tetraploid potato breeding. A total of 1008 clones from 43 full-sib families were evaluated for total tuber yield (TTY) and specific gravity (SG) in seven trials. Five models were compared to assess the importance of non-additive effects: a base model (M1), a mixed linear model with and without additive × additive epistatic effects (M2pE and M2wE), and a mixed linear model including non-additive genetic effects with and without additive × additive epistatic effects (M3pE and M3wE). The M3wE and M2wE models provided the best fit for TTY and SG, respectively. These results suggest that non-additive gene effects were crucial in determining TTY, whereas gene action for SG was predominantly additive. Thus, the proposed approach estimates breeding values and total genotypic values at no additional cost, while facilitating the study of inheritance for complex traits and simultaneous selection of parents and clones in early stages of potato breeding.

Keywords *Solanum tuberosum*; Plant breeding; Linear mixed model; Genetic effect partitioning.

1. Introduction

Potato (*Solanum tuberosum* L.) is the most important non-grain crop for global food security. It can be consumed directly as a minimally processed food or through industrialized products (*e.g.,* chips and frozen products). Potato has wide adaptation and high productivity, making it a crucial crop for continuous production in the coming years, especially when faced with the complex scenario involving climate change and the increased demand for food driven by population growth (Devaux et al. 2014; Devaux et al. 2021; FAO 2022).

Although the average global potato yield has increased by 70% over the last 60 years, it still represents only 13% of the maximum yield potential (Haverkort and Struik 2015; FAO 2022). However, the gap between potential and current yields can be minimized through the development of superior cultivars. Historically, potato breeding has been performed through phenotypic recurrent selection (Gopal 2015; Jansky and Spooner 2018), usually using large populations and strong selection intensity in the early stages to reduce the population size to manageable levels (Jansky 2009; Haynes et al. 2012; Bradshaw 2017; Stich and Van Inghelandt 2018; Bradshaw 2022). However, the complexity of tetrasomic inheritance, combined with a high level of parental heterozygosity and the long selection cycles for multiple traits, has limited the genetic gain in this crop (Jansky 2009; Haynes et al. 2012; Slater et al. 2013; Gopal 2015; Bradshaw 2017).

The rate of genetic gain from a breeding population is directly proportional to the selective accuracy and magnitude of available additive genetic variability, and inversely proportional to the interval between cycles (Bradshaw 2022). Despite these findings, the selection of parents remains a challenging task because the performance of individuals is not always associated with the average performance of their offspring (Gopal 1998). The non-additive fraction of genotypic effects is not utilized in the process of sexual reproduction (Muñoz et al. 2014). Therefore, the study of combining ability becomes a valuable tool for identifying superior parents and crosses in potato breeding programs (Gopal 2015; Bradshaw 2017).

Despite the usefulness of combining ability, the incompatibility between certain parents (Jansky 2009) complicates the achievement of a balanced diallel cross, though it does not prevent the assessment of the genetic merit of the offspring. Alternatively, Slater et al. (2014a,b) utilized a mixed linear model (also known as the animal model), integrating an additive relationship matrix suitable for autotetraploid species, to predict breeding values in scenarios involving complex pedigrees (Kerr et al. 2012; Hamilton and Kerr 2018). However, they did not account for non-additive genetic effects.

Tetrasomic inheritance adds complexity to the genotypic value of an individual due to the increased number of intra- and inter-locus interactions (Kempthorne 1955; Endelman et al. 2018; Bradshaw 2022). Consequently, the absence of an appropriate algorithm for constructing dominance kinship matrices based on the complex pedigrees of autopolyploid species makes the classical modelling of non-additive effects impractical (Muñoz et al. 2014; Endelman et al. 2018). Alternatively, genomic relatedness matrices can be utilized (Endelman et al. 2018; Stich and Van Inghelandt 2018). However, the cost of genotyping exceeds that of phenotyping in the early stages of potato breeding programs (Stich and Van Inghelandt 2018; Bradshaw 2022). In this sense, the approach proposed by Oakey et al. (2006) for wheat overcomes the aforementioned constraints, enabling the parsimonious partitioning of genotypic effects into additive and non-additive components during the selection of wheat lines. The rationale proposed by the authors was to include a vector of uncorrelated random effects in the animal model to capture residual (non-additive) genetic effects. Integrating non-additive effects into the model proposed by Slater et al. (2014a,b) could refine the selection process in tetraploid potato breeding, facilitating the selection of superior varieties or parents for the next breeding cycle.

The objective of this study was to investigate the implications of integrating additive and non-additive genetic effects into a mixed linear model, with an emphasis on genotypic variance partitioning and the estimation of selective accuracy for parents and clones in early stages of a tetraploid potato breeding program, either for direct use or for crossing.

2. Material and methods

2.1 Field experiments

2.1.1 Germplasm, experimental plan, and crop management

A total of seven trials (clonal tests) were conducted. The clones were derived from two tetraploid populations, POP1 and POP2, consisting of multiple biparental crosses involving 31 and 12 families, respectively (Table 1), generated by the Potato Breeding Program at the Federal University of Lavras (UFLA). The populations originated from different parents, with some cultivars and clones from crosses performed within the program. POP1 parents were selected based on tuber shape, dry matter content, and tuber yield, as this population was intended for selection of clones for the chip industry. POP2 parents were resistant to PVY (*Potato Virus Y*), PVX (*Potato Virus X*), and PLRV (*Potato Leafroll Virus*). The pedigree of the populations and their genetic relationships are provided in the Supplementary Material (Figure 1) and visualized in the heatmap in Figure 1, where the kinship degree is represented by color variation (Figure 1). The trials were conducted at the Center for Scientific and Technological Development in Agriculture of the Federal University of Lavras (UFLA), in Lavras, Minas Gerais, Brazil (21°12'19.8"S, 44°58'48.8"W, 919 m altitude), in a soil classified as Typic Hapludox (Latossolo Vermelho Amarelo; Santos et al. 2018).

The trials were evaluated from 2013 to 2022 across three different seasons with varying heat stress levels based on average temperatures: no heat stress (WHS; 18.0 to 18.5 °C), moderate heat stress (MHS; 18.1 to 22.3 °C), and high heat stress (HHS 21.1 to 22.5 °C). The trials took place from April to October (WHS), January to May (MHS), and November to March (HHS).

Details of each trial are presented in Table 1. Four field trials followed an augmented block design (ABD) (Federer 1956), while three trials utilized a partially replicated design (P-REP), with approximately 20% of plots containing duplicate clones (p_N) (Cullis et al. 2006). Different clones were used in the two populations, and all analyses were based on these populations.

Table 1. Details of the experimental design for field trials, including the number of rows, columns, families, clones, checks, plots, and fraction of plots containing repeated clones in the P-REP design.

Trial †	Design	Number of levels						p_N
		Rows	Columns	Families	Clones	Checks	Plots	
POP1(HHS17)	ABD	27	20	31	491	2	531	7.16
POP1(MHS17)	ABD	18	31	31	491	2	531	7.16
POP1(WHS18)	ABD	27	20	31	491	2	531	7.16
POP2(WHS18)	ABD	11	83	12	597	4	717	16.74
POP2(HHS20)	P-REP	31	24	12	312	4	400	21.25
POP2(WHS21)	P-REP	13	31	12	304	3	400	23.00
POP2(WHS22)	P-REP	16	25	12	308	3	376	22.07

† POP1 = clone population 1; POP2 = clone population 2; WHS = no heat stress; MHS = moderate heat stress; HHS = high heat stress; The numbers 17, 18, 20, 21, and 22 indicate the experiment years (2017, 2018, 2020, 2021, and 2022, respectively). ABD = augmented block design; P-REP = partially replicated design; p_N = fraction of the plots occupied by repeated clones, calculated as $p_N = (N - Ntrat) / N$, where N is the number of plots and $Ntrat$ is the number of clones.

The plots consisted of a single row of five plants, except for the POP2 trials in 2018, where each plot contained a single row of three plants. The spacing was 0.30 m between plants and 0.80 m between rows across all trials. Plants were harvested 90 to 120 days after planting. Crop management followed the recommended practices for potato cultivation in the region. Soil preparation involved ploughing, harrowing, and rotary hoeing. Fertilization at planting included applications of 120 kg ha^{-1} N, 420 kg ha^{-1} P_2O_5, and 240 kg ha^{-1} K_2O. Additionally, side-dressing application of 60 kg ha^{-1} N and 60 kg ha^{-1} K_2O was performed 30 days after planting. Irrigation was provided through a sprinkler system to meet the crop's evapotranspiration requirements. Weekly applications of insecticide and fungicide were carried out to mitigate late blight during the winter and early blight during the dry season. In the summer, acaricides and treatments for controlling *Myzus persicae* were applied.

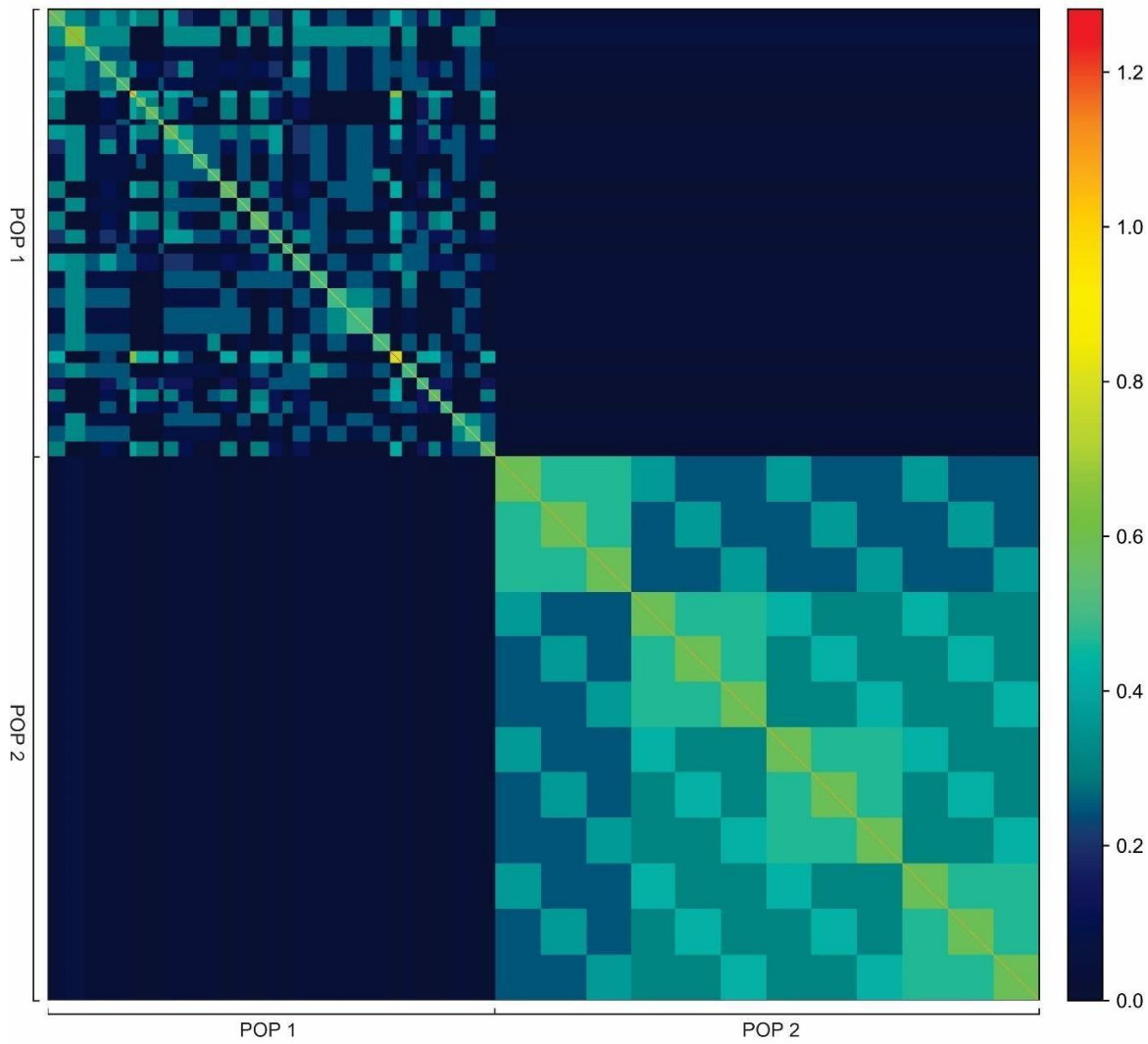

Figure 1. Heatmap depicting the pedigree of the POP1 and POP2 populations, emphasizing their genetic relationships.

2.1.2 Phenotyping

Two agronomic traits were assessed: total tuber yield (TTY - kg ha^{-1}) and specific gravity (SG). TTY was determined based on the total fresh weight of tubers harvested from the plot. SG was determined by the weight of tubers in air divided by the difference between the weight of tubers in air and the weight of tubers in water; tuber weight in air and water was measured using a hydrostatic balance with samples of approximately 2.5 kg (Schippers 1976).

2.2 Statistical analyses

2.2.1 Single-trial analysis (ST)

Trial plots were arranged in a grid with *r* rows and *c* columns; the matrix form of the mixed linear model is presented in Equation (1):

$$\mathbf{y} = \mathbf{1}\boldsymbol{\mu} + \boldsymbol{Z}_g u_g + \boldsymbol{Z}_r u_r + \boldsymbol{Z}_c u_c + \boldsymbol{e} \quad (1)$$

where $\mathbf{y}^{(N \times 1)}$ is the vector of phenotypic observations, where N is the number of plots; $\mathbf{1}^{(N \times 1)}$ is a vector in which, in which all elements are equal to one; $\boldsymbol{\mu}^{(1 \times 1)}$ is the intercept; $\mathbf{u}_g^{(g \times 1)}$ is the genotypic random effects vector of clones associated with the matrix $\boldsymbol{Z}_g^{(N \times g)}$, where g is the number of clones; $\mathbf{u}_r^{(r \times 1)}$ is the row random effects vector associated with matrix $\boldsymbol{Z}_r^{(N \times r)}$, where r is the number of rows; $\mathbf{u}_c^{(c \times 1)}$ is the column random effects vector associated with matrix $\boldsymbol{Z}_c^{(N \times c)}$, where c is the number of columns; and $\mathbf{e}$ is the random error vector.

It was assumed that the random effects vectors $\mathbf{u}_g$, $\mathbf{u}_r$, $\mathbf{u}_c$, and $\mathbf{e}$ (Equation 1) are mutually independent and follow a multivariate Gaussian distribution with a mean of zero and (co)variance matrices: var($\mathbf{u}_g$) = $\boldsymbol{G}_g$, var($\mathbf{u}_r$) = $\boldsymbol{G}_r$, var($\mathbf{u}_c$) = $\mathbf{G}_c$ and var($\mathbf{e}$) = $\boldsymbol{R}$. The structures used for each of these (co)variance matrices for model M1 are presented in Table 2.

The genotypic effects vector ($\mathbf{u}_g$) described in Equation (1) can be partitioned into additive ($\mathbf{u}_a$) and non-additive ($\mathbf{u}_s$) genetic effects, as shown in Equation (2) (Oakey et al. 2006; Hunt et al. 2013; Cowling et al. 2015), resulting in the M3wE model (Table 2). Thus, the additive relationship matrix was integrated into the model, and the incidence matrix $\boldsymbol{Z}_g$ was adapted by concatenating it with a matrix of zeros [0, $\boldsymbol{Z}_g$], where the zero matrix represents the non-phenotyped ancestors present in the additive relationship matrix. The variance of the genotypic effects vector ($\mathbf{u}_g$) from Equation (2) is presented in Equation (3).

$$\mathbf{u}_g = \mathbf{u}_a + \mathbf{u}_s \tag{2}$$

$$\text{var}(\mathbf{u}_g) = \boldsymbol{A}\sigma^2_a + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{I}_s \end{bmatrix} \sigma^2_s \tag{3}$$

where $\mathbf{A}^{(a \times a)}$ is the additive relationship matrix, a is the number of individuals in the pedigree, $\boldsymbol{I}_s^{(s \times s)}$ is an identity matrix, s represents the number of clones evaluated, and σ^2_a and σ^2_s are the variance components associated with the additive ($\mathbf{u}_a$) and non-additive ($\mathbf{u}_s$) effect vectors, respectively. Notably, the exclusion of the non-additive effects vector ($\mathbf{u}_s$) represents a return to the traditional animal model (M2wE, Table 2) used by Slater et al. (2014a,b).

To investigate the potential confounding between additive and additive × additive effects, models M2pE and M3pE were also fitted by integrating the epistatic effects vector $\mathbf{u}_{aa}$. The (co)variance structure associated with the $\mathbf{u}_{aa}$ vector is presented in Equation (4).

$$\text{var}(\mathbf{u}_{aa}) = \boldsymbol{A} \odot \boldsymbol{A}\sigma^2_{aa} \tag{4}$$

where $\boldsymbol{A} \odot \boldsymbol{A}^{(a \times a)}$ is the additive × additive epistatic relationship matrix, a is the number of individuals in the pedigree, σ^2_{aa} is the variance component associated with the additive × additive epistatic effects vector ($\mathbf{u}_{aa}$), and $\odot$ symbolizes the Hadamard product.

Table 2. (Co)variance structures of the adjusted models: M1 (base model), M2wE (animal model without additive × additive epistatic effect), M2pE (animal model including additive × additive epistatic effect), M3wE (animal model including non-additive effects without additive × additive epistatic effect) and M3pE (animal model including non-additive effects plus additive × additive epistatic effect).

(Co)variance matrix	M1	M2wE	M2pE	M3wE	M3pE
$\boldsymbol{G}_r$	$\sigma^2_r \boldsymbol{I}_r$	$\sigma^2_r \boldsymbol{I}_r$	$\sigma^2_r \boldsymbol{I}_r$	$\sigma^2_r \boldsymbol{I}_r$	$\underset{r}{\sigma^2} \boldsymbol{I}_r$
$\boldsymbol{G}_c$	$\sigma^2_c \boldsymbol{I}_c$	$\sigma^2_c \boldsymbol{I}_c$	$\sigma^2_c \boldsymbol{I}_c$	$\sigma^2_c \boldsymbol{I}_c$	$\underset{c}{\sigma^2} \boldsymbol{I}_c$
$\boldsymbol{G}_g$	$\sigma^2_g \boldsymbol{I}_g$				
$\boldsymbol{G}_a$		$\sigma^2_a \mathbf{A}$	$\sigma^2_a \boldsymbol{A}$	$\sigma^2_a \boldsymbol{A}$	$\underset{a}{\sigma^2} \boldsymbol{A}$
$\boldsymbol{G}_s$				$\sigma^2_s \boldsymbol{I}_s$	$\underset{s}{\sigma^2} \boldsymbol{I}_s$
$\boldsymbol{G}_{aa}$			$\underset{aa}{\sigma^2} \boldsymbol{A} \odot \boldsymbol{A}$		$\underset{aa}{\sigma^2} \boldsymbol{A} \odot \boldsymbol{A}$
$\boldsymbol{R}$	$\underset{e}{\sigma^2} \boldsymbol{I}_N$	$\underset{e}{\sigma^2} \boldsymbol{I}_N$	$\underset{e}{\sigma^2} \boldsymbol{I}_N$	$\underset{e}{\sigma^2} \boldsymbol{I}_N$	$\underset{e}{\sigma^2} \boldsymbol{I}_N$

$\boldsymbol{G}_r$, $\boldsymbol{G}_c$, $\boldsymbol{G}_g$, $\boldsymbol{G}_a$, $\boldsymbol{G}_s$, $\boldsymbol{G}_{aa}$, and $\boldsymbol{R}$ are matrices of (co)variance associated with row, column, genotypic, additive, non-additive, epistatic additive × additive, and error effects, respectively. $\underset{r}{\sigma^2}$, $\underset{c}{\sigma^2}$, $\underset{g}{\sigma^2}$, $\underset{a}{\sigma^2}$, $\underset{s}{\sigma^2}$, $\underset{aa}{\sigma^2}$, and $\underset{e}{\sigma^2}$ variance components associated with row, column, genotypic, additive, non-additive, epistatic additive × additive, and error, respectively. $\boldsymbol{I}_r$, $\boldsymbol{I}_c$, $\boldsymbol{I}_g$, $\boldsymbol{I}_s$ and $\boldsymbol{I}_N$ are identity matrices associated with row, column, genotypic, non-additive, and error effects, respectively. $\mathbf{A}$ is the additive relationship matrix, and $\boldsymbol{A} \odot \boldsymbol{A}$ is the additive × additive epistatic relationship matrix.

The additive relationship matrix ($\boldsymbol{A}$) was estimated using the AGHmatrix R package (Amadeu et al. 2016; R Core Team 2023) from the pedigree of each population utilizing an algorithm suitable for autopolyploid species (Kerr et al. 2012; Hamilton and Kerr 2018) and a double reduction rate of $w = 0.10$ (Slater et al. 2014a,b).

Variance components were estimated using the REML method (Patterson and Thompson 1971), and the predicted EBLUPs were derived using the equations of mixed models by Henderson (Henderson et al. 1959). All analyses were conducted using the Echidna Mixed Models software (Gilmour 2023) version 1.79. Subsequent analyses in the following sections were performed using the R software (R Core Team 2023).

2.2.2 Comparison of the models

The relative contributions of the variance components were calculated to facilitate result interpretation, each variance component expressed as a proportion of the total variance (sum of all the variance components of the model). The mean relative contributions of each effect to the variance components and their respective approximate standard errors were estimated using the delta method (Supplementary Material, Note S1).

The models were compared using the Akaike Information Criterion (AIC) (Akaike, 1974) (Equation 5) and a correspondence analysis between the top 20% of individuals in clonal selection (based on total genetic effects) and the top 5% of individuals in parent selection (based

on additive genetic effects). This analysis included the Czekanowski coefficient (Qiao et al. 2000) (CC, Equation 6) and the Spearman correlation coefficient (r_s) to assess the ranking consistency of clones and parents. Additionally, the variance components of the fitted models were evaluated using the Likelihood Ratio Test (LRT) (Equation 7) (Felsenstein 1981; Swofford et al. 1996; Huelsenbeck and Crandall 1997).

$$AIC = -2\ell + 2p \quad (5)$$

$$CC = x/(x + y) \quad (6)$$

$$LRT = -2\ln(\ell_1/\ell_2) \quad (7)$$

where ℓ is the logarithm of the maximum point of the residual log-likelihood function; p is the number of variance parameters; x is the number of clones selected by both strategies; and y is the number of clones diverging between strategies. For selection strategies, ℓ_1 is the maximum point of the residual log-likelihood function of the reduced model (excluding the tested effect), and ℓ_2 is the maximum point of the residual log-likelihood function of the full model.

2.2.2 Multi-environment–trial analysis (MET)

Similar to the single-trial analysis model, the total genotypic effects vector can be predicted for the multi-environment analysis using the base model, combining the genotypic effects vectors $\mathbf{u}_g$ within environments, as presented in Equation (8), capturing the G×E (genotype-by-environment interaction) analysis.

$$\mathbf{y} = \mathbf{1}\boldsymbol{\mu} + \mathbf{X}_t\boldsymbol{\tau}_t + \mathbf{Z}_g\mathbf{u}_g + \mathbf{Z}_{gt}\mathbf{u}_{gt} + \mathbf{Z}_r\mathbf{u}_r + \mathbf{Z}_c\mathbf{u}_c + \mathbf{e} \quad (8)$$

where $\mathbf{y}^{(N \times 1)}$ is the vector of phenotypic observations, where N is the number of plots; $\mathbf{1}^{(N \times 1)}$ is a vector in which all elements are equal to one; $\boldsymbol{\mu}^{(1 \times 1)}$ is the intercept; $\boldsymbol{\tau}_t$ is the vector of environmental fixed effects associated with the matrix $\mathbf{X}_t^{(N \times t)}$; t is the number of environments; $\mathbf{u}_g^{(g \times 1)}$ is the genotypic random effects vector of clones associated with the matrix $\boldsymbol{Z}_g^{(N \times g)}$, where g is the number of clones; $\mathbf{u}_{gt}$ is the random interaction effects vector associated with the matrix $\mathbf{Z}_{gt}^{(N \times gt)}$, where g is the number of clones and t is the number of environments; $\mathbf{u}_r^{(r \times 1)}$ is the row random effects vector associated with matrix $\boldsymbol{Z}_r^{(N \times r)}$, where r is the number of rows; $\mathbf{u}_c^{(c \times 1)}$ is the column random effects vector associated with matrix $\boldsymbol{Z}_c^{(N \times c)}$, where c is the number of columns; and $\mathbf{e}$ is the random error vector. Three models were used to estimate the genetic components and their interactions with the environment. Model M1 considers the total genotypic effect and its interaction with the environment. Model M2 includes only the additive genetic effect and its interaction with the environment. Finally, model M3 partitions the genotypic effect into additive and non-additive components, also incorporating the interactions

of both with the environment.**2.2.3 Accuracies of additive, non-additive, and genotypic effects and relative efficiency**

The accuracies associated with the additive effects ($r_{\hat{a}a}$) (Butler et al. 20; Cowling et al. 2015), non-additive effects ($r_{\hat{s}s}$), genotypic effects ($r_{\hat{g}g}$), and relative efficiency (RE) were estimated using Equations (9), (10), (11), and (12) (Cowling et al. 2015), respectively. The RE measures the efficiency of clonal selection compared to parental selection.

$$r_{\hat{a}a} = \sqrt{1 - \frac{\upsilon_a}{(1+F)\sigma_a^2}} \tag{9}$$

$$r_{\hat{s}s} = \sqrt{1 - \frac{\upsilon_s}{\sigma_s^2}} \tag{10}$$

$$r_{\hat{g}g} = \sqrt{1 - \frac{\upsilon_g}{(1+F)\sigma_a^2 + \sigma_s^2}} \tag{11}$$

$$RE = \frac{r_{\hat{g}g}}{r_{\hat{a}a}} \tag{12}$$

where υ_a, υ_s and υ_g are the values of the variance of the prediction error (PEV) of the additive, non-additive, and genotypic effects, respectively; and F is the inbreeding coefficient.

The PEVs of the additive (υ_a) and non-additive (υ_s) effects were obtained directly from the diagonal elements of the respective submatrices within the inverse of the coefficient matrix (C^{-1}) of the system of equations of mixed models (Henderson et al. 1959). Conversely, the PEV associated with the vector of total genotypic effects (υ_g) of the M3wE model was obtained from the diagonal of the matrix presented in Equations (13) and (14). The diagonal of this matrix provides the PEV of the linear combination between vectors $\mathbf{u}_a$ and $\mathbf{u}_s$.

$$\text{var}\,(\mathbf{L}_g\mathbf{u}_g) = \mathbf{L}_g\mathbf{C}^{-1}\mathbf{L}_g^T \tag{13}$$

$$\mathbf{C} = \mathbf{W}^T\mathbf{R}^{-1}\mathbf{W} \tag{14}$$

where $\mathbf{L}_g{}^{(g \times \beta)}$ is the matrix of linear combinations between the $\mathbf{u}_a$ and $\mathbf{u}_s$ vectors of the M3wE model, where g is the number of total predicted genotypic effects and β is the total number of effects included in the M3wE model (fixed and random); $\mathbf{C}^{(\beta \times \beta)}$ is the matrix of the coefficients of the system of equations of mixed models; $\mathbf{W}$ is the matrix of the model that concatenates the incidence matrices of the fixed and random effects of the M3wE model, where $\mathbf{W}^T = (\mathbf{1}, \mathbf{Z}_a, \mathbf{Z}_s, \mathbf{Z}_r, \mathbf{Z}_c)^T$. Narrow-sense heritability was calculated according to the approach proposed by Schmidt et al. (2019), equation (15).

$$h^2 = \frac{\sigma^2 A}{\sigma^2 A + \sigma^2 NA + \sigma^2 E}$$

3. Results

3.1 Comparison of the models and partitioning of the genotypic effect for single-trial analysis

Although AIC and ℓ results were similar, M3wE provided the best fit for TTY, while M2wE provided the best fit for SG among the tested models, as both had the lowest AIC in most trials (Supplementary Material, Table 1.1). Furthermore, the inclusion of the additive × additive epistatic effect did not lead to a significant increase in ℓ in most trials, except for the TTY trait. This was consistent for both the TTY (M3wE vs. M3pE) and SG (M2wE vs. M2pE) traits (Supplementary Material, Table 1.1, Table 1.2).

The genetic component of variance represented by σ^2_g in M1 and by σ^2_a in M2wE was significant for both traits. In the M3wE model, σ^2_a was significant for both traits in most cases, except in POP1 (HHS17) and POP2 (WHS22) for TTY (Supplementary Material, Table 1.2). The non-additive component of variance was significant in all trials for TTY and not significant in most trials for SG (Supplementary Material, Table 1.2; Figure 2).

The average magnitude of the difference in the relative contribution of genotypic variance (σ^2_g vs. $\sigma^2_a + \sigma^2_s$) between models M1 and M3wE was greater for SG (56% and 65%, respectively) than for TTY (59% and 60%, respectively) (Supplementary Material, Table 1.2; Figure 2). Notably, on average, the relative contribution of the additive variance component (σ^2_a) in the M2wE model matched the relative contribution of the genotypic variance component (σ^2_g) in the M1 model for both traits (Supplementary Material, Table 1.2; Figure 2). The relative contribution of the σ^2_a in the M2wE model was similar for both traits (TTY: 56% and SG: 57%) (Supplementary Material, Table 1.2; Figure 2). However, on average, the relative contribution of σ^2_a in the M2wE model was approximately three times higher than in the M3wE model for TTY and twice as high for SG (Supplementary Material, Table 1.2, Figure 1). The relative contribution of the additive component for SG in the M3wE model was approximately twice that observed for TTY (Supplementary Material, Table 1.2; Figure 2).

The contribution of the additive component to the total genotypic variation in the M3wE model was, on average, 24% for TTY and 52% for SG, while the contribution of the non-

additive component was 76% for TTY and 48% for SG (Supplementary Material, Table 1.2, Table 1.3; Figure 2).

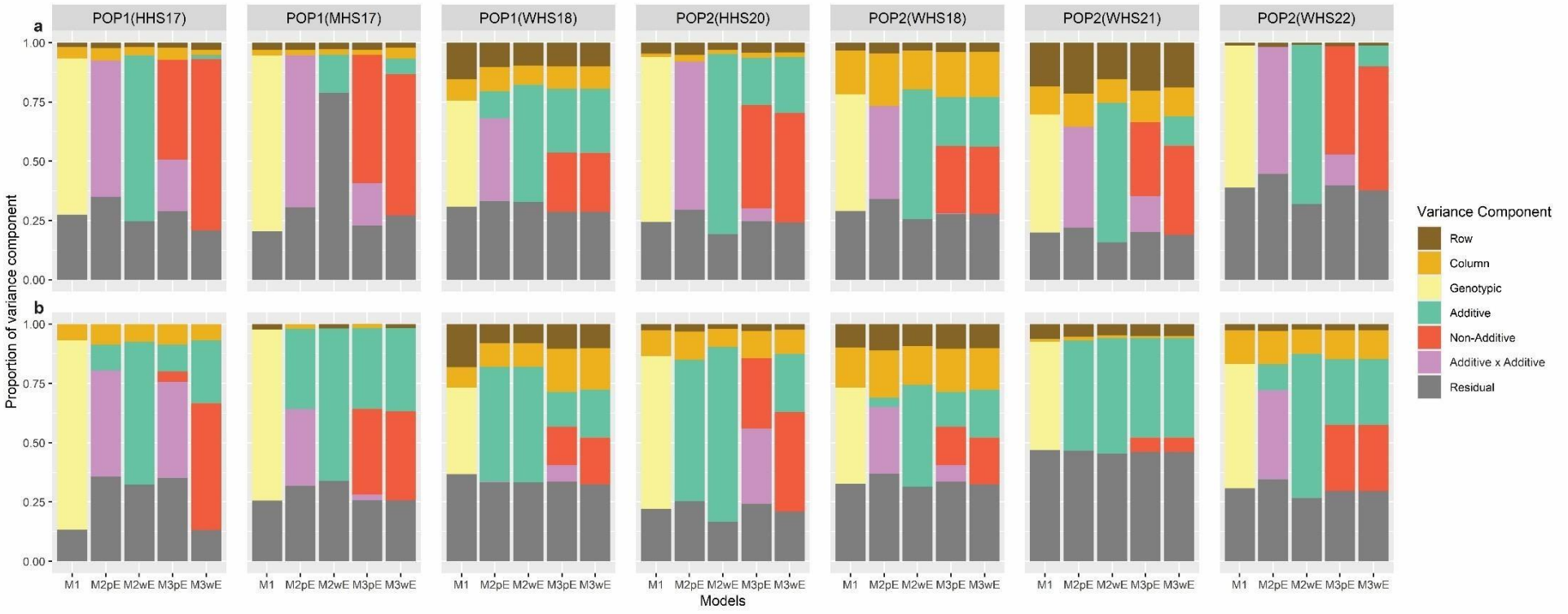

Figure 2: Contribution of the variance components (Row, Column, Genotypic, Additive, Non-Additive, Additive × Additive, and Residual) estimated from the models M1, M2wE, M2pE, M3wE, and M3pE for the traits. **a.** total tuber yield (TTY) and **b.** specific gravity (SG).

Spearman correlation coefficients (r_s) were significant ($P \leq 0.01$) for both traits, ranging from 0.94 to 1.00 for TTY and from 0.84 to 0.99 for SG, indicating a strong linear relationship between the genotypic effect vectors obtained from the M1 ($\mathbf{u}_g$) and M3 ($\mathbf{u}_a + \mathbf{u}_s$) models (Table 3). The Czekanowski coefficient (CC) ranged from 0.81 to 0.99 for TTY and from 0.65 to 0.96 for SG, demonstrating a high degree of coincidence in clonal selection. On average, r_s and CC were higher for TTY (r_s = 0.98 and CC = 0.95) compared to SG (r_s = 0.95 and CC = 0.87) for clonal selection (Table 3). For parental selection, r_s ranged from 0.45 to 0.94 for TTY and from 0.84 to 1.00 for SG (Table 3). The CC ranged from 0.10 to 0.70 for TTY and from 0.50 to 1.00 for SG. On average, both r_s and CC were higher for SG (r_s = 0.93 and CC = 0.81) than for TTY (r_s = 0.75 and CC = 0.51) (Table 3).

The analysis of selective accuracy (rs) and selection coincidence (CC) for the traits tuber yield (TTY) and dry matter content (SG) revealed significant differences between clonal selection and parental selection. In general, the mean values of rs and CC were higher for clonal selection in all populations and years evaluated, reflecting the predominance of non-additive effects in the genetic control of TTY.

For TTY, the mean coincidence between clones selected by different replicates was 0.95, while the coincidence between selected parents was only 0.51. This contrast was even more evident in the POP2(WHS22) population, in which clonal selection showed perfect coincidence between replicates (CC = 0.99), while parental selection coincided in only 10% of selected individuals (CC = 0.10). This discrepancy highlights the low stability in parental selection for productivity, suggesting that most of the variability observed for TTY is attributed to non-additive effects, which are not transmitted to the progenies.

In contrast, for SG, the differences between the selection criteria were less pronounced. The average coincidence of clonal selection was 0.87, while parental selection reached 0.81. These results indicate a greater contribution of additive genetic effects to the control of SG, which favors the efficiency of parental selection. However, even in this trait, some populations presented relevant differences. For example, in POP2(HHS20), the coincidence of clonal selection was 0.95, while parental selection resulted in only 0.50.

Table 3. Spearman correlation (r_s) and Czekanowski coefficient (CC) associated with clonal [$\mathbf{u}_g$ (M1) vs. $\mathbf{u}_a + \mathbf{u}_s$ (M3wE)] and parental selection [$\mathbf{u}_a$ (M2wE) vs. $\mathbf{u}_a$ (M3wE)] for total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG) traits.

Trait	Trial †	Clonal Selection		Parental Selection	
		r_s	CC	r_s	CC
TTY	POP1(MHS17)	1.00	0.99	0.83	0.60
	POP1(HHS17)	0.99	0.98	0.61	0.50
	POP1(WHS18)	0.94	0.81	0.94	0.70
	POP2(WHS18)	0.97	0.92	0.87	0.65
	POP2(HHS20)	0.99	0.96	0.82	0.60
	POP2(WHS21)	0.99	0.97	0.75	0.40
	POP2(WHS22)	0.99	0.99	0.45	0.10
	Average	0.98(0.62‡)	0.95(0.60‡)	0.75	0.51
SG	POP1(MHS17)	0.99	0.87	0.95	0.80
	POP1(HHS17)	0.99	0.96	0.91	0.65
	POP1(WHS18)	0.84	0.65	1.00	1.00
	POP2(WHS18)	0.94	0.87	0.92	0.85
	POP2(HHS20)	0.99	0.95	0.84	0.50
	POP2(WHS21)	0.93	0.84	1.00	1.00
	POP2(WHS22)	0.98	0.95	0.91	0.85
	Average	0.95(0.94§)	0.87(0.84§)	0.93	0.81

† POP1 = clone population 1; POP2 = clone population 2; WHS = no heat stress; MHS = moderate heat stress; HHS = high heat stress; The numbers 17, 18, 20, 21, and 22 indicate the experiment years (2017, 2018, 2020, 2021, and 2022, respectively). ‡ Comparison between the vectors $\mathbf{u}_g$ (M1) and $\mathbf{u}_a$ (M3wE). § Comparison between the vectors $\mathbf{u}_g$ (M1) and $\mathbf{u}_a$ (M2wE).

3.2 Accuracies of additive, non-additive, total genotypic effects, heritability, and relative efficiency

The results presented in this section refer to the M3wE model for TTY and the M2wE model for SG, as these models exhibited the best fit according to the criteria presented in the previous section.

The accuracy of the additive effects ($r_{\hat{a}a}$) ranged from 0.49 to 0.67 for TTY and from 0.67 to 0.81 for SG. On average, $r_{\hat{a}a}$ was higher for SG (0.73) than for TTY (0.57). The accuracy of the non-additive effects ($r_{\hat{s}s}$) ranged from 0.61 to 0.75 for TTY and, with an average of 0.66, indicating a moderate magnitude but a higher value than $r_{\hat{a}a}$. Moreover, both $r_{\hat{s}s}$ and $r_{\hat{g}g}$ were higher in the experiments designed using P-REP for TTY (Table 4). For SG, the results suggest that additive effects were more relevant to the performance of the clones. The accuracy of the genotypic effects ($r_{\hat{g}g}$) was higher than that of the others ($r_{\hat{a}a}$ and $r_{\hat{s}s}$) in all experiments for both traits, highlighting the superiority of clonal selection through vector ranking of genotypic effects ($\mathbf{u}_g = \mathbf{u}_a + \mathbf{u}_s$). In this context, clonal selection efficiency ranged from 13% to 61% for TTY and, on average, was 40% higher than parental selection (Table 4).

The heritability for TTY and SG exhibited significant variation across populations and trials. For TTY, heritability values were low (0.24 to 0.45) (Table 4). This indicates that environmental factors had a stronger role on the observed variability than genetic factors, thereby complicating efficient genetic selection. The overall heritability was 0.33, reflecting a low genetic contribution. Conversely, for SG, heritability was higher, with values ranging from 0.44 to 0.65, indicating a stronger genetic contribution to trait variability, facilitating genetic selection (Table 4). The overall heritability value for SG was 0.53, indicating good potential for genetic gains through selection. These results highlight the importance of accounting for differences among populations and trials when designing genetic improvement strategies.

Table 4. Average accuracies of additive effects ($r_{\hat{a}a}$), non-additive effects ($r_{\hat{s}s}$), total genotypes ($r_{\hat{g}g}$), and heritability (h^2) for total tuber yield (TTY, Mg ha $^{-1}$) and specific gravity (SG).

Trait	Trial †	$r_{\hat{a}a}$	$r_{\hat{s}s}$	$r_{\hat{g}g}$	h^2	Efficiency ‡
TTY	POP1(MHS17)	0.49	0.65	0.79	0.24	1.61
	POP1(HHS17)		0.70§			
	POP1(WHS18)	0.67	0.56	0.76	0.45	1.13
	POP2(WHS18)	0.63	0.61	0.74	0.40	1.17
	POP2(HHS20)	0.54	0.73	0.83	0.29	1.54
	POP2(WHS21)	0.54	0.75	0.85	0.29	1.57
	POP2(WHS22)		0.72§			
	Average	0.57	0.66	0.79	0.33	1.40
SG	POP1(MHS17)	0.77			0.59	
	POP1(HHS17)	0.81			0.65	
	POP1(WHS18)	0.77			0.59	
	POP2(WHS18)	0.75			0.56	
	POP2(HHS20)	0.68			0.46	
	POP2(WHS21)	0.67			0.44	
	POP2(WHS22)	0.68			0.46	
	Average	0.73			0.53	

† POP1 = clone population 1; POP2 = clone population 2; WHS = no heat stress; MHS = moderate heat stress; HHS = high heat stress; The numbers 17, 18, 20, 21, and 22 indicate the experiment years (2017, 2018, 2020, 2021, and 2022, respectively). ‡ Efficiency: ratio $r_{\hat{g}g}/r_{\hat{a}a}$. § Not included in the mean estimate.

3.3 Comparison of models for MET analysis

In the genotype × environment interaction analysis, (σ^2_{ge}), model M3 provided the best fit for TTY, while M2 provided the best fit for SG, based on a lower AIC value, following the same pattern observed in the individual analyses (Supplementary Material, Table 2.1).

The relative contribution of the genotype × environment interaction component (σ^2_{ge}) was significant for both traits in model M1. However, this component was more relevant for TTY, exhibiting a higher relative average (4%), indicating greater complexity in its inheritance. For SG, the average contribution of the interaction was lower (0.81%), suggesting that its inheritance may be simpler, potentially following a purely additive pattern. Model M2 exhibited a higher average relative contribution of the additive component (σ^2_a) (4.81% for TTY and 5.38% for SG) than the genotypic variance component (σ^2_g) (3.14% for TTY and 4.37% for SG) in model M1 for both TTY and SG, highlighting the importance of additive genetic effects (Supplementary Material, Table 2.2). However, in model M3 the average additive effect was smaller (1.04%) than in model M2 (4.81%) for TTY, suggesting that a portion of the genetic variation previously attributed to the additive effect may involve non-additive components. The

average non-additive variance (σ_s^2) was 2.26%, further highlighting the significance of this component and indicating that dominant and epistatic gene interactions contribute to the inheritance of TTY (Supplementary Material, Table 2.2).

The additive effect decreased from 4.81 (M2) to 1.04 (M3), suggesting that a substantial portion of the genetic variability can be explained by the newly integrated non-additive terms, further emphasizing the influence of non-additive inheritance for TTY (Supplementary Material, Table 2.2). The interaction σ_{ae}^2 (additive × environment) was significant, indicating that the heritability of the trait is not constant over the years, which may hinder selection based solely on additive effects. The interaction σ_{se}^2 (non-additive × environment) was also significant, highlighting that the effects of dominance and epistasis vary across years. Additionally, this finding demonstrate that clone performance may be inconsistent across different years. Thus, improving TTY requires considering both additive and non-additive effects in the selection process (Supplementary Material, Table 2.2).

For SG, the σ_{ae}^2 interaction effect was higher (1.84%) in M2 than in M1 (0.81%), revealing a greater influence of the environment on the heritability of the trait (Supplementary Material, Table 2.2). In the M3 model, the non-additive effect (1.80%) and its interaction with the environment (0.14%) were low, demonstrating that SG is less influenced by dominance and epistasis compared to TTY. Furthermore, the additive × environment interaction decreased from 1.62% (M2) to 1.43% (M3), suggesting reduced instability in the heritability of the trait over time, reaffirming that additive effects constitute the majority of SG inheritance (Table S3, Supplementary Material). These results corroborate the individual analyses, where the partition of effects clearly shows that TTY has predominantly non-additive inheritance, while SG exhibits additive inheritance (Supplementary Material, Table 2.2).

The comparison of the interaction components of models M1 and M3 (σ^2_{ge} vs. $\sigma^2_{ae} + \sigma^2_{se}$) showed that the average relative contribution was higher for TTY (4.04% and 4.80%) than for SG (0.81% and 1.57%). The same pattern was observed for M2, where the average contribution of the additive component was also higher for TTY compared to SG, suggesting that the interaction is more important for TTY due to the complexity of its inheritance (Supplementary Material, Table 2.2).

In the analysis of the interaction components, the row/environment effect showed substantially higher values in the POP1 (MHS17) trial compared to the others (Supplementary Material, Table 2.2). This result indicates that, in this specific environment, there was more significant variation associated with the longitudinal arrangement of the plots, reflecting a more

pronounced spatial influence on the data. In the other trials, this component had a considerably smaller contribution, suggesting a smaller impact of variation along the lines on the phenotypic expression of the genotypes. This difference highlights the particularity of the MHS17 environment with the spatial structure of the experiment. Thus, the results obtained not only demonstrate the uniqueness of the POP1 (MHS17) environment but also highlight the need for special attention to this type of variation in future experiments.

4. Discussion

4.1 ST analysis

Given the relevance of potato for global food security (Devaux et al. 2014; Devaux et al. 2021), breeders have focused their efforts on the continuous development of cultivars. However, major challenges, including the complexity of tetrasomic inheritance, the high levels of parental heterozygosity and the long breeding cycles for multiple traits, have limited the genetic gain of the crop in terms of tuber yield. Slater et al. (2016) also highlighted the complexity of the traits of interest, and that their low heritability make it difficult to obtain significant genetic gains. Moreover, the strong G × E interaction in potato leads to inconsistent genotype responses across different environments and years. According to Ortiz et al. (2020), this environmental variability makes it challenging to select stable and adaptable genotypes, thereby reducing genetic progress (Haynes et al. 2012; Slater et al. 2014a; Bradshaw 2017; Jansky and Spooner 2018; Bradshaw 2022). In this context, despite the genetic advances made over the last 150 years in vine maturity and tuber quality in the USA, tuber yield has remained constant over time (Douches et al. 1996; Jansky 2009).

The lack of genetic gain for tuber yield is closely related to its complex inheritance pattern due to the substantial importance of non-additive gene action and inbreeding depression (Mendoza and Haynes 1974; Jansky 2009; Zhang et al. 2019). Gopal (2015) reports a series of studies where specific combining ability exceeded general combining ability, confirming the significance of non-additive gene action in the genetic control of tuber yield. In this scenario, the performance of the clones is not a reliable indicator of the superiority of the offspring (Gopal 1998). Later, Gopal (2015) suggested the used of combining ability as a tool for selecting parents in potato breeding. However, the incompatibility of some crosses (Jansky 2009) makes it hard to obtain a balanced diallel. Alternatively, Slater et al. (2014a,b) proposed the use of an animal model integrating an additive relationship matrix suitable for autotetraploid species. However, the proposed model did not integrate non-additive genetic effects.

The superiority of the M3wE model along with the significance of the variance components σ^2_a and σ^2_s confirms the importance of non-additive gene action in the genetic control of TTY. Moreover, the absence of non-additive genetic effects in the animal model (M2wE) led to an inflation of σ^2_a. Muñoz et al. (2014), studying pine populations, highlighted that excluding non-additive genetic effects in the animal model inflates both the additive genetic effects and additive genetic variance. Class and Brommer (2020), studying a wild population of bluecap birds, found that disregarding dominance genetic variance inflated estimates of additive genetic variance for different traits, particularly when maternal effects were omitted. Furthermore, Muñoz et al. (2014) argue that overestimating additive variance inflates predicted genetic gains, misleadingly suggesting a genetic architecture simpler than it actually is. Notably, although several studies highlight the relevance of non-additive effects for TTY, Endelman et al. (2018) and Amadeu et al. (2020) reported that non-additive variance contributes minimally to the total genotypic variance of TTY in tetraploid potato populations.

In contrast to TTY, the superiority of the M2wE model, along with the absence of significance of σ^2_s in most trials and the significance of σ^2_a in all trials, demonstrates the predominance of additive gene action in the genetic control of SG. The M2wE model has a simpler structure than M3wE, as it includes only additive components. This simplification enhances statistical parsimony. Sood et al. (2020) reported that more complex models often overfit data for traits with predominantly additive inheritance, such as SG, reducing predictive accuracy. Moreover, focusing on additive effects, as in SG, aligns with selection strategies used for traits with high heritability. Additionally, the model exhibits fewer dominance deviations.

Furthermore, integrating non-additive genetic effects (M3wE) increased genotypic variance compared to the M1 model. Slater et al. (2014a,b), using the animal model, reported high narrow-sense heritability for SG in diploid (0.73) and tetraploid (0.74) potato populations, indicating predominantly additive gene action in its genetic control. However, Endelman et al. (2018) found that additive genetic variance was strongly inflated by the additive × additive epistatic variance component in tetraploid potato population for SG. Bernardo (2010) and Muñoz et al. (2014) reported that, in the animal model, part of the non-additive variance, such as the additive × additive epistatic, can be confounded with additive variance. These findings align with those of Haynes (2001), Haynes (2008), Gopal (2015), and Amadeu et al. (2020), who reported a significant contribution of non-additive effects to SG in diploid and tetraploid potato populations.

Comparing the results of clonal selection and parental selection highlights a central challenge in the genetic improvement of tetraploid potatoes: the discrepancy between the phenotypic performance of clones and their value as parents. This divergence was particularly evident for tuber yield (TTY), whose average coincidence of selection between replicates was substantially higher in clonal selection (0.95) than in parental selection (0.51). The low coincidence observed between the selected parents, even within the same population, suggests that parental performance is highly influenced by non-additive effects and complex interactions that are not predictable based solely on the total phenotypic value of the clones.

This finding reinforces a recurring point in the literature: complex quantitative traits such as TTY are strongly influenced by dominance and epistasis, especially in autotetraploid species with a high degree of heterozygosity (Gopal, 2015; Gallais, 2003). In such cases, the total genotypic value of a clone may be excellent, but its genetic contribution to the progeny – restricted to the additive heritable fraction – may be limited. This phenomenon is known as "disconnection between phenotypic merit and additive genetic merit" (Bradshaw, 2022), and compromises the accuracy of parental selection when it is based solely on the phenotypic performance of the clones.

In the case of dry matter content (SG), parental selection presented values closer to clonal selection (0.81 vs. 0.87), indicating a greater participation of additive effects in the genetic control of this trait. This suggests that, for SG, parental selection based on additive estimates may be more effective than for TTY. However, considerable variations were still observed between populations and environments, as in POP2(HHS20), where parental coincidence was only 0.50, while clonal coincidence was 0.95. These results reinforce the idea that, even in traits with higher additive heritability, environmental variability and the complexity of polyploid inheritance must be considered (Schmidt et al., 2019).

In addition, the discrepancy between selection criteria may be aggravated by the limitations inherent in phenotypic evaluation, especially in the early stages of breeding programs, where selection accuracy tends to be lower due to the lower number of replicates and high environmental variability. In view of this, strategies that allow for the precise partitioning of genetic effects, such as the use of mixed models with pedigree (animal model), become indispensable. These models allow for the separate estimation of additive and non-additive effects, providing a more reliable basis for the selection of parents and for the optimization of crosses (Oakey et al., 2007; Slater et al., 2014).

In summary, the results indicate that, in tetraploid potato, clonal selection remains an efficient approach for traits with a strong influence of non-additive effects, such as TTY. On the other hand, parental selection requires greater methodological refinement, and the use of models that consider the complex genetic architecture of the species is recommended to obtain satisfactory selective accuracy and consistent genetic gains throughout the breeding cycles.

Although integrating additive × additive epistatic effect did not significantly impact genetic variance for SG, this does not imply that the effect is unimportant. Muñoz et al. (2014) reported that pedigree-based relationship matrices offer a less precise variance component partition than genomic relationship matrices. Additionally, the model did not account for other inter-locus interactions. However, integrating first-order epistasis improves selection accuracy, as also reported by Endelman et al. (2018) and Wilson et al. (2021).

Despite the complex inheritance of quantitative traits in tetraploid potatoes, breeders often select superior clones based solely on genotypic values (Andrade et al. 2020; Fernandes Filho et al. 2021), disregarding genetic relationships. Nevertheless, the results of the present study indicated that clonal selection remains effective for identifying superior clones for both traits, even when using only the additive parentage matrix (**A**) derived from the pedigree. However, validating this result in the context of genomic selection requires integrating the genomic (**G**) or hybrid (**H**) kinship matrix (Amadeu et al. 2016). Notably, unlike TTY, integrating the additive relationship matrix effectively identified individuals with the highest additive genetic value for SG. This effectiveness is attributed to the strong linear relationship between σ^2_g and σ^2_a, the higher narrow-sense heritability compared to TTY, and the lower magnitude of the genotype × environment interaction (Haynes 2001; Slater et al. 2014b; Wang et al. 2017; Endelman et al. 2018). For these reasons, intense selection for SG is applied in the early stages of potato breeding programs (Endelman et al. 2018). These findings align with genetic improvements in SG over the last century, highlighting its importance for processing cultivars. These cultivars account for over 50% of the potato-growing area in North America, highlighting that SG is crucial for cultivars developed for processing purposes (Douches et al. 1996; Love et al. 1998).

The parental selection based on additive effects was strongly influenced by the inclusion of non-additive effects (M2wE vs. M3wE) for TTY. The absence of non-additive effects in the animal model may confound additive and non-additive effects, leading to inflated predicted genetic gains, as non-additive genetic variance is not transmitted through sexual reproduction (Muñoz et al. 2014). Parental selection is inherently less efficient for TTY than

clonal selection, as the latter utilizes all genetic variation in the selection process. Endelman et al. (2018) emphasized that the partial transmission of non-additive effects helps maintain favorable allele blocks while reducing recombination in polyploid genomes. According to Wolfe et al. (2021), accounting for dominance effects is crucial when selecting parents in polyploid crops, particularly in species where clonal reproduction is prevalent, to increase selection efficiency. Werner et al. (2023) support these findings by demonstrating the importance of a comprehensive genetic approach to selecting clones both as individuals and as potential parents, considering not only additive variance but also dominance effects. This highlights the importance of developing new strategies to enhance parental selective accuracy and shorten intercrossing cycles for improving annual genetic progress in TTY for tetraploid potato populations.

One of the strategies proposed by McCann et al. (2012) is the use of more robust experimental designs in the early stages of potato breeding programs to increase selective efficiency. In this context, integrating replicates as early as possible in potato breeding programs has been recommended. Among available experimental designs, the partially replicated design (P-REP) demonstrated potential in the early stages of potato breeding programs (Cullis et al. 2006; Paget et al. 2017). This design helps overcome seed limitations, increasing the number of tested clones, and can be adapted for evaluations in multiple environments (Cullis et al. 2006; Williams et al. 2011; Haynes et al. 2012; Williams et al. 2014; Paget et al. 2017). Additionally, P-REP enables partitioning of additive and non-additive genetic effects, as well as the joint modelling of genetic effects, spatial trends, and competition (Hunt et al. 2013. Finally, P-REP is associated with a higher percentage of plots per genotype (p_N) compared to the traditional augmented block design (Table 1), reducing confounding between non-additive genetic and environmental effects.

In the approach proposed by Oakey et al. (2006), the distinction between non-additive genetic and environmental effects is directly proportional to the percentage of repeated genotypes and the number of replicates per genotype. The absence of a suitable algorithm for obtaining the pedigree dominance kinship matrix for autopolyploid species hinders the modelling of non-additive effects via the classical approach (Muñoz et al. 2014; Endelman et al. 2018). However, the framework proposed by Oakey et al. (2006) overcomes the constraints of the approach proposed by Slater et al. (2014a,b), facilitating the partitioning of genotypic effects into additive and non-additive effects at no additional cost, making its implementation

feasible in the early stages of a potato breeding program. This approach can be readily extended to genomic selection (Oakey et al. 2016), facilitating the development of parsimonious models.

4.2 MET analyses

The genotype × environment models highlighted the differences in the inheritance of the TTY and SG traits, emphasizing the complexity of their genetic variability. The results revealed a genetic pattern consistent with previous findings in potato breeding, indicating that non-additive effects strongly influence productivity, while quality traits, such as tuber weight and dry matter content, are primarily additive (Slater et al. 2016; Endelman et al. 2018; Enciso-Rodríguez et al. 2018).

The results observed for TTY showed that the genetic variance initially attributed to the additive effect in the M2 model was redistributed to the non-additive effects in the M3 model. This suggests that dominance and epistasis are crucial factors in the expression of TTY, as widely reported in the literature (Bradshaw 2017; Li et al. 2021). Studies on tuber yield and hybrid vigor in potato indicated that heterosis is frequently observed, with inheritance strongly influenced by non-additive effects. Slater et al. (2016) reported that in tetraploid potatoes, dominance and epistatic effects are common and strongly influence TTY. This explains the significant non-additive × environment interaction observed in the M3 model, indicating that clone performance varies across years and locations, complicating tuber yield prediction. The strong genotype × environment interaction in models M1 and M3 further confirms the significant influence of environmental variations on TTY.

The significant non-additive effects highlight the need to explore heterosis in potato breeding. Bradshaw (2017) suggests hybrid crosses to enhance favorable gene expression via dominance and epistasis. These results suggest that clone and parent selection strategies should integrate non-additive effects, including models that partition genetic variance components.

The lowest AIC values presented in the M2 model for SG emphasize the importance of additive effects, which effectively capture most of this trait's genetic variation. These results align with Bradshaw (2022), who described SG as a predominantly additive trait with stable inheritance over time. In the M3 model, non-additive effects and their environmental interactions were minimal, indicating that SG is less influenced by dominance and epistasis than TTY. Endelman et al. (2018) emphasize that traits with a strong additive basis, such as SG, are ideal for recurrent selection programs due to their greater long-term predictability. The reduction in additive × environment interaction from 1.62% (M2) to 1.43% (M3) indicates

greater temporal stability in the heritability of this trait. This is a positive result that supports the selection of clones or parents by enabling the use of a simpler model.

Genomic selection has become a key strategy in potato breeding programs, enhancing selection gains and significantly reducing the time required to release new cultivars. This approach is particularly valuable for traits that are controlled by complex genetic factors (Slater et al. 2016). However, a major challenge in the early stages of these breeding programs is the elevated genotyping expenses, primarily due to the large number of clones involved. Nevertheless, despite the advantages of genomic selection, Sood et al. (2020) evaluated scenarios comparing relationship matrices **A** and **H** and found that prediction accuracy varied minimally between clones, regardless of whether their parents had been genotyped. This reveals the usefulness of pedigree-based methods in simpler breeding programs. Additionally, pedigree approaches efficiently capture additive effects, which predominate in relatively simple traits, such as SG. Bradshaw (2022 reported that many agronomic traits in potatoes exhibit strong additive inheritance, reinforcing the suitability of pedigree-based strategies. With appropriate statistical methods, non-additive effects can also be modelled. Furthermore, the economic viability and potential to explore heterosis and epistatic combinations make pedigree-based strategies viable solutions in resource-limited scenarios.

The method used in the present study captured the interaction between effects and the environment. This reinforced the inheritance pattern of each trait, with SG strongly linked to additive effects, and TTY affected by the non-additive × environment interaction, indicating the influence of dominance and epistasis. Therefore, using kinship matrices to capture interactions enables efficient selection in small breeding programs, reducing the need for mass genotyping and, at more advanced stages, genomic selection can be implemented without compromising prediction accuracy (Sood et al. 2020).

5 Conclusion

Non-additive gene action is crucial in the genetic control of total tuber yield (TTY) in tetraploid potato breeding, while specific gravity is predominantly controlled by additive genetic effects. Omitting non-additive genetic effects from the animal model overestimates additive genetic variance in TTY due to confounding with non-additive genetic variance, leading to biased predictions of genetic gains from parental selection. The approach applied in this study can be readily implemented in the early stages of a tetraploid potato breeding program at no additional cost, facilitating inheritance studies of complex quantitative traits and the simultaneous selection of parents and clones.

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Supplementary material

Supplementary notes

Note S1. Relative contributions of variance components

For each model tested (M1, M2wE, M2pE, M3wE or M3pE), the vector of relative contributions ($\boldsymbol{\omega}$) takes the form presented in equation Eq. S1.

$$\boldsymbol{\omega}^T = \left[\frac{\boldsymbol{\kappa}_1}{\boldsymbol{\kappa}^T\boldsymbol{\kappa}} \quad \frac{\boldsymbol{\kappa}_2}{\boldsymbol{\kappa}^T\boldsymbol{\kappa}} \quad \cdots \quad \frac{\boldsymbol{\kappa}_i}{\boldsymbol{\kappa}^T\boldsymbol{\kappa}}\right] \qquad \text{(Eq. S1)}$$

where $\boldsymbol{\kappa}$ is the vector of variance components from tested model (M1, M2wE, M2pE, M3wE or M3pE).

The standard errors for relative contributions of variance components ($\boldsymbol{\kappa}_i$) were obtained by delta method (Masuda, 2019; Gold et al., 2020), as shown in equations Eq. S2 and Eq. S3.

$$SE_i = \sqrt{\boldsymbol{\theta}^T\boldsymbol{\nabla}_{AI}^{-1}\boldsymbol{\theta}} \qquad \text{(Eq. S2)}$$

$$\boldsymbol{\theta}^T = \left[\frac{\partial\boldsymbol{\omega}_i}{\partial\boldsymbol{\kappa}_1} \quad \frac{\partial\boldsymbol{\omega}_i}{\partial\boldsymbol{\kappa}_2} \quad \cdots \quad \frac{\partial\boldsymbol{\omega}_i}{\partial\boldsymbol{\kappa}_i}\right] \qquad \text{(Eq. S3)}$$

where $\boldsymbol{\theta}$ is the vector of partial derivatives of relative contributions of variance components from tested model (M1, M2wE, M2pE, M3wE or M3pE) and $\boldsymbol{\nabla}_{AI}^{-1}$ inverse of average information matrix from tested model (M1, M2wE, M2pE, M3wE or M3pE).

Table 1.1. Summary of models M1, M2wE, M2pE, M3wE, and M3pE for total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG) traits: Maximum point of the residual log-likelihood (ℓ) and Akaike information criterion (AIC).

Trait	Fitting Parameters	Trial†	M1	M2wE	M2pE	M3wE	M3pE
TTY	ℓ	POP1(MHS17)	**-1393.08**	-1402.45	-1393.65	-1392.82	-1391.36
		POP1(HHS17)	-1069.16	-1073.41	-1066.60	-1067.16	**-1065.00**
		POP1(WHS18)	-1340.46	-1333.78	-1330.35	**-1330.35**	-1330.35
		POP2(WHS18)	-1496.76	-1477.32	-1476.33	**-1475.78**	-1476.00
		POP2(HHS20)	-1157.18	-1152.11	-1151.26	**-1150.50**	-1150.49
		POP2(WHS21)	-1041.30	-1039.53	-1037.89	**-1036.92**	-1037.00
		POP2(WHS22)	-1032.67	-1034.40	-1032.10	**-1031.32**	-1030.97
	AIC	POP1(MHS17)	**2794.18**	2812.91	2797.30	2795.65	2795.00
		POP1(HHS17)	2146.33	2154.81	2143.21	2144.33	**2142.00**
		POP1(WHS18)	2878.57	2675.58	2673.05	**2670.70**	2672.70
		POP2(WHS18)	3001.53	2962.65	2962.67	**2961.55**	2963.55
		POP2(HHS20)	2322.36	2312.22	2312.52	**2311.00**	2312.97
		POP2(WHS21)	2090.61	2087.07	2085.78	**2083.85**	2085.74
		POP2(WHS22)	2073.34	2076.79	2074.20	**2072.64**	2073.94
SG	ℓ	POP1(MHS17)	2207.25	2225.31	2226.57	**2228.65**	2228.67
		POP1(HHS17)	1794.84	1844.08	**1847.67**	1804.94	1847.68
		POP1(WHS18)	2210.61	**2230.45**	2230.45	2230.45	2230.45
		POP2(WHS18)	2544.03	**2561.90**	2562.59	2562.85	2562.95
		POP2(HHS20)	1631.06	1637.07	**1638.47**	1638.40	1638.88
		POP2(WHS21)	1531.15	**1547.67**	1547.67	1547.72	1547.72
		POP2(WHS22)	1521.76	**1530.01**	1530.35	1530.86	1530.86
	AIC	POP1(MHS17)	-4406.50	-4442.63	-4443.13	**-4447.30**	-4445.34
		POP1(HHS17)	-3581.69	-3680.16	**-3685.34**	-3599.88	-3683.36
		POP1(WHS18)	-4413.23	**-4452.88**	-4450.88	-4450.91	-4448.90
		POP2(WHS18)	-5080.06	**-5115.81**	-5115.18	-5115.71	-5113.91
		POP2(HHS20)	-3254.12	-3266.15	**-3266.94**	-3266.79	-3265.73
		POP2(WHS21)	-3054.30	**-3087.34**	-3085.33	-3085.44	-3083.44
		POP2(WHS22)	-3035.52	**-3052.02**	-3050.70	-3051.72	-3049.72

†POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022).

Table 1.2. Contribution of the variance components (Row, Column, Genotypic, Additive, Non-Additive, Additive × Additive, and Residual in %) estimated from the models M1, M2wE, M2pE, M3wE, and M3pE for total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG).

Trait	Trial†	M1			
		Row	Colunm	Genotypic	Residual
TTY	POP1(MHS17)	2.95**	2.40*	74.12*	20.53
	POP1(HHS17)	1.95ns	4.78**	65.76**	27.51
	POP1(WHS18)	15.46**	8.99**	44.70**	30.85
	POP2(WHS18)	3.35**	18.45**	49.20**	29.00
	POP2(HHS20)	4.70**	1.42ns	69.54**	24.34
	POP2(WHS21)	18.45**	11.94**	49.70**	19.91
	POP2(WHS22)	1.18ns	0.00ns	59.94**	38.88
	Average ±SE	6.86 ±3.72	6.80 ±2.48	58.84 ±7.51	27.43 ±6.94
SG	POP1(MHS17)	2.35ns	0.00ns	72.08**	25.57
	POP1(HHS17)	0.00ns	6.82**	79.89**	13.29
	POP1(WHS18)	18.20**	8.63**	36.45**	36.45
	POP2(WHS18)	9.92**	16.91**	40.45**	32.72
	POP2(HHS20)	2.67*	10.80**	64.53**	22.00
	POP2(WHS21)	6.31**	1.04ns	45.72**	46.93
	POP2(WHS22)	2.72*	14.04**	52.49**	30.75
	Average ± SE	6.04 ± 2.76	8.31 ± 2.97	55.93 ± 7.45	29.72 ± 6.92

Table 1.2. Continuation.

Trait	Trial†	M2wE				M2pE				
		Row	Columm	Additive	Residual	Row	Columm	Additive	Additive × Additive	Residual
TY	POP1(MHS17)	2.84^{ns}	2.26**	15.99**	78.91	2.98*	2.37**	0.00^{ns}	64.10**	30.55
	POP1(HHS17)	1.88**	3.45**	70.00**	24.67	2.32^{ns}	5.26**	0.00^{ns}	57.58**	34.84
	POP1(WHS18)	9.67**	8.11**	49.50**	32.72	10.31**	10.19**	11.40^{ns}	34.90**	33.20
	POP2(WHS18)	3.32**	16.45**	54.70**	25.53	4.55**	22.20**	0.00^{ns}	39.20^{ns}	34.05
	POP2(HHS20)	3.10**	1.71^{ns}	76.00**	19.20	5.22**	2.80^{ns}	0.00^{ns}	62.55^{ns}	29.43
	POP2(WHS21)	15.50**	10.00**	58.80**	15.70	21.05**	14.00**	0.00^{ns}	42.50^{ns}	22.00
	POP2(WHS22)	0.95^{ns}	0.00^{ns}	67.18**	31.87	1.72^{ns}	0.00^{ns}	0.00^{ns}	53.58**	44.70
	Average ± SE	5.32 ±2.63	6.01 ±2.19	56.01 ±8.53	32.65 ±7.17	6.94±3.40	8.09±2.79	1.63±44.34	50.59±9.87	32.60±8.07
SG	POP1(MHS17)	1.81^{ns}	0.00^{ns}	64.34**	33.85	0.00^{ns}	1.97^{ns}	33.85**	32.33^{ns}	31.85
	POP1(HHS17)	0.00^{ns}	7.5**	60.25**	32.25	0.00^{ns}	8.70**	10.81**	44.74**	35.75
	POP1(WHS18)	8.14**	9.90**	48.72**	33.24	8.13**	9.91*	48.50**	0.19^{ns}	33.27
	POP2(WHS18)	9.22**	16.43**	42.96**	31.39	11.10**	19.90**	4.00^{ns}	28.08^{ns}	36.92
	POP2(HHS20)	1.90*	7.81**	73.61**	16.68	3.10**	12.00**	0.00^{ns}	59.60^{ns}	25.30
	POP2(WHS21)	4.80**	1.00^{ns}	48.80**	45.40	5.40*	1.5^{ns}	46.40**	0.00^{ns}	46.70
	POP2(WHS22)	2.27*	10.27**	60.76**	26.70	2.90*	14.05**	10.91**	37.61^{ns}	34.53
	Average ± SE	4.02 ± 2.14	7.47 ± 2.65	57.06 ± 9.47	31.37 ± 8.62	4.28±2.06	9.59±3.18	21.98±19.70	28.94±16.14	34.73±9.06

Table 1.2. Continuation.

		M3wE					M3pE					
		Row	Column	Additive	Non-Additive	Residual	Row	Column	Additive	Non-Additive	Additive ×Additive	Residual
TTY	POP1(MHS17)	2.08^{ns}	4.70**	6.48*	59.60**	27.14	2.95*	2.30*	0.00^{ns}	54.06**	17.85^{ns}	22.84
	POP1(HHS17)	2.94*	2.30*	1.70^{ns}	72.21**	20.85	2.10^{ns}	5.11**	0.00^{ns}	42.12**	21.70**	28.93
	POP1(WHS18)	9.94**	9.54**	27.00**	24.85**	28.67	9.94**	9.54**	26.95**	24.90**	0.00^{ns}	28.67
	POP2(WHS18)	3.85**	19.10**	21.00**	28.35**	27.70	3.86**	19.13**	20.72**	28.18**	0.35^{ns}	27.76
	POP2(HHS20)	4.14**	2.04^{ns}	23.46**	46.18*	24.18	4.28**	2.12^{ns}	19.97**	43.57*	5.32^{ns}	24.74
	POP2(WHS21)	18.92**	12.20**	12.32**	37.56*	19.00	20.36**	13.21**	0.00^{ns}	31.18**	15.06^{ns}	20.19
	POP2(WHS22)	1.30^{ns}	0.00^{ns}	8.74^{ns}	52.25**	37.71	1.47^{ns}	0.00^{ns}	0.00^{ns}	45.63**	13.14^{ns}	39.76
	Average ± SD	6.17 ± 3.01	7.14 ± 2.52	14.96 ± 9.75	49.06 ± 11.03	26.15 ± 6.78	6.42±3.13	7.35±2.65	9.66±15.78	38.52±8.49	10.49±14.56	27.56±7.27
SG	POP1(MHS17)	1.65^{ns}	0.00^{ns}	35.08**	37.60**	25.67	0.00^{ns}	1.70^{ns}	34.06**	36.17**	2.28^{ns}	25.81
	POP1(HHS17)	0.00^{ns}	6.84**	26.54**	53.5**	13.12	0.00^{ns}	8.67**	11.30**	4.38^{ns}	40.51**	35.14
	POP1(WHS18)	8.25**	9.94**	47.32**	1.34^{ns}	33.15	8.24**	9.94**	47.32**	1.33^{ns}	0.00^{ns}	33.15
	POP2(WHS18)	10.03**	17.70**	20.12**	19.70^{ns}	32.45	10.32**	18.30**	14.66**	16.23^{ns}	7.02^{ns}	33.47
	POP2(HHS20)	2.45*	10.04**	24.57**	41.95^{ns}	20.99	2.96*	11.45**	0.00^{ns}	29.70**	31.73^{ns}	24.16
	POP2(WHS21)	5.04**	0.82^{ns}	42.00**	6.11^{ns}	46.03	5.04**	0.82^{ns}	42.00**	6.10^{ns}	0.00^{ns}	46.04
	POP2(WHS22)	2.63*	12.16**	27.70**	27.94^{ns}	29.57	2.63**	12.20**	27.64**	27.93^{ns}	0.00^{ns}	29.60
	Average ± SD	4.30 ± 2.12	7.48 ± 2.77	33.85 ± 16.00	31.15 ± 14.28	28.73 ± 7.07	4.17±2.4	9.00±3.09	25.29±17.99	17.40±15.52	11.65±11.98	32.48±7.95

[†]POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022). Average ± SE represents the relative contribution and average standard error of each variance component. $^{**}P \leq 0.01$, $^{*}P \leq 0.05$, and $^{ns}P > 0.05$ are the significance for variance components.

Table 1.3. Variance components (Row, Column, Genotypic, Additive, Non-Additive, Additive × Additive, and Residual) estimated from the models M1, M2wE, M2pE, M3wE, and M3pE for the traits total tuber productivity (TTY, Mg ha^{-1}) and specific gravity (SG).

Trait	Trial†	M1			
		σ_r^2	σ_c^2	σ_g^2	σ_e^2
TTY	POP1(MHS17)	1.01	2.49	83.30	14.32
	POP1(HHS17)	3.31	2.70	34.24	23.08
	POP1(WHS18)	12.10	7.03	35.01	24.16
	POP2(WHS18)	1.61	8.87	23.61	13.93
	POP2(HHS20)	8.34	2.56	124.00	43.41
	POP2(WHS21)	26.51	17.16	71.43	28.61
	POP2(WHS22)	19.00	0.00	96.61	62.66
SG ($\times 10^6$)	POP1(MHS17)	0.00	6.62	51.46	12.90
	POP1(HHS17)	1.68	0.00	77.53	18.25
	POP1(WHS18)	14.74	6.99	29.53	29.74
	POP2(WHS18)	1.72	2.93	70.13	5.67
	POP2(HHS20)	2.01	8.12	48.51	16.53
	POP2(WHS21)	7.38	1.08	52.38	53.95
	POP2(WHS22)	2.49	12.85	48.03	28.14

Table 1.3. Continuation.

Trait	Trial†	M2wE				M2pE				
		σ_r^2	σ_c^2	σ_a^2	σ_e^2	σ_r^2	σ_c^2	σ_a^2	σ_{aa}^2	σ_e^2
TTY	POP1(MHS17)	3.23	2.57	18.18	89.79	2.45	3.08	0.00	66.45	31.68
	POP1(HHS17)	1.32	2.44	49.17	17.33	1.10	2.50	0.00	27.41	16.59
	POP1(WHS18)	8.60	7.21	44.02	29.11	7.59	7.46	8.36	25.6	24.37
	POP2(WHS18)	1.95	9.55	31.75	14.83	1.96	9.60	0.00	16.94	14.73
	POP2(HHS20)	7.49	4.14	183.36	46.23	8.15	4.30	0.00	97.20	45.73
	POP2(WHS21)	28.75	18.68	109.45	29.22	28.94	18.77	0.00	58.31	28.89
	POP2(WHS22)	2.06	0.00	145.98	69.24	2.54	0.00	0.00	78.77	65.72
SG ($\times 10^6$)	POP1(MHS17)	1.53	0.00	54.40	28.60	1.40	0.00	24.09	23.01	22.67
	POP1(HHS17)	0.00	8.30	70.10	37.97	0.00	7.83	9.74	40.29	32.18
	POP1(WHS18)	7.00	8.50	41.90	28.60	6.98	8.50	41.60	16.85	28.54
	POP2(WHS18)	18.20	32.50	85.00	62.10	17.86	32.03	6.32	45.16	59.39
	POP2(HHS20)	1.91	7.87	74.20	16.80	2.04	7.73	0.00	39.26	16.62
	POP2(WHS21)	6.00	1.04	61.00	56.80	6.00	1.03	60.99	39.69	56.82
	POP2(WHS22)	2.53	11.40	67.70	29.80	2.40	11.87	9.22	31.96	9.92

Table 1.3. Continuation.

Trait	Trial†	M3wE					M3pE					
		σ_r^2	σ_c^2	σ_a^2	σ_s^2	σ_e^2	σ_r^2	σ_c^2	σ_a^2	σ_s^2	σ_{aa}^2	σ_e^2
TTY	POP1(MHS17)	2.39	3.31	1.89	81.13	23.41	2.46	3.18	0.00	58.27	19.24	24.62
	POP1(HHS17)	1.08	2.45	3.38	31.09	14.15	1.03	2.52	0.00	20.74	10.68	14.24
	POP1(WHS18)	7.96	7.67	21.59	19.91	22.96	7.96	7.66	21.59	19.60	0.00	22.96
	POP2(WHS18)	1.90	9.42	10.36	13.99	13.67	1.90	9.42	10.20	13.88	0.17	13.68
	POP2(HHS20)	7.63	3.76	43.24	85.10	44.56	7.72	3.81	35.84	78.56	9.60	44.56
	POP2(WHS21)	28.01	18.22	18.30	55.76	28.05	28.26	18.34	0.00	43.28	20.90	28.03
	POP2(WHS22)	21.27	0.00	14.32	85.60	61.78	2.27	0.00	0.00	70.74	20.38	61.64
SG ($\times 10^6$)	POP1(MHS17)	1.20	0.00	25.69	27.53	13.37	1.21	0.00	24.80	26.30	1.66	18.80
	POP1(HHS17)	0.00	6.50	26.30	53.34	13.40	0.00	7.85	10.20	3.96	36.70	31.80
	POP1(WHS18)	7.04	8.48	40.41	1.14	28.31	7.04	8.48	40.40	1.14	0.00	28.30
	POP2(WHS18)	1.78	3.14	35.84	35.07	5.77	17.79	31.51	25.19	27.95	12.10	57.64
	POP2(HHS20)	1.92	7.86	19.24	32.86	16.44	2.02	7.77	0.00	20.12	21.52	16.39
	POP2(WHS21)	6.18	7.98	50.80	7.40	55.70	6.10	1.00	50.88	7.40	0.00	55.77
	POP2(WHS22)	2.50	11.56	26.32	26.56	28.11	2.50	11.56	26.32	26.55	0.00	28.11

†POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022).

1. Supplementary tables MET analysis

Table 2.1 Summary of models M1, M2 and M3 for total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG) traits: Maximum point of the residual log-likelihood (ℓ) and Akaike information criterion (AIC).

Trait	Fitting Parameters	Trial†	M1	M2	M3
TTY	ℓ	POP1	-3819.87	-3817.07	-3811.71
		POP2	-4729.04	-4697.61	-4695.59
	AIC	POP1	7661.75	7656.14	**7649.42**
		POP2	9486.086	9423.226	**9423.17**
SG	ℓ	POP1	6238.00	6270.36	6273.02
		POP2	6342.84	6366.451	6371.90
	AIC	POP1	-12266.20	**-12518.74**	-12520.05
		POP2	-12657.70	**-12704.90**	-12711.80

†POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022).

Table 2.2. Contribution of the variance components of the interactions (Row/Environment, Column/ Environment, Genotypic, Genotypic × Environment, Additive, Additive × Environment, Non-additive, Non-additive × Environment and Residual in %) estimated from the models M1, M2 and M3 for the traits total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG).

Trait	Trial†	M1				
		Row/Environment	Column/ Environment	Genotypic	Genotypic × Environment	Residual
TTY	POP1(MHS17)	52.01**	0.79**	3.00**	3.36**	6.33
	POP1(HHS17)	0.73**	0.56**			19.91
	POP1(WHS18)	3.10**	1.80**			8.36
	POP2(WHS18)	0.39**	2.11**			2.47
	POP2(HHS20)	1.39	1.85	3.29	4.72	29.89
	POP2(WHS21)	7.30**	4.70**			12.20
	POP2(WHS22)	0.40**	0.00ns			29.41
	Average ± SE	9.36 ± 2.26	1.68 ± 1.00	3.14 ± 1.00	4.04 ± 1.00	15.45 ± 1.35
SG	POP1(MHS17)	31.66**	2.37**	8.45**	1.34**	21.94
	POP1(HHS17)	0.00ns	0.41**			14.68
	POP1(WHS18)	5.05**	2.74**			11.35
	POP2(WHS18)	0.19**	0.33**			0.66
	POP2(HHS20)	0.02	0.08	0.29	0.28	0.50
	POP2(WHS21)	0.11**	0.04**			1.61
	POP2(WHS22)	0.24**	13.08**			82.89
	Average ± SE	5.32 ± 1.00	2.72 ± 1.06	4.37 ± 0.72	0.81 ± 0.56	19.04 ± 0.10

Table 2.2 Continuation.

Trait	Trial†	M2				
		Row/Environment	Columm/ Environment	Additive	Additive × Environment	Residual
TTY	POP1(MHS17)	50.32**	0.72**	4.80**	3.82**	6.68
	POP1(HHS17)	0.82**	0.44**			19.84
	POP1(WHS18)	2.27**	1.81**			8.49
	POP2(WHS18)	0.47**	2.18**			2.47
	[illegible]	[illegible]	[illegible]	4.82**	6.03**	[illegible]
	POP2(WHS21)	7.50**	4.84**			12.31
	POP2(WHS22)	0.45**	0.00ns			29.01
	Average ± SE	9.03 ± 2.22	1.74 ± 1.00	4.81 ± 0.53	4.92 ± 0.46	15.01 ±1.31
SG	POP1(MHS17)	30.84**	2.51**	10.40**	2.83**	22.00
	POP1(HHS17)	0.00ns	0.47**			14.06
	POP1(WHS18)	3.02**	3.13**			10.73
	POP2(WHS18)	0.20**	0.34**			0.67
	[illegible]	[illegible]	[illegible]	0.36**	0.42**	[illegible]
	POP2(HHS20)	0.02**	0.08**			1.62
	POP2(WHS21)	0.12**	0.03**			[illegible]
	POP2(WHS22)	0.25	13.00			82.73
	Average ± SE	4.91 ± 1.00	2.79 ± 1.08	5.38 ± 0.17	1.62 ± 0.17	18.85 ± 1.45

Table 2.2 Continuation.

Trait	Trial†	M3						
		Row/Environment	Colunm/ Environment	Additive	Additive × Environment	Non-additive	Non- additive × Environment	Residual
TTY	POP1(MHS17)	52.16**	0.77**	0.81**	1.78ns	2.36**	2.22**	6.34
	POP1(HHS17)	0.84**	0.47**					20.18
	POP1(WHS18)	2.29**	1.92**					7.85
	POP2(WHS18)	0.48**	2.23**					2.41
	[illegible]	[illegible]	[illegible]					[illegible]
	POP2(WHS21)	7.72**	4.96**					12.33
	POP2(WHS22)	0.46**	0.00ns					29.68
	Average ± SD	9.34 ± 2.25	1.79 ± 1.00	1.04 ± 0.10	2.76 ±0.24	2.26 ± 1.04	2.04 ± 1.56	15.10 ± 1.36
SG	POP1(MHS17)	31.88**	2.47**	4.90**	2.84**	3.58**	0.00ns	22.36
	POP1(HHS17)	0.00ns	0.42**					14.19
	POP1(WHS18)	3.26**	3.17**					10.90
	POP2(WHS18)	0.19**	0.34**					0.64
	POP2(HHS20)	0.02**	0.08**	0.28**	0.03ns	0.03ns	0.29**	0.17
	POP2(WHS21)	0.11**	0.04**					1.57
	POP2(WHS22)	0.23**	12.99**					82.99
	Average ± SD	17.84 ± 1.00	2.78 ± 1.08	2.59 ± 0.03	1.43 ± 1.00	1.80 ± 0.09	0.14 ± 1.00	18.97 ± 1.00

†POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022). Average ± SE represents the relative contribution and average standard error of each variance component. $^{**}P \leq 0.01$, $^{*}P \leq 0.05$, and $^{ns}P > 0.05$ are the significance codes for variance components

Table 2.3 Variance components interactions of (Row/Environment, Column/ Environment, Genotypic, Genotypic × Environment, Additive, Additive ×Environment, Non-additive, Non-additive × Environment and Residual) estimated from the models M1, M2 and M3 for the traits total tuber yield (TTY, Mg ha^{-1}) and specific gravity (SG).

Trait	Trial†	M1				
		σ^2_{re}	σ^2_{ce}	σ^2_g	σ^2_{ge}	σ^2_e
TTY	POP1(MHS17)	202.96**	3.11**	11.74**	13.12**	24.71
	POP1(HHS17)	2.85**	2.20**			77.69
	POP1(WHS18)	12.13**	7.04**			32.65
	POP2(WHS18)	1.59**	8.60**			10.04
	POP2(HHS20)	6.46**	7.53**	13.40**	19.20**	120.46
	POP2(WHS21)	29.70**	19.12**			49.66
	POP2(WHS22)	1.65**	0.00^{ns}			119.71
SG	POP1(MHS17)	89.19**	6.68**	23.80**	3.78**	61.81
	POP1(HHS17)	0.00^{ns}	1.14**			41.34
	POP1(WHS18)	14.22**	7.72**			31.98
	POP2(WHS18)	18.72**	31.66**			64.02
	POP2(HHS20)	1.88**	7.83**	28.05**	27.42**	155.93
	POP2(WHS21)	10.86**	4.21**			15.55
	POP2(WHS22)	23.56**	0.00^{ns}			80.06

Table 2.3 Continuation.

Trait	Trial†	M2				
		σ^2_{re}	σ^2_{ce}	σ^2_a	σ^2_{ae}	σ^2_e
TTY	POP1(MHS17)	201.94**	2.87**	19.27**	15.32**	26.80
	POP1(HHS17)	3.30**	7.25**			79.60
	POP1(WHS18)	9.09**	1.74**			34.05
	POP2(WHS18)	2.00**	9.26**	20.49**	25.63**	10.50
	POP2(HHS20)	5.89**	9.54**			111.79
	POP2(WHS21)	31.88**	20.58**			52.33
	POP2(WHS22)	1.91**	0.00ns			123.35
SG	POP1(MHS17)	87.06**	7.09**	29.35**	7.98**	62.01
	POP1(HHS17)	0.00ns	1.33**			39.69
	POP1(WHS18)	8.53**	8.83**			30.27
	POP2(WHS18)	18.87**	33.14**	34.88**	40.84**	65.04
	POP2(HHS20)	1.72**	7.81**			17.57
	POP2(WHS21)	11.42**	3.06**			15.63
	POP2(WHS22)	22.15**	12.58**			80.08

Table 2.3 Continuation.

Trait	Trial†	M3						
		σ^2_{re}	σ^2_{ce}	σ^2_a	σ^2_{ae}	σ^2_s	σ^2_{se}	σ^2_e
TTY	POP1(MHS17)	202.61**	3.00**	3.14**	6.91ns	9.17**	8.61**	24.63
	POP1(HHS17)	3.24**	1.81**					78.39
	POP1(WHS18)	8.90**	7.45**					30.50
	POP2(WHS18)	1.94**	9.10**	5.17**	15.31**	8.83**	7.65ns	9.84
	POP2(HHS20)	6.02**	9.15**					110.26
	POP2(WHS21)	31.55**	20.28**					50.42
	POP2(WHS22)	1.88**	0.00ns					121.37
SG	POP1(MHS17)	88.09**	6.82**	13.53**	7.85**	9.90**	0.00ns	61.78
	POP1(HHS17)	0.00ns	1.15**					39.22
	POP1(WHS18)	9.01**	8.77**					30.12
	POP2(WHS18)	18.57**	32.34**	26.95**	2.51ns	2.96ns	27.81**	6.61
	POP2(HHS20)	1.83**	7.72**					2.95
	POP2(WHS21)	10.96**	4.15**					15.11
	POP2(WHS22)	22.40**	12.54**					62.07

†POP1 and POP2 represent the two different breeding populations. The WHS, MHS, and HHS codes represent the different levels of heat stress: no heat stress, moderate heat stress and high heat stress, respectively. Codes 17, 18, 20, 21, and 22 represent the year in which each experiment was carried out (2017, 2018, 2020, 2021, and 2022). $^{**}P \leq 0.01$, $^{*}P \leq 0.05$, and $^{ns}P > 0.05$ are the significance codes for variance components.

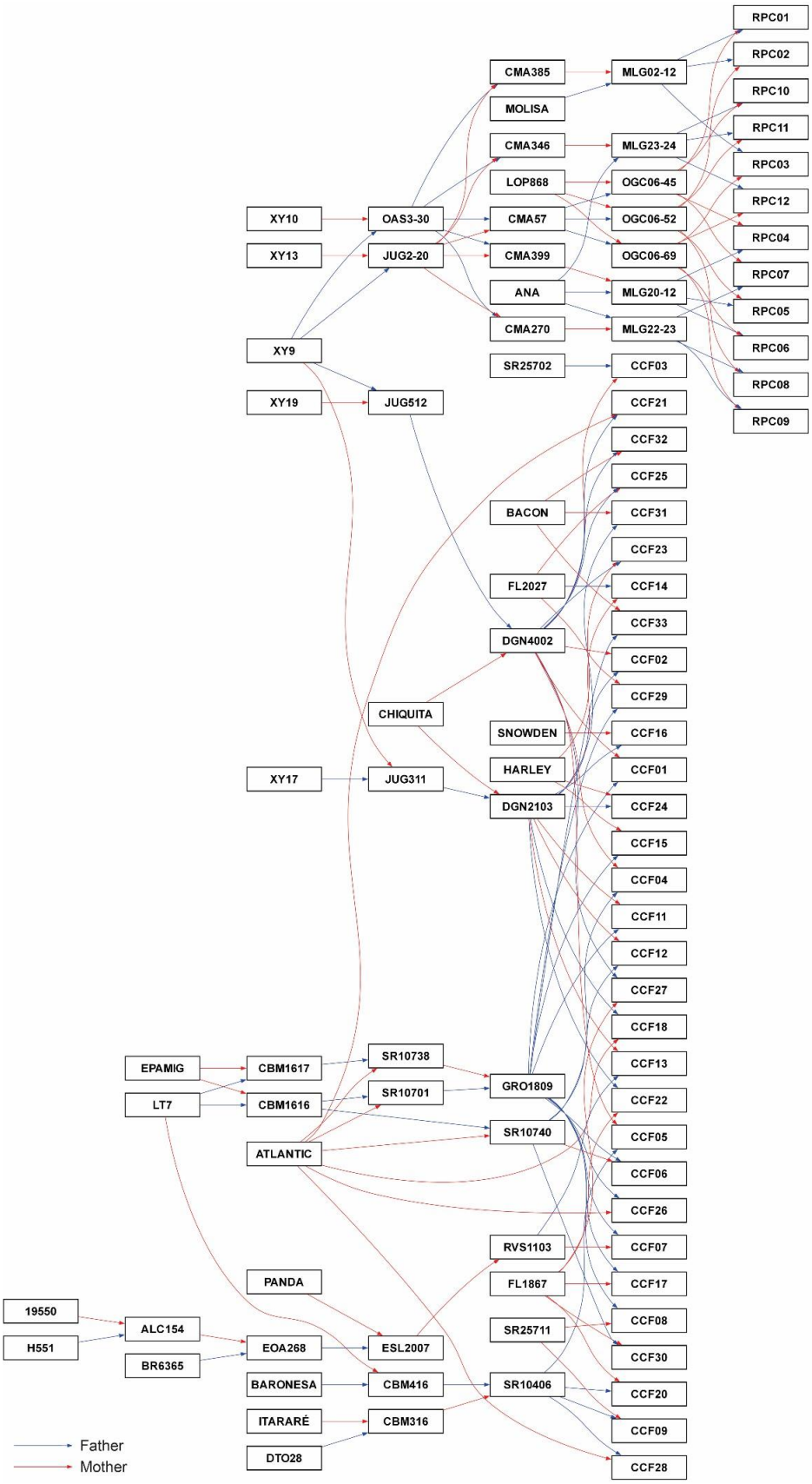

Figure 1. Genealogical overview of the two (POP1 e PO2) populations used to construct the pedigree.

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ARTIGO 2- TROPICAL BREEDING OF TETRAPLOID POTATO: YIELD, SPECIFIC GRAVITY, AND SOFT ROT RESISTANCE

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Luciana Aparecida Miguel1 https://orcid.org/0000-0002-5720-6267[1] *, Tiago de Souza Marçal[1]

[1] Department of Biology, Federal University of Lavras, Lavras, MG, Brazil

* Corresponding authors: luciana.apamiguel@gmail.com

Abstract

Potato has had a long increase in productivity during the last years, but its productive potential is still low and little explored considering the crop potential. In tropical climates, breeding is further affected due to additional challenges such as heat stress, short photoperiods and strong pressure from pests and diseases. The objectives of this study were to dissect the genetic effects into additive and non-additive effects for tuber yield, dry matter content and resistance to soft rot; to estimate the additive, non-additive and total accuracies for tuber yield, dry matter content and resistance to soft rot; and to perform clonal and parental selection based on multiple traits. A total of 356 potato clones from the C0 cycle of recurrent selection for soft rot at the Federal University of Lavras (UFLA), originating from 15 families, were used. The agronomic traits evaluated were total tuber yield (TTY), dry matter content (SG), total large tuber yield (YLT) and average large tuber mass (ATW), and the resistance traits were mean lesion diameter (ALD) and mean lesion depth (ALDp). Three models were used to evaluate the importance of non-additive effects: a base model (M1), a mixed linear model considering additive genetic effects M2 and a mixed linear model including non-additive genetic effects. Factor analysis was used to investigate the association between agronomic and resistance traits. The results showed that, in general, the M2 (additive) model was the best to explain the inheritance of the traits, with the exception of TTY and ALD. The resistance trait ALD showed practically the same accuracy as ALDp, therefore, both were effective in evaluating resistance to soft rot in potatoes. The agronomic trait SG showed a strong association with the resistance traits ALD and ALDp, suggesting an indirect selection through SG for soft rot.

Keywords Bacterial Diseases; Plant Breeding; Factor Analysis; Inheritance Study.

1 Introduction

Potato (*Solanum tuberosum* L.) is one the major staple foods for global food security (Devaux et al. 2014; Devaux et al. 2021; FAO, 2022) and can be consumed fresh or processed. To develop cultivars suitable for fresh or processed markets, potato breeders need to select clones based on several traits, such as yield, quality, appearance, and resistance to major diseases (Jansky, 2009; Jansky and Spooner, 2018). In tropical climates, heat stress, short photoperiods, and the strong pressure from pests and diseases impose additional challenges for potato breeding. For this reason, the combined impact of both abiotic and biotic stresses can

significantly reduce the tuber yield and dry matter content in tropical climates (Fernandes Filho, 2020; Kroschel et al., 2020; Andrade et al., 2021; Patiño-Torres et al., 2021; Martins et al., 2023). In this context, highlight the potato bacterial diseases caused by *Pectobacterium* and *Dickeya*s pecies, such as blackleg and soft rot. These bacteria, being difficult to control, can lead to significant losses both in the field and during storage (Czajkowski et al., 2011; Charkowski, 2018; Charkowski et al., 2020).

The challenge in controlling soft rot makes genetic resistance the most sustainable alternative to mitigate yield losses caused by this disease (Czajkowski et al., 2011; Charkowski, 2015; Lebecka et al., 2021; Ma et al., 2022).However, while some studies have indicated moderate to high heritability for the severity of this disease (Rebecca and Zimnoch-Guzowsha, 2004; Lebecka et al., 2021; Ma et al., 2022), the genetic architecture of resistance to soft rot is not fully understood, despite of the many QTLs identified thus far (Lebecka et al., 2005; Lebecka et al., 2021; Fenstemaker et al., 2024). In this context, it is crucial to dissect the phenotypic variance of key quantitative traits into genetic additive, genetic non-additive, and environment components to infer gene action, as well as to refine the parental and clonal selection strategies in tetraploid potato breeding.

Thus, for each cycle of multi-trait recurrent selection, the potato breeders need to identify both the best clones and parents, aiming to release new cultivars and intercross the selected parents to achieve a new selection cycle (Gopal, 2015; Bradshaw, 2017).In this scenario, multivariate analysis, such as factor analysis, offers the opportunity to extract linear combinations that capture inter-trait information to create "super-traits" that facilitate decision-making (Rocha et al., 2018). Furthermore, the rate of genetic gain across breeding cycles is closely associated with both the accuracy of predicted breeding values and the magnitude of additive genetic standard deviations (Bradshaw, 2022). For this reason, it is essential to partition the phenotypic variance to achieve the accuracy of genetic effects and, consequently, to infer selection efficiency (Martins et al., 2023).

In addition to partitioning phenotypic variance components, it is also necessary to dissect phenotypic values into additive and non-additive genetic effects to enable both clonal and parental selection. Although the *per se* performance of clones can be useful for clonal selection, it is not a reliable indicator for parent selection for some traits, such as tuber yield (Gopal, 2015). Gopal (1998) reported a low correlation between mid-parent values and offspring average. This happens due to the complexities of tetrasomic inheritance and clones' high level of heterozygosity. In this context, the genotypic value of an individual can be

significantly affected by the non-additive genetic effects originating from the intra- and interlocus interactions (Kempthorne, 1954; Gopal, 2015; Endelman et al., 2018; Bradshaw, 2022).

Currently, molecular markers are indispensable for dissecting the genetic architecture of complex quantitative traits in tetraploid potato breeding (Endelman et al., 2018). Nevertheless, genotyping costs exceed those of phenotyping during the early stages of potato breeding programs due to the large size of breeding populations managed at this stage (Stich e Inghelandt, 2018; Bradshaw, 2017; Bradshaw, 2022). Alternatively, Oakey et al. (2006) proposed a parsimonious framework to dissect genetic effects into additive and non-additive effects for complex quantitative traits. This approach is useful for data analysis using the pedigree data in practical potato breeding situations, without incurring additional costs, enabling to extension of the framework reported by Slater et al. (2014).

Partitioning components of phenotypic variance and the estimation of selective accuracy of economically important traits (such as yield, quality, and disease resistance) is crucial for developing a successful potato breeding program. The objectives of this study were to: (i) partition genetic effects into additive and non-additive effects of tuber yield, specific gravity, and soft rot resistance, (ii) estimate additive, non-additive, and total accuracies of tuber yield, specific gravity, and soft rot resistance, and (iii) perform both multi-trait clonal and parental selection. For this study, we used the parsimonious framework proposed by Oakey et al. (2006) to partition phenotypic variance of complex quantitative traits through residual maximum likelihood and linear mixed model methods, and estimate accuracies, which can be used for making selection decisions. Finally, these data will allow us to understand the major factors of the phenotypic variation of tuber yield, dry matter content, soft rot resistance, and the selection potential of the breeding population evaluated.

2 Material and Methods

2.1 Evaluated Clones

In this study, 356 potato clones from the C_0 cycle of recurrent selection for soft rot at the Federal University of Lavras (UFLA) were obtained and evaluated. The C0 cycle breeding population was obtained through a half-diallel mating design with six parents, resulting in 15 crosses (Table 1). These parents were originally selected based on resistance to soft rot and tuber yield.

Table 1. Description of biparental crosses, clonal families, and the number of clones obtained per family.

Crosses	Family	Number of Clones
PRM348 × CBM22-19	MOF01	21
RVS 06-37 × CBM09-10	MOF02	18
ESL 58 × CBM09-10	MOF03	22
ESL 58 × GSI 01-17	MOF04	19
CBM22-19 × RVS 06-37	MOF05	28
CBM22-19 × ESL 58	MOF06	23
PRM348 × RVS 06-37	MOF07	33
PRM348 × GSI 01-17	MOF08	30
GSI 01-17 × CBM09-10	MOF09	20
ESL 58 × RVS 06-37	MOF10	20
PRM348 × ESL 58	MOF11	24
CBM22-19 × GSI 01-17	MOF12	24
RVS 06-37× GSI 01-17	MOF13	35
PRM348 × CBM09-10	MOF14	17
CBM22-19 × CBM09-10	MOF15	22

Source: own elaboration (2025).

2.2 Description of the Field Trial

The field trial was conducted at the Center for Scientific and Technological Development in Lavras, Minas Gerais, during the winter season (May to August) of 2017. The augmented block design (Federer, 1956) was used for the field trial with 15 blocks and five checks, the cultivars Agata, Asterix, BRS- F63 Camila, Cupido, and clone CBM16-16. The plots consisted of a single row with five plants spaced 0.3 m apart within rows and 0.8 m between rows.

The crop management was performed according to the recommendations for the potato crop for the state of Minas Gerais. The soil tillage practices included plowing, harrowing, and rotary hoeing. At planting, 120 kg ha^{-1} of N (nitrogen), 420 kg ha^{-1} of P_2O_5 (phosphorus), and 240 kg ha^{-1} of K_2O (potassium) were applied using 1500 kg ha^{-1} of the 08-28-16 fertilizer. Thirty days after planting, topdressing with 60 kg ha^{-1} of N and 60 kg ha^{-1} of K_2O was done using 300 kg ha^{-1} of the formulated 20-00-20 fertilizer. Sprinkler irrigation on demand to meet the crop evapotranspiration demand.

For the field trial, two traits were evaluated: total tuber yield (TTY, Mg ha^{-1}) and tuber specific gravity (SG). The TTY trait was estimated based on the ratio between the total mass of tubers harvested in the plot and its area (1.2 m^2), subsequently converted to tons per hectare. The SG was estimated using the ratio between the mass of tubers in air and water, where SG = mass of tubers in air / (mass of tubers in air – mass of tubers in water), based on a sample of approximately 2 kg per plot (Schippers, 1976).

2.3 Description of the Laboratory Experiment

The reaction of the clones to soft rot was evaluated in the Bacteriology Laboratory located in the Department of Plant Pathology at UFLA. Tubers harvested from the field experiment were used. After inoculation, they were placed in BOD chambers, adopting the 5×68 α-lattice design with three repetitions and two controls per block (Agata and CBM09-10), with each BOD representing an incomplete block. The Agata cultivar was used as a susceptibility control, while the CBM09-10 clone was used as a resistance control (Assis, 2007). The plots consisted of one tuber.

For the inoculation process, the tubers were washed with water and neutral soap and disinfected in a 1:1 solution of 2% sodium hypochlorite and distilled water for 5 minutes. They were then rinsed with sterilized distilled water to remove excess hypochlorite. The bacterial inoculation into the tuber was performed using a sterile tip to create two holes 15 mm deep and 6 mm in diameter on opposite longitudinal sides of each tuber. With a micropipette, 50 µl of the bacterial suspension was deposited into each hole. After inoculation, the holes were sealed with petroleum jelly, and the tubers were placed in plastic trays that had been washed and disinfected with 70% alcohol, containing moist cotton linings to maintain humidity. The trays were then wrapped in plastic bags to form a humid chamber and subsequently placed in BOD for 72 hours at 28ºC. After 72 hours, the lesions were washed under running water to remove the rotted tissue, and the diameter and depth of the lesionswere measured with a digital caliper. Finally, 6 mm was subtracted from the diameter measurements and 15 mm from the depth measurements, corresponding to the holes made during inoculation. The reaction to soft rot was characterized by the average lesion diameter (ALD) and average lesion depth (ALDp).

2.3 Statistical analyses

2.3.1 Fitted models

Trial plots were arranged in a grid with *r* rows and *c* columns; the matrix form of the mixed linear model is presented in Equation (1):

$$\mathbf{y} = \mathbf{1}\boldsymbol{\mu} + \boldsymbol{Z}_g u_g + \boldsymbol{Z}_r u_r + \boldsymbol{Z}_c u_c + \boldsymbol{e} \quad (1)$$

where $\mathbf{y}^{(N \times 1)}$ is the vector of phenotypic observations, where N is the number of plots; $\mathbf{1}^{(N \times 1)}$ is a vector, in which all elements are equal to one; $\boldsymbol{\mu}^{(1 \times 1)}$ is the intercept; $\mathbf{u}_g^{(g \times 1)}$ is the genotypic random effects vector of clones associated with the matrix $\boldsymbol{Z}_g^{(N \times g)}$, where g is the number of clones; $\mathbf{u}_r^{(r \times 1)}$ is the row random effects vector associated with matrix $\boldsymbol{Z}_r^{(N \times r)}$, where r is the number of rows; $\mathbf{u}_c^{(c \times 1)}$ is the column random effects vector associated with matrix $\boldsymbol{Z}_c^{(N \times c)}$, where c is the number of columns; and $\mathbf{e}$ is the random error vector.

It was assumed that the random effects vectors $\mathbf{u}_g$, $\mathbf{u}_r$, $\mathbf{u}_c$, and $\mathbf{e}$ (Equation 1) are mutually independent and follow a multivariate Gaussian distribution with a mean of zero and (co)variance matrices: var($\mathbf{u}_g$) = $\boldsymbol{G}_g$, var($\mathbf{u}_r$) = $\boldsymbol{G}_r$, var($\mathbf{u}_c$) = $\mathbf{G}_c$ and var($\mathbf{e}$) = $\boldsymbol{R}$. The structures used for each of these (co)variance matrices for model M1 are presented in Table 2.

The genotypic effects vector ($\mathbf{u}_g$) described in Equation (1) can be partitioned into additive ($\mathbf{u}_a$) and non-additive ($\mathbf{u}_s$) genetic effects, as shown in Equation (2) (Oakey et al., 2006; Hunt et al., 2012; Cowling et al., 2015), resulting in the M3 model (Table 2). Thus, the additive relationship matrix was integrated into the model, and the incidence matrix $\boldsymbol{Z}_g$ was adapted by concatenating it with a matrix of zeros [0, $\boldsymbol{Z}_g$], where the zero matrix represents the non-phenotyped ancestors present in the additive relationship matrix. The variance of the genotypic effects vector ($\mathbf{u}_g$) from Equation (2) is presented in Equation (3).

$$\mathbf{u}_g = \mathbf{u}_a + \mathbf{u}_s \tag{2}$$

$$\text{var}(\mathbf{u}_g) = \boldsymbol{A}\sigma^2_a + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{I}_s \end{bmatrix} \sigma^2_s \tag{3}$$

where $\mathbf{A}^{(a \times a)}$ is the additive relationship matrix, a is the number of individuals in the pedigree, $\boldsymbol{I}_s^{(s \times s)}$ is an identity matrix, s represents the number of clones evaluated, and σ^2_a and σ^2_s are the variance components associated with the additive ($\mathbf{u}_a$) and non-additive ($\mathbf{u}_s$) effect vectors, respectively. Notably, the exclusion of the non-additive effects vector ($\mathbf{u}_s$) represents a return to the traditional animal model (M2, Table 2) used by Slater et al. (2014b).

Tabela 2. Structures of (co)variance of the fitted models: M1 (base model), M2 (animal model), M3 (animal model including non-additive effects).

(Co)variance matrix[1]	M1	M2	M3
$\mathbf{G}_r$	$\sigma_r^2\mathbf{I}_r$	$\sigma_r^2\mathbf{I}_r$	$\sigma^2_r\mathbf{I}_r$
$\mathbf{G}_c$	$\sigma_c^2\mathbf{I}_c$	$\sigma_c^2\mathbf{I}_c$	$\sigma^2_c\mathbf{I}_c$
$\mathbf{G}_g$	$\sigma_g^2\mathbf{I}_g$		
$\mathbf{G}_a$		$\sigma_a^2\mathbf{A}$	$\sigma^2_a\mathbf{A}$
$\mathbf{G}_s$			$\sigma^2_s\mathbf{I}_s$
$\mathbf{R}$	$\sigma_e^2\mathbf{I}_N$	$\sigma_e^2\mathbf{I}_N$	$\sigma^2_e\mathbf{I}_N$

[1]$\mathbf{G}_r$, $\mathbf{G}_c$, $\mathbf{G}_g$, $\mathbf{G}_a$, $\mathbf{G}_s$e$\mathbf{R}$: Matrices of (co)variance associated with the effects of row, column, genotypic, non-additive, and error, respectively;σ^2_r, σ^2_c, σ^2_g, σ^2_a,σ^2e σ^2_s $\sigma^2_e$are variance components associated with row, column, genotypic, additive, non-additive, and error $\mathbf{I}_r$, $\mathbf{I}_c$, $\mathbf{I}_g$, $\mathbf{I}_s$e $\mathbf{I}_N$ are identity matrices related to row, column, genotypic, non-additive, and error, respectively; A is the additive relationship matrix. Source: Miguel et al., (2025).

An additive relationship matrix (***A***) was constructed using R software (R Core Team, 2022) through the AGHmatrix package (Amadeu et al., 2016) from the pedigree of each population, employing a suitable algorithm for autopolyploid species (Kerr et al., 2012; Hamilton and Kerr, 2018) and a double reduction rate of w = 0.10 (Slater et al., 2014b).

The variance component estimates of the models presented in Table 2 were obtained using the REML method (Patterson and Thompson, 1971), and the EBLUPs were predicted using the equations of mixed models by Henderson (Henderson et al., 1959). All analyses were conducted using Echidna Mixed Models software (Gilmour, 2024) version 1.85. Subsequent sections' analyses were carried out using R software (R Core Team, 2024).

2.2.2 Comparison of the models

The relative contributions of the variance components were calculated to aid in the interpretation of the results, with each component expressed as a proportion of the total variance (i.e., the sum of all variance components in the model). Mean relative contributions were also provided for the variance components of each effect along with their respective approximate standard errors using the delta method. The Akaike Information Criterion (AIC) was utilized for model comparison, as presented in equation (4) (Akaike, 1974). The significance of variance components was assessed using the likelihood ratio test (LRT) method, as shown in equation (5):

$$AIC = -2\ell + 2p \quad (4)$$

$$LRT = -2\ln(\ell_1/\ell_2) \quad (5)$$

where ℓ is the logarithm of the maximum point of the residual log-likelihood function, p is the number of variance parameters. For selection strategies, ℓ_1 is the maximum point of the residual

log-likelihood function of the reduced model (without the tested effect), and ℓ_2 is the maximum point of the residual log-likelihood function of the full model

2.2.3 Accuracies and selection

The accuracies associated with the additive effects ($r_{\hat{a}a}$) (Butler et al., 2017; Cowling et al., 2015), non-additive effects ($r_{\hat{s}s}$) and genotypic effects ($r_{\hat{g}g}$) were estimated using expressions (6), (7) and (8), respectively. The RE measures the efficiency of clonal selection compared to parental selection.

$$r_{\hat{a}a} = \sqrt{1 - \frac{\upsilon_a}{(1+F)\sigma_a^2}} \tag{6}$$

$$r_{\hat{s}s} = \sqrt{1 - \frac{\upsilon_s}{\sigma_s^2}} \tag{7}$$

$$r_{\hat{g}g} = \sqrt{1 - \frac{\upsilon_g}{(1+F)\sigma_a^2 + \sigma_s^2}} \tag{8}$$

in which υ_a, υ_s and υ_g are the values of the variance of the prediction error (PEV) of the additive, non-additive and genotypic effects, respectively; F is the inbreeding coefficient.

The PEVs of the additive (υ_a) and non-additive (υ_s) effects were directly obtained from the diagonal of the inverse of the left-hand side of the mixed model equations system (Henderson et al., 1959). Meanwhile, the PEV associated with the vector of total genotypic effects (υ_g) from model M3 was obtained from the diagonal of the matrix presented in equation (10). The diagonal of this matrix provides the PEV of the linear combination between the vector $\mathbf{u}_a$ and $\mathbf{u}_s$.

$$\text{Var}(\mathbf{L}_g\mathbf{u}_g) = \mathbf{L}_g\mathbf{C}^{-1}\mathbf{L}_g^T \tag{9}$$

$$\mathbf{C} = \mathbf{W}^T\mathbf{R}^{-1}\mathbf{W} \tag{10}$$

where $\mathbf{L}_g^{(g \times \beta)}$ is the matrix of linear combinations between the $\mathbf{u}_a$ and $\mathbf{u}_s$ vectors of the M3 model, where g is the number of total predicted genotypic effects andβ is the total number of effects included in the M3wE model (fixed and random); $\mathbf{C}^{(\beta \times \beta)}$ is the matrix of the coefficients of the system of equations of mixed models; $\mathbf{W}$ is the matrix of the model that concatenates the incidence matrices of the fixed and random effects of the M3wE model, where $\mathbf{W}^T = (\mathbf{1}, \mathbf{Z}_a, \mathbf{Z}_s, \mathbf{Z}_r, \mathbf{Z}_c)^T$.

Clonal and parental selection was performed using factor analysis of the FAI-BLUP selection index (Rocha et al., 2018). Selection was in the positive direction for the traits TTY

and SG, and in the negative direction for the traits ALD and ALDp, selecting the top 20 individuals evaluated.

3 Resultados

3.1 Models and partitioning of the genotypic effect

The choice of the most appropriate model was based on the Akaike Information Criterion (AIC) values, with the model with the lowest AIC being considered the best fit to the data. Overall, model M2 presented the best fit for most agronomic and resistance traits, evidencing the predominance of additive effects in the evaluated traits. However, for total tuber yield (TTY), the most appropriate model was M1, which suggests that the total genotypic effect, without decomposition, is more representative in this case. For the ALD (lesion diameter) trait, model M3 was the most informative, indicating that both additive and non-additive effects contribute significantly to the expression of this trait (Supplementary Material, Table S1). For the traits TTY, SG and YLT, there was no significant gain in log-likelihood (ℓ) between the models, indicating that the additional complexity of the M2 or M3 models did not substantially improve the fit (Supplementary Material, Table S1).

The decomposition of variance components in model M1 revealed that genotypic variance (σ_g^2) was significant for all agronomic traits, being higher for SG (40.03 ± 9.49) and TTY (33.30 ± 8.15). These results suggest sufficient genetic variability to promote gain by selection. For ATW and YLT, residual variance represented most of the phenotypic variation (74.00 ± 6.57 and 73.94 ± 9.47, respectively), with smaller proportions of genotypic variance, suggesting that these traits are strongly influenced by non-genetic factors (Supplementary Material, Table S2). In model M2, additive components (σ_a^2) were significant for all traits, evidencing the contribution of genes with fixable additive effects on the total genetic variance. The SG trait maintained the highest σ_a^2 among the agronomic traits (42.20 ± 10.76), indicating that selection based on additive genetic values can be highly efficient for this trait (Supplementary Material, Table S2).

For TTY, σ_a^2 was reduced (13.70 ± 9.02), which, combined with the high value of the residual variance (55.41 ± 9.09), suggests that other genetic components (e.g., dominance and epistasis) and environmental factors play an important role. Among the resistance traits, ALD presented an additive component almost twice as high as that observed for ALDp (45.10 ± 3.95 *vs*. 24.71 ± 4.48) (Supplementary Material, Table S2).

In the M3 model, the inclusion of the non-additive component (σ_a^2) allowed greater detailing of the genetic architecture. For TTY and ALD, the non-additive components (σ_s^2) were

significant and expressive (30.82 ± 8.69 and 24.15 ± 7.64, respectively), reinforcing the existence of dominance or epistasis effects relevant to these traits (Supplementary Material, Table S2). On the other hand, for SG, ATW, YLT and ALDp, the non-additive component (σ_s^2) was null or not significant, indicating that these traits are predominantly controlled by additive effects, which facilitates the selection of superior parents based on predicted values (Supplementary Material, Table S2).

The joint interpretation of the models highlights the need for distinct strategies for each trait in the context of potato genetic improvement. For traits such as SG, ATW and YLT, the predominance of additive heritability suggests that parental selection (through additive genetic values) can be highly effective. In contrast, for TTY and ALD, non-additive effects play an important role, making clonal selection more appropriate. In these cases, the use of elite clones or specific hybrids can maximize genetic gain by exploiting heterosis and genetic complementarity.

3.2 Accuracies and selection

For the agronomic traits, the value of $r_{\hat{g}g}$ was estimated only for TTY, presenting a moderate correlation of 0.66, reflecting a reasonable prediction of the total genotypic variance. For the other traits, the correlations refer to the additive variance ($r_{\hat{a}a}$) (Table 3). The highest value was observed for SG (0.74), indicating high accuracy in predicting the additive effects for this trait, consistent with previous results that showed significant additive variance. Next, the traits ATW and YLT presented values of 0.62 and 0.61, respectively, indicating moderate accuracy in predicting the additive effects. The overall average accuracy of the additive components for the agronomic traits was 0.65 (Table 3).

In the case of the resistance traits, the estimated correlations refer to the aditive ($r_{\hat{a}a}$) and non-additive ($r_{\hat{s}s}$) omponents. For ALDp, the value of $r_{\hat{a}a}$ was estimated, which presented a value of 0.69, indicating that the non-additive effects were predicted with good accuracy for this trait (Table 3).

These results reinforce the findings of models M2 and M3, in which SG and ALDp demonstrated a strong additive component, while ALD and TTY were mainly influenced by non-additive effects. The correlations obtained validate the accuracy of the models in separating genetic effects and indicate that selection can be conducted based on reliable predictions of genetic effects for the different traits, respecting their respective inheritance natures (Table 3).

Table 3. Accuracies of additive effects ($r_{\hat{a}a}$), non-additive effects ($r_{\hat{s}s}$) and total genotypic effects ($r_{\hat{g}g}$) for the field traits total tuber yield (TTY, Mg ha^{-1}), specific gravity (SG), average mass of large tubers (ATW), total yield of large tubers (YLT) and laboratory traits average tuber lesion diameter (ALD) and average tuber lesion depth (ALDp).

Trial	Trait†	$r_{\hat{g}g}$	$r_{\hat{a}a}$	$r_{\hat{s}s}$
AGRONOMIC	TTY	0.66		
	SG		0.74	
	ATW		0.62	
	YLT		0.61	
	Average		0.65	
RESISTANCE	Trait†	$r_{\hat{g}g}$	$r_{\hat{a}a}$	$r_{\hat{s}s}$
	ALD			0.69
	ALDp		0.70	

† Identification of the traits evaluated the agronomic and resistance.
Source: own elaboration (2025).

The factor analysis of clonal selection (Table 4) showed that the first two factors extracted jointly explained a substantial proportion of the total variance observed in the characteristics analyzed. The factor loadings indicated that Factor 1 (FA1) is strongly related to the variables SG (0.776), ALD (-0.777) and ALDp (-0.756), suggesting that this factor represents an axis of variation associated with a higher specific gravity and lower average lesion diameter and depth (Table 4). The variable SG showed a positive association with FA1, while ALD and ALDp showed a negative association, which may indicate an inverse relationship between specific gravity and tuber resistance characteristics.

On the other hand, Factor 2 (FA2) was strongly influenced exclusively by the variable TTY (-0.998), clearly representing an axis of total productivity. The other characteristics showed loadings very close to zero in this factor, indicating that FA2 describes the variation associated with production in isolation (Table 4).

In addition to parental selection (Table 5), factor analysis also identified two main factors (FA1 and FA2), which jointly explain most of the variability observed among the evaluated traits. Factor 1 (FA1) showed strong correlations with the variables SG (0.839) and ALD (-0.838). The positive correlation between SG (specific gravity) and FA1, combined with the negative correlation of ALD (mean diameter of the tuber lesion), suggests an inverse relationship between these two variables. In other words, plants with higher SG tend to present lower ALD values, and vice versa (Table 5).

Factor 2 (FA2), in turn, was strongly associated with the variable TTY (0.996) (Table 5). The magnitude of the factor loading of TTY in FA2 and the low correlation of this variable with FA1 indicate that productivity varies practically independently of the other traits analyzed. The commonalities reinforce the adequacy of the model, indicating that the two factors explain the variability of the characteristics well. TTY presented a commonality of 0.999, that is, practically all of its variation was captured by the model (Table 5). SG and ALD were also well represented, with commonalities greater than 0.70, reflecting a good adequacy of the factorial structure.

Table 4. Results of the factor analysis for clonal selection for traits total tuber yield (TTY, Mg ha-1), specific gravity (SG), the total yield of large tubers (YLT) and laboratory traits average tuber lesion diameter (ALD) and average tuber lesion depth (ALDp).

Traits	FA1	FA2	Comunalidades
SG	0.776535	-0.014	0.6032018
ALD	-0.77706	-0.0062	0.6038576
TTY	-0.05371	-0.9982	0.9992454
ALDp	-0.75571	-0.0346	0.5723006

Source: own elaboration (2025).

Table 5. Results of the factor analysis for parental selection for traits total tuber yield (TTY, Mg ha-1), specific gravity (SG) and laboratory traits average tuber lesion diameter (DMLT).

Traits	FA1	FA2	Comunalidades
SG	0.838546	0.041121	0.7048502
ALD	-0.83849	-0.02086	0.7035035
TTY	-0.09145	0.995748	0.9998784

Source: own elaboration (2025).

Based on the scatter plot constructed from the main components FA1 (45%), associated with SG and ALD, and FA2 (25%) associated with TTY, it was possible to classify the evaluated individuals into four distinct quadrants, allowing a joint analysis of performance (FA1 axis) and stability (FA2 axis), both for clonal and parental selection. This approach made it possible to identify superior genotypes for direct selection and composing strategic crosses (Table 4).

In the clonal selection graph (Figure 1), the clones located in quadrant I, with positive values for both components, simultaneously presented high TTY and high SG. These genotypes, highlighted in green in the graph, represent the most promising clones, bringing together desirable characteristics for direct selection and possible recommendation. The presence of individuals in this quadrant demonstrates the efficiency of the selection process

used, since reconciling productivity and specific gravity is one of the main challenges in genetic improvement.

In quadrant II, there are clones with low SG (negative FA1 values) but with high TTY (FA2 values above average), represented in brown (Figure 1). Although these clones do not stand out in terms of productivity, their stability can be explored in crossing programs, especially with clones from quadrant IV, aiming to combine these complementary characteristics.

The clones from quadrant III, marked in black, presented negative values for both principal components, which indicates low performance combined with low TTY and SG. These clones are considered the least desirable and are not recommended for selection or as parents, since they do not present agronomic advantages in either of the two dimensions evaluated.

In quadrant IV, there are clones with high SG (positive FA1 values) but with TTY below average (negative FA2 values) (Figure 1). Represented in blue, these clones demonstrate good productive potential, but with unstable SG, which may limit their direct recommendation. However, they are interesting candidates for crossbreeding with clones from quadrant II, aiming to generate descendants that combine high performance with greater stability.

The controls, indicated in red, are distributed between quadrants II and III. Some of them present relatively good SG, but performance below the average (quadrant II), while others are associated with low TTY and SG (quadrant III) (Figure 1). Notably, no control was allocated to quadrant I, which reinforces the superior potential of some experimental clones with the material currently used as a reference. Thus, the results demonstrate the presence of superior clones among those evaluated, especially those located in quadrant I, which should be prioritized in advanced stages of the breeding program.

In parental selection (Figure 2), the main components FA1 (60%) associated with SG and ALD and FA2 (21%) associated with TTY allow an accurate analysis of the population in terms of performance (FA1 axis) and stability (FA2 axis), serving as a strategic tool for parental selection in the breeding program. Dividing the graph into quadrants makes it possible to identify groups of genotypes with different agronomic profiles and make informed decisions about selection and crossings (Table 5).

Quadrant I, corresponding to clones with positive values for FA1 and FA2, represents clones with high TTY and high SG. These clones, highlighted in the graph in light green, are considered the most promising for direct selection, as they combine superior productivity with

SG consistency across environments. Therefore, they constitute the best candidates for parents in breeding programs aimed at launching widely adapted cultivars.

Quadrant II contains clones with negative values for FA1 and positive for FA2: low SG but high TTY. When combined with more productive clones (such as those in quadrant IV), they can contribute to the generation of hybrids with a greater balance between performance and predictability.

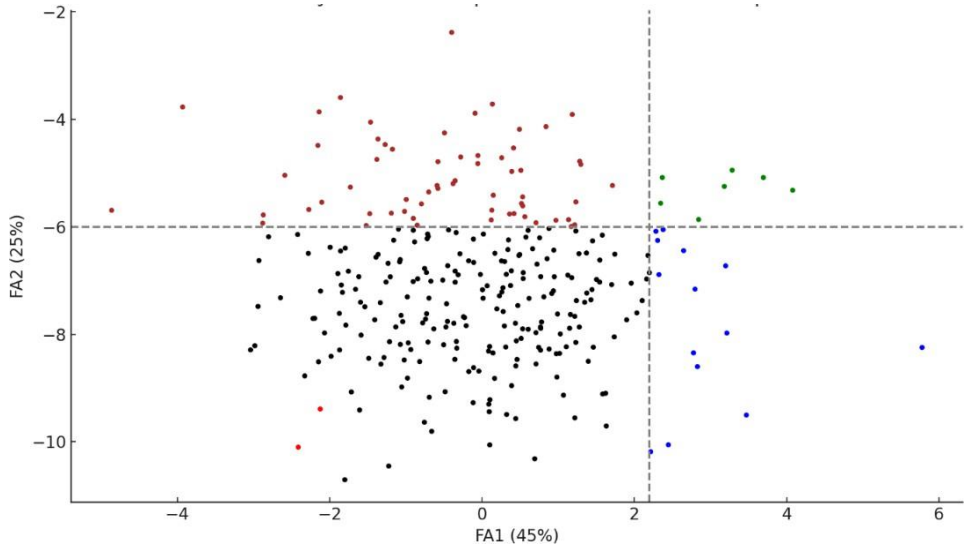
Quadrant III, where clones present negative values for both FA1 and FA2, brings together the worst performances in both criteria: low TTY and SG. The clones in this group, indicated in brown, are not recommended for selection or use as parents, and it is preferable to discard them from the breeding program.

Quadrant IV, which brings together clones with positive values for FA1 and negative for FA2, contains clones with high SG but low TTY. Represented in the graph in blue, these clones demonstrate high productive potential, but their instability may limit their direct adoption as cultivars. However, they are highly interesting as parents in crosses with clones in quadrant II, aiming to obtain descendants that combine productivity and stability.

The controls, highlighted in red, are scattered between quadrants II and III, indicating that, for the most part, they perform below or similar to the average of the experimental population. No control is positioned in quadrant I, which shows that several experimental clones outperform the materials. Clones from quadrants I and IV should be prioritized for parental selection, with those from quadrant I being the most recommended for direct selection. Crossing strategies between quadrants II (SG) and IV (TTY) have also proven effective in obtaining lines with a favorable combination of agronomic characteristics, contributing to the success of the next stages of the breeding program.

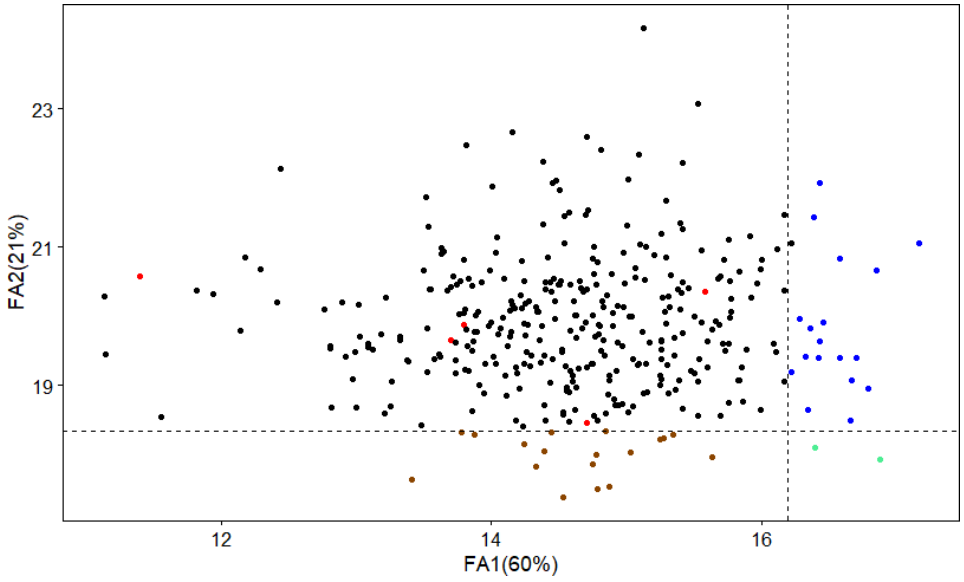
In addition, for crosses between these individuals, it is necessary to verify whether they are from different families, since most of the selected clones are from the same families. It is important to carefully evaluate and choose individuals who complement each other.

Figure 1. Clonal selection graph based on factor analysis for the SG, TTY, and ALD traits, factors FA1 and FA2. Selected clones are above or to the left of the dashed line and are represented by dots; brown dots indicate clones selected for the SG and ALD trait; blue dots indicate clones selected for TTY; red indicates the control Ágata, and green dots indicate clones selected for both factors (MOF14-15).



Source: own elaboration (2025).

Figure 2. Parental selection graph based on factor analysis for the SG, ALD, and ALDp traits, FA1 and FA2.Selected clones are above or to the left of the dotted line and are represented by dots; brown dots indicate clones selected for the SG trait; blue dots indicate clones selected for ALD; red dots indicate the controls (Asterix, CBM16-16, and Cupido), and green dots indicate clones selected for both traits (MOF03-15 and MOF03-18).



Source: own elaboration (2025).

4 Discussion

Given the global importance of the potato crop, both in terms of consumption and its contribution to food security, genetic improvement of this species remains in constant development. However, the high degree of heterozygosity of the parents, the complexity of tetrasomic inheritance and long selection cycles have limited genetic progress for important traits, such as productivity, dry matter content and disease resistance (Haynes et al., 2012; Slater et al., 2014a; Bradshaw, 2017; Jansky and Spooner, 2018; Bradshaw, 2022; Miguel et al., 2025). In this context, it is essential to investigate the inheritance of these traits to develop more efficient selection strategies.

Genotypic variance analyses indicated significant genetic variability among clones for all traits evaluated, demonstrating the feasibility of selection. For agronomic traits, the results suggest that total tuber yield (TTY) is predominantly conditioned by non-additive gene action, while specific gravity (SG) presents predominantly additive inheritance. These findings corroborate the works of Slater et al. (2014a) and Sood et al. (2022), in which greater heritability in the narrow sense was observed for SG compared to TTY. Gopal (2015) and Arcaute et al. (2022) also reported that the general combining ability for SG is higher than the specific ability, reinforcing the predominance of additive gene action. On the other hand, the results for TTY indicate a more complex inheritance pattern, requiring selection strategies that contemplate non-additive effects, such as specific crosses and recurrent selection between families (Miguel et al., 2025).

Regarding resistance to soft rot, both lesion diameter (ALD) and lesion progression (ALDp) presented distinct inheritances. ALD demonstrated a greater contribution of additive variance and better experimental precision, while ALDp showed a greater influence of non-additive effects. This suggests that, although both traits are related to disease resistance, the underlying genetic architecture differs between them. Similar results were obtained by Lebecka and Zimnoch-Guzowska (2004), who reported high heritability for resistance to soft rot in diploid potato populations, with predominantly additive inheritance. However, the results of this study indicate that, at least for ALDp, non-additive effects also play a relevant role, which should be considered in breeding programs. The same authors also highlight that resistance to soft rot does not present a significant correlation with agronomic traits, which may explain the lower association of ALDp with SG or TTY.

Factor analysis, used for clonal and parental selection, allowed the dimensionality of the data to be reduced and latent groups of correlated traits to be identified, as suggested by the

foundations of this multivariate technique (Johnson and Wichern, 2007; Ferreira, 2008). This approach is especially useful in genetic improvement studies involving multiple correlated phenotypic variables, as it allows the identification of factors that concentrate the common variance between traits, optimizing simultaneous selection (Cruz et al., 2012; Rocha et al., 2018).

In clonal selection, factor analysis revealed that TTY is strongly associated with the second factor (FA2), while ALD and SG were associated with the first factor (FA1), both with high commonalities. This indicates that these factors adequately synthesize the observed variability and allow the selection of clones that simultaneously combine desirable traits. The association between ALD and SG suggests that clones with higher dry matter content tend to have lower lesion severity, and vice versa. This correlation had already been pointed out by Assis (2007) as a possible route of indirect selection, although Wolters and Collins (1995) reported low-magnitude genetic correlation between the same traits. The divergence between studies may reflect differences in the populations evaluated, the pathogens tested, or the environmental conditions.

In parental selection, the factor analysis maintained the pattern of association: SG and ALD in FA1 and TTY in FA2, with the addition of the high commonality of ALDp, indicating its relationship with TTY in this context. This consistency between clonal and parental reinforces the robustness of the factual groupings. The stability of the factors and the high explained variance provide greater security in the choice of clones based on these latent variables, as pointed out by Ferreira (2008) and corroborated by Rocha et al. (2018) in the context of plant breeding.

The visualization of the scatter plots of the factors, which group the clones into four quadrants, allowed a practical categorization of the individuals. The upper right quadrant (Q1), which brings together clones with superior performance in both factors, is the most desirable from a breeding point of view, as it combines high yield, resistance to soft rot, and technological quality. The lower left quadrant (Q3), on the other hand, contains clones with inferior performance, being potential sources of recombination in crosses with high-performance parents, such as those positioned in Q1 or Q2.

The strategy of crossing individuals from contrasting quadrants is particularly interesting for traits with complex and non-additive inheritance, such as TTY and ALDp, as it increases the chance of recombination of favorable alleles and expression of positive transgressions. As proposed by Resende (2016), the combined use of multivariate analyses and

mixed models can intensify the gains from selection, especially when the extracted factors are strongly correlated with the original variables and with each other.

It was also observed that more than half of the clones selected for SG and ALD coincided with each other in clonal and parental selection, evidencing their dual utility: as candidates for composing commercial cultivars and as parents for new combinations. Lebecka and Zimnoch-Guzowska (2004) recommend that the selection of parents in potatoes be based on repeated phenotypic evaluations and that crosses between 4x-2x species can generate progenies with greater resistance. Thus, the use of resistant diploid clones as parents of tetraploids can be a viable alternative for the genetic control of soft rot, especially when combined with high specific gravity and productivity.

Therefore, based on the factual groupings and observed heritability patterns, it is recommended to adopt two independent recurrent selection programs: one focused on SG and resistance to soft rot (FA1), with an emphasis on additive action, and another focused on yield (FA2), with strategies aimed at taking advantage of non-additive variance. Additional evaluations in different environments are essential to confirm the stability of the correlations between the traits and the consistency of the factors, as emphasized by Lebecka and Zimnoch-Guzowska (2004).

5 Conclusion

In general, the M2 (additive) model was the best to explain the inheritance of the traits, with the exception of TTY and ALD. The ALD resistance trait showed practically the same accuracy as ALDp, and were therefore effective in evaluating resistance to soft rot in potatoes. However, the agronomic trait SG showed a strong association with the ALD and ALDp resistance traits, evidencing that selection for soft rot can be performed indirectly through SG.

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Supplementary material

Table S1. Summary of models M1, M2 and M3for total tuber yield (TTY, Mg ha^{-1}), specific gravity (SG), the average mass of large tubers (ATW), the total yield of large tubers (YLT) and laboratory traits average tuber lesion diameter (ALD) and average tuber lesion depth (ALDp2) traits: Maximum point of the residual log-likelihood (ℓ) and Akaike information criterion (AIC).

Fitting Parameters	Trait	M1	M2	M3
ℓ	TTY	-1240.25	-1243.36	-1239.74
	SG	-531.20	-518.07	-518.03
	ATW	-1527.23	-1520.42	-1520.42
	YLT	-1183.28	-1180.61	-1180.61
	ALD	-1428.56	-1423.55	-1421.67
	ALDp	-1322.57	-1315.67	-1315.44
AIC	TTY	**2488.51**	2494.72	2489.50
	SG	1070.40	**1044.14**	1046.07
	ATW	3062.46	**3048.85**	3050.85
	YLT	2374.56	**2369.23**	2371.23
	ALD	2863.12	2853.11	**2851.35**
	ALDp	2651.14	**2637.34**	2638.88

Source: own elaboration (2025).

Table S2. Contribution of the variance components (Row, Column, Genotypic, Additive, Non-Additive, Block and Residual in %) estimated from the models M1, M2, and M3 for traits total tuber productivity (TTY, Mg ha^{-1}), specific gravity (SG), the average mass of large tubers (ATW), the total yield of large tubers (YLT) and laboratory traits average tuber lesion diameter (ALD) and average tuber lesion depth (ALDp). Continue.

Trial	Trait	M1			
		Row	Column	Genotypic	Residual
AGRONOMIC	TTY	19.80** ± 5.76[1]	11.50** ± 4.00	33.30** ± 8.15	35.45 ± 7.77
	SG	7.51** ± 3.43	2.10* ± 1.96	40.03** ±9.49	50.38 ± 9.28
	ATW	6.21** ± 3.25	3.85* ± 2.62	16.00** ± 5.78	74.00 ± 6.57
	YLT	7.00** ±3.48	0.00^{ns} ± 0.00	19.16** ± 9.37	73.94 ± 9.47
RESISTANCE	Trait	Block		Genotypic	Residual
	ALD	6.27** ± 9.65		35.45** ±11.58	58.30 ± 13.96
	ALDp	10.47** ± 4.29		19.20** ±3.38	70.33 ± 4.59

Table S2. Conclusion

Trial	Trait†	M2				M3				
		Row	Column	Additive	Residual	Row	Column	Additive	Non-Additive	Residual
AGRONOMIC	TTY	19.00**± 5.64	12.23**± 4.53	13.70**± 9.02	55.41± 9.09	19.48**± 5.71	11.61**±4.31	2.89^{ns}±4.00	30.82**±8.69	35.20±7.72
	SG	7.20**± 3.20	2.10*± 1.71	42.20**± 10.76	48.60 ± 10.10	7.25**± 3.25	2.10*± 1.83	36.77**±21.12	5.40^{ns}±19.19	48.51±9.76
	ATW	6.15**± 3.19	3.72*± 2.54	14.23**± 5.51	76.00± 6.27	6.15**± 3.18	3.73*± 2.54	14.23**±5.52	0.00^{ns}±0.00	75.90±6.28
	YLT	7.00**± 3.45	0.00^{ns}± 0.00	13.00**± 6.97	80.15± 7.28	7.00**± 3.45	0.00^{ns}± 0.00	13.00**±6.97	0.00^{ns}±0.00	80.15±7.28
RESISTANCE	Trait	Block		Additive	Residual	Block		Additive	Non-Additive	Residual
	ALD	5.10**± 2.34		45.10**± 3.95	49.87± 3.84	6.00**± 2.73		12.30**±9.39	24.15*±7.64	57.60±4.17
	ALDp	9.55**± 3.97		24.71**± 4.48	65.73± 4.98	10.00**± 4.14		14.80**±10.31	6.91^{ns}±7.38	68.32±5.30

† Represents agronomic traits evaluated in field experiments and resistance traits evaluated in laboratory experiments. [1] Represents average standard error of each variance component. $^{**}P \leq 0.01$, $^{*}P \leq 0.05$, and $^{ns}P > 0.05$ are the significance for variance components.
Source: own elaboration (2025).

Table S3. Variance components (Row, Column, Genotypic, Additive, Non-Additive, Block, and Residual) estimated from the models M1, M2 and M3for the for traits total tuber productivity (TTY, Mg ha^{-1}), specific gravity (SG), the average mass of large tubers (ATW), the total yield of large tubers (YLT) and laboratory traits average tuber lesion diameter (ALD) and average tuber lesion depth (ALDp).

Trial	Trait	M1			
		σ^2_r	σ^2_c	σ^2_g	σ^2_e
AGRONOMIC	TTY	32.33**	18.72**	54.36**	58.00
	SG	0.38**	0.10*	2.02**	2.54
	ATW	45.48**	28.21*	116.93**	541.70
	YLT	9.17**	0.00^{ns}	25.48**	98.32
RESISTANCE	Trait	σ^2_b		σ^2_g	σ^2_e
	ALD	0.46**		2.62**	4.30
	ALDp	0.60**		1.10**	4.01

Table S3. Conclusion.

Trial †	Trait	M2				M3				
		σ_r^2	σ_c^2	σ_a^2	σ_e^2	σ_r^2	σ_c^2	σ_a^2	σ_s^2	σ_e^2
AGRONOMIC	TTY	30.48^{**}	20.00^{**}	22.38^{**}	90.50	31.91^{**}	19.01^{**}	4.73^{ns}	50.47^{**}	57.64
	SG	0.39^{**}	0.11^{*}	2.30^{**}	2.66	0.38^{**}	0.11^{*}	2.00^{**}	0.28^{ns}	2.60
	ATW	27.20^{**}	44.87^{*}	103.90^{**}	553.75	44.86^{**}	27.20^{*}	103.83^{**}	0.00^{ns}	553.70
	YLT	9.26^{**}	0.00^{ns}	17.31^{**}	107.32	9.26^{**}	0.00^{ns}	17.31^{**}	0.00^{ns}	107.32
RESISTANCE	Trait	σ_b^2		σ_a^2	σ_e^2	σ_b^2		σ_a^2	σ_s^2	σ_e^2
	ALD	0.44^{**}		4.00^{**}	4.34	0.45^{**}		0.92^{**}	1.81^{*}	4.31
	ALDp	0.58^{**}		1.52^{**}	4.04	0.59^{**}		0.87^{**}	0.41^{ns}	4.02

† Represents agronomic traits evaluated in field experiments and resistance traits evaluated in laboratory experiments. [1] Represents average standard error of each variance component. $^{**}P \leq 0.01$, $^{*}P \leq 0.05$, and $^{ns}P > 0.05$ are the significance for variance components.
Source: own elaboration (2025).

TERCEIRA PARTE

2 CONSIDERAÇÕES FINAIS

O presente trabalho abordou, de forma inovadora e aprofundada, a complexa arquitetura genética de características quantitativas no melhoramento de batata tetraploide (*Solanum tuberosum* L.), com foco na partição dos efeitos aditivos e não aditivos para otimizar as estratégias de seleção clonal e parental. Foram avaliadas características de alta relevância agronômica e econômica, como produtividade total de tubérculos (TTY), teor de matéria seca (SG) e resistência à podridão mole, uma das doenças bacterianas mais prejudiciais à cultura.

A modelagem estatística baseada em modelos lineares mistos, com a incorporação de informações de pedigree, permitiu a decomposição da variância genotípica nos seus principais componentes. Os resultados evidenciaram que a produtividade é fortemente influenciada por efeitos genéticos não aditivos, enquanto a gravidade específica apresenta controle predominantemente aditivo. Para os caracteres de resistência à podridão mole, foi observada contribuição significativa de ambos os componentes, sendo o diâmetro da lesão (ALD) associado a maior precisão experimental do que a profundidade da lesão (ALDp).

A aplicação de diferentes modelos (M1, M2 e M3) em análises individuais e multiambientais possibilitou identificar o modelo mais adequado para cada traço e objetivo de seleção. Modelos que consideraram os efeitos não aditivos (M3) proporcionaram melhor ajuste para TTY e ALD, enquanto modelos focados em efeitos aditivos (M2) foram mais eficientes para SG e ALDp. A análise de acurácia indicou superioridade da seleção clonal em relação à parental, principalmente para características sob maior influência de efeitos não aditivos.

A análise fatorial também contribuiu para a compreensão das correlações genéticas entre os caracteres, evidenciando associações favoráveis entre SG e resistência à podridão mole. Essa correlação possibilita a seleção indireta, viabilizando o avanço simultâneo de clones com alto teor de matéria seca e maior resistência às doenças, sem comprometer o rendimento.

A discrepância observada entre os clones selecionados para uso direto e aqueles indicados como genitores reforça a importância da partição dos efeitos genéticos. Clones com alta performance fenotípica nem sempre apresentam valor genético aditivo elevado, o que pode comprometer a eficiência dos cruzamentos. Portanto, estratégias que integrem a seleção clonal e parental com base na partição dos efeitos genéticos são fundamentais para maximizar o progresso genético.

Por fim, este trabalho contribui significativamente para o avanço do melhoramento genético da batata, oferecendo um referencial técnico e metodológico robusto para a tomada de decisão em programas de melhoramento, especialmente em fases iniciais. A integração de

abordagens estatísticas avançadas com dados fenotípicos de qualidade mostrou-se eficaz e de baixo custo, tornando-se uma alternativa promissora à seleção genômica em programas com recursos limitados. Assim, espera-se que os resultados aqui obtidos auxiliem no desenvolvimento de cultivares mais produtivas, estáveis e resistentes, contribuindo para a sustentabilidade da cadeia produtiva da batata no Brasil e no mundo.

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