BLUP (Best Linear Unbiased Predictors) analysis for the selection of superior genotypes in the yellow diploid potato (*Solanum tuberosum* group Phureja)

Análisis BLUP (Best Linear Unbiased Predictors) en etapas avanzadas de selección en papa criolla (*Solanum tuberosum* Grupo Phureja)

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Evaluation field of promising genotypes of yellow diploid potato. Photo: L.E. Rodríguez.
ABSTRACT
One of the major challenges that breeders face is the differential response of genotypes from one environment to another, known as the genotype × environmental interaction (GxE). The optimal procedure restricted maximum likelihood/best linear unbiased predictor (REML/BLUP) allows the simultaneous estimation of genetic parameters and the prediction of genotypic values. The BLUP predictors are presented as an alternative to the narrowing of biased values. It is based on the variances by genotype to determine its response value, as a complement of the selection index (SI). The ESIM (Eigenvalue Selection Index) allows selecting genotypes based on two or more variables or selection characters as long as the economic matrix possesses the appropriate values to highlight the desired response variable. Three stages of selection were evaluated in an advanced diploid potato improvement program. BLUP values were obtained for the yield and specific gravity variables and from them the genetic parameters and the SI were obtained. The genetic gain for yield corresponded to 1.228 kg/plant with a heritability ($H^2$) = 0.82, while GA for GE was 0.02 with an $H^2$ = 0.935. The SI from the BLUP values selected in the final stages three new cultivars (Criolla Dorada, Criolla Ocarina and Criolla Sua Pa) that were registered at the Instituto Colombiano Agropecuario (ICA). Although BLUE and BLUP are highly correlated, the BLUP / ESIM analysis gives an advantage to the predictor because it reduces the responses to the environmental effect, efficiently selecting genotypes with high agronomic potential.

Additional key words: potato breeding; selection index; ESIM; genetic parameters.

RESUMEN
Uno de los principales desafíos que enfrentan los mejoradores es la respuesta diferencial de los genotipos de un entorno a otro, conocida como la interacción genotipo × ambiente (GxE). El procedimiento óptimo restringido de máxima verosimilitud/mejor predictor imparcial lineal (REML / BLUP) permite la estimación simultánea de parámetros genéticos y la predicción de
INTRODUCTION

The yellow diploid potato (Solanum tuberosum L. grup Phureja) (Huamán and Spooner, 2002) is one of the most important plant genetic resources in Colombia. This potato is also known by its nutritional value, color, flavor, texture and rapid cooking (Rivera et al., 2011; Peña et al., 2015; Gómez et al., 2018). It poses good efficiency potential, higher early blooming, an absence of tuber dormancy, resistance to biotic and abiotic factors, specific adaptations to different environments and an unexplored source of genes usable in plant breeding programs (Rodríguez, 2013). Individuals from group Phureja have been characterized as a good source for iron and zinc (Burgos et al., 2007).

Efficiency and nutritional quality are influenced by the environmental effects (Bonierbale et al. 2004, Rodríguez-Pérez, 2010; Hammond et al., 2011; PGSC, 2011; Li et al., 2013) and genetic expression. Likewise, they control the weight and starch content. These variables, when estimated,
can increase the accuracy of selection in advanced stages of breeding (Rivera et al., 2011; Li et al., 2013). To do so, it becomes necessary to rigorously discriminate characters of high heritability and easy phenotypical characterization, such as shape and color. Multiplication rates and late selection occurs for variables such as efficiency and characters with low heritability in further stages of selection (Poehlman and Allen, 2003).

The success of a plant breeding program depends on the capacity to deliver genotypes that guarantee high performance in terms of efficiency and/or quality across a range of environmental conditions. Genotype by environment interaction (GXE) is the result of a differential response of genotypes across environments. Analyses and estimations of GXE have the potential to generate information on the characteristics of genotypes, identifying the superior ones for specific environmental conditions. This potato has wide adaptability and high efficiency potential, as determined by GXE. The most desirable cultivar is the one combining high efficiency and stability.

Federer and Raghavarao (1975) point out that the analysis of variance is useful for estimating the variance components associated with genotypes, environments and their interaction. This provides information on the stability of genotypes that, calculated across heritability in a broad sense ($H^2$), enables the establishment of new genotypes and possible parental plants in a breeding program. One option for an estimation of the average value of genotypes or families can be obtained by a minimum-quadratic estimation (Littell et al., 2006). Under the assumption of normality and independence from errors this provides the best linear unbiased estimate (BLUE) (Littell et al., 2006; Ticona-Benavente and Silva, 2015).

For the improvement of the potato, an assessment of new genotypes by the establishment of augmented designs that enable the assessment of hundreds of genotypes without the use of replicas is recommended (Federer, 1998; Benavente et al., 2011). Moreover, within the predictive power of BLUE, heritability or information from parental plants are not considered, thus removing power from the selection analysis (Ticona-Benavente and Silva, 2015). The removal of assumed presuppositions within BLUE led Henderson (1953,1984) and Patterson and Thompson (1971) to structure the basis for the best linear unbiased predictor (BLUP) (Henderson, 2012; Ticona-Benavente and Silva, 2015), used to estimate the random effects in a mixed model (Piepho et al., 2008). This allowed predictions of a more accurate genetic value in search of new varieties and genetic values of parental selection (Piepho et al., 2008; Ticona-Benavente and Silva, 2015).
BLUP values show predictive accuracy when compared to other procedures, since the pedigree information is often included via the numerator relation matrix, which is often susceptible to analysis via a simple mixed model. The estimation of genetic values is mainly based on models with fixed effects. This eliminates variations and brings the response value closer to the genotypic response (Piepho et al., 1994; Piepho, 2008). Some of the work on selection in advanced stages (close to obtaining a variety) based on BLUP methodologies has been carried out in species such as beans (Ferreira et al., 2008), yams (Borges et al., 2010), oil palm (Flori and Hamon, 2001), sugar cane (Barbosa et al., 2014), sorghum (Filho and Tardin, 2014), corn (Bernardo, 1995,1996; Olivoto et al., 2017), and cassava (Ceballos et al., 2016).

In plant breeding, besides BLUP, the implementation of a Selection Index (SI), enables the selection of individuals for incorporation into a further stage of assessment. This process is carried out based on the phenotypic values observed for several traits of each candidate individual (Cerón-Rojas et al., 2006). As defined by Smith (1936), SI originally assigns subjective economic weight to each trait with the disadvantage that it requires large amounts of information making weight assignment difficult. Thus, the Eigen value selection index method (ESIM) appears to be an alternative for the selection of genotypes in advanced stages of a selection program, since it takes into account the proportion of traits contributing to the SI. These can involve two or more variables in the construction of the index with differential economic values, prioritized by relevant variables according to the species (Cerón-Rojas et al., 2006, 2016).

Although some work has been done in simulated data for potato (Slater et al., 2014; Ticona-Benavente and Silva, 2015) the estimation of BLUP and the application of ESIM are pioneer methods for the analysis of selection programs for the diploid potato. The objective of this study was the implementation of BLUP and ESIM as a strategy for the selection of superior families and genotypes in three advanced selective stages in the yellow diploid potato breeding program at the Universidad National de Colombia.

MATERIALS AND METHODS

Advanced lines of yellow diploid potato genotypes (Solanum tuberosum Group Phureja) were developed by hybridization obtained from crosses of different diploid parents (Tab. 1) cultivated
and selected in different years and locations, in a process of participative selection research with small farmers.

Table 1. Genealogy of 25 generation F1 families, parentheses indicate the number of genotypes evaluated by family.

| Family Code (N° of seeds) | Genealogy                                      | Family Code (N° of seeds) | Genealogy                                      |
|---------------------------|------------------------------------------------|---------------------------|------------------------------------------------|
| 08-001 (125)              | \{S. bukasovii \textit{473452-15} ×}           | 08-056 (70)               | \{UN-col 38 × Criolla Latina\}                |
|                           | Criolla Guaneña\}                             |                           |                                                |
| 08-028 (183)              | \{S. bukasovii \textit{473452-12} ×}           | 08-041 (75)               | \{Criolla Colombia × Criolla Galeras\}         |
|                           | Guaneña\}                                     |                           |                                                |
| 09-004 (190)              | \{S. bukasovii \textit{265865-9 × 98-71.9} \} | 08-042 (90)               | \{Criolla Colombia × Criolla Latina\}         |
| 08-045 (20)               | \{S. stenotomum \textit{195188-7 ×}           | 08-051 (100)              | \{Criolla Latina × Criolla Colombia\}         |
|                           | Group phureja \textit{704218}\}              |                           |                                                |
| 08-057 (20)               | \{S. stenotomum \textit{195188-10 ×}          | 08-046 (130)              | \{Criolla Galeras × Criolla Colombia\}        |
|                           | Group phureja \textit{704218}\}              |                           |                                                |
| 08-048 (95)               | \{S. stenotomum \textit{195188-12 ×}          | 09-003 (20)               | \{98-71-9 × Criolla Colombia\}                |
|                           | Criolla Colombia\}                            |                           |                                                |
| 08-052 (96)               | \{S. stenotomum \textit{703285 ×}            | 08-044 (5)                | \{Criolla Guaneña × Criolla Latina\}          |
|                           | Criolla Colombia\}                            |                           |                                                |
| 08-049 (45)               | \{Latina × S. stenotomum (gon 1)\}            | 08-004 (65)               | \{Criolla Guaneña × Criolla Galeras\}         |
| 08-047 (85)               | \{Criolla Colombia × S. stenotomum \textit{703315}\} | 08-055 (65)               | \{Criolla Latina × UN-col 38\}                |
| 08-043 (85)               | \{Criolla Colombia × S. stenotomum \textit{703285-1}\} |                           |                                                |
| 09-001 (155)              | \{S. goniocalyx \textit{704481 ×}            |                           |                                                |
|                           | Criolla Colombia\}                            |                           |                                                |
| 09-002 (120)              | \{S. goniocalyx \textit{703825 ×}            | 98-71.9;26                | \{Criolla Colombia × S. goni (Amarilla Tumbay)\} |
|                           | Criolla Colombia\}                            |                           |                                                |
| 09-005 (100)              | \{S. goniocalyx \textit{703279 ×}            | C. Galeras                | \{Criolla Colombia × S. goni (Amarilla Tumbay)\} |
|                           | Criolla Colombia\}                            |                           |                                                |
| 08-040 (95)               | \{UN-col 3 × Criolla Latina\}                 | C. Guaneña                | \{S. goni (Amarilla Tumbay) × (Criolla Colombia)\} |
| 08-039 (85)               | \{UN-col 30 × UN-col 62\}                    | C. Latina                 | \{Criolla Colombia × S. goni (Amarilla Tumbay)\} |
| 08-054 (65)               | \{UN-col 38 × Criolla Galeras\}              | C. Colombia                | \{Clonal selection of round and yellow Genotypes\} |

From materials of familiar selection obtained in two stages and after characterization based on variables of shape and color, three additional selection stages were established: three (SS3), four (SS4) and five (SS5). These allow an advancement in the obtained population. SS3 corresponded to the establishment of four evaluations of diploid potato using 100 advanced genotypes chosen by
participative selection processes with farmers in the municipalities of Facatativá (Cundinamarca), Medellín (Antioquia), Pasto (Nariño) and Chipaque (Cundinamarca). SS4 corresponded to the evaluation of 30 genotypes selected in SS3 in two municipalities, Facatativá (Cundinamarca) and Pasto (Nariño). SS5 corresponded to the evaluation of eight genotypes and two witnesses that were evaluated in eleven settlements that represent the productive system "papa criolla" in Colombia, (Carlosama, Cumbal, Ipialpud, Jamondino, Mosquera, Obonuco, Tuquerres, in Nariño and San Ramon, Santa Bárbara, Subachoque and Zipaquirá, in Cundinamarca) located between 2400 and 2800 m over two consecutive semesters.

For the three stages of selection, a design of full blocks was randomly established, with four repetitions. The experimental unit was made up of 40 m$^2$ plots with a distance of 1.0 m between furrows, and 0.3 m between sites. Each plant was fertilized with 30 g of compound N-P-K (10-20-20). Variables evaluated were tuber yield (TY) and specific gravity (SG) according to Araujo et al. (2020).

Bearing in mind that the data corresponds to three multi-environmental evaluations in order to obtain the mean of each genotype in each settlement. The BLUP (Henderson, 1984) were calculated assuming the genotypes were random effects and settlements were fixed effects.

The value for heritability ($H^2$) was obtained in a wide sense for each essay and each settlement. The settlements where heritability was under 0.5 were eliminated, since the high variance values might imply an elevated error value. Calculations were made using settlements where heritability was $H^2= 0.5$; meaning a genetic gain (GG) and its percentage (GAM), following Poehlman and Allen’s (2003) procedure.

For the determination of the ESIM specific values of SI were used in each stage, from the matrix of correlation between efficiency and specific gravity (Cerón-Rojas, 2006, 2008). To obtain the individual index for each genotype, the corresponding BLUP values were used, along with the MIXED procedure of software SAS 9.4. In order to prove that the effect of settlement was statistically meaningful, Ward’s method of variance cluster was used through an ANOVA analysis to classify the settlements according to the TY variable. For the classification of genotypes, the quadrant method (Francis and Kanenberg, 1978), based on the mean and CV of the cultivar across the environments was used.
Finally, correlation values between BLUP and BLUE of response variables were used as a method for the verification of the impact of using variance components as fixed or random effects in each of the stages of an advanced breeding program.

RESULTS AND DISCUSSION

For the variable TY, based on BLUP values, the predicted mean for SS3 was 1.489 kg/plant, for SS4 0.429 kg/plant and for SS5 0.929 kg/plant (Tab. 2). Average values –non BLUP- for SS3, Es4 and Es5 were 1.520, 0.443, and 0.964 kg/plant, respectively.

Changes between observed values and predicted BLUP values for TY were rather similar, in accordance with Barbosa et al. (2014). Although the GAM value of the population analyzed decreases 64.55% (SS3) 26.56% (SS4), 16.55% (SS5), (Tab. 2), it indicates that it is a logical consequence to take superior genotypes to advanced stages. This means that, as a response to the selection of values observed for predicting familiar or genetic values, it is a relative improvement for the heritability value and a constant decrease in variation (as occurred in this study) where the value of heritability for TY in two states shifted from 0.63 to 0.82 and CV decreased from 36.78 a 3.70%, thus confirming Ticona-Benavente and Pinto (2012) (Tab. 2).

Bearing in mind that the selection states are consecutive, it is guaranteed that the TY gain, based on the addition of the GG values at the end of stage five, corresponds to 1.228 kg/plant. This is high if taken into account that the genetic advancement of potatoes consists of the multiplication of material in a vegetative manner that may be related to the environmental effect. This produces a positive consequence in the response variable for some of the environments such as a better offer for the genotypes (Cotes et al., 2000; Rivadeneira et al., 2016).
Table 2. Genetic parameters for tuber yield and specific gravity.

| Parameter                        | Tuber yield | Specific gravity |
|----------------------------------|-------------|-----------------|
|                                  | Selection stage |                  |
| Factors                          | Three | Four | Five | Three | Four | Five |
| Repetitions                      | 3     | 3    | 4    | 3     | 3    | 4    |
| Settlements                      | 4     | 2    | 17   | 4     | 2    | 21   |
| Settlement variance              | 1372078.6 | 8993.69 | 101596.0 | 1.29E-05 | 1.90e-04 | 9.05E-05 |
| Genot. Variance                  | 241353.89 | 8051.51 | 2764.89 | 2.16E-05 | 1.97E-05 | 1.32E-05 |
| Genot. Variance x Sett.          | 405231 | 2.76E-13 | 6614.08 | 1.62E-05 | 1.03E-06 | 8.27E-06 |
| Error variance                   | 470416.77 | 39568.3 | 14003.75 | 1.66E-04 | 1.84E-04 | 4.36E-05 |
| General mean                     | 1.489  | 0.429 | 0.929 | 1.072  | 1.082 | 1.087 |
| CV (%)                           | 36.78  | 28.69 | 3.70  | 0.572  | 0.773 | 0.124 |
| $H^2$                            | 0.630  | 0.540 | 0.820 | 0.546  | 0.386 | 0.935 |
| GG                               | 0.961  | 0.114 | 0.153 | 0.006  | 0.007 | 0.007 |
| GAM (%)                          | 64.55  | 26.56 | 16.55 | 56.30  | 64.800 | 66.10 |

CV: Variation quotient; $H^2$: heritability in wide sense; GG: Genetic Gain; GAM: GG in %.

One of the criteria for this type of analysis is that the values for inheritability under 0.5 (Carlosama 12A, Cumbal 12A, San Ramón 12B, Túquerres 12A, Túquerres 12B) were not taken into account, which is the reason why only 17 settlements were included for TY. For SS3, the value $H^2=0.63$ for the efficiency character indicates that it is related to an effective selection of superior families over the first few generations matching that reported by Ticona-Benavente and Silva (2015).

The high value for $H^2 = 0.82$ for SS5 corresponds to a value across all settlements. This value may be related to an efficient selection pressure, which led to proper selection of superior individuals, thus ensuring high heritability for superior individuals. The values for these genetic parameters may increase based on the efficiency of BLUP methodology, keeping in mind that the selection of individuals must have an organoleptic characteristics component (special shape and color). This affects the final selection, focused on obtaining genotypes with a high commercial potential regarding the tetraploid potato (Ticona-Benavente and Silva, 2015).

Additionally, efficiency is a variable considerably affected by the environment, and that might also have been influenced by the inclusion of diversity generated in the population by introducing
wild parents and bred diploids.

For the variable SG, the mean predicted for SS3 was 1.072, for SS4 1.082 and for SS5 1.087, using BLUP values. The average values without prediction –no BLUP- for ES3, ES4 and SS5 were 1.080, 1.081, and 1.088, respectively. It is evident that the adjustment by BLUP methodology determined that the average predicted value for SG would change, decreasing from 1.083 to 1.080. (Tab. 2). However, individual responses by selection display higher variability, which might imply the incorporation of characteristics such as shape and color (Robinson, 1991; Piepho et al., 2008), thus generating a better estimation under the BLUP proposal.

In agreement with the variable TY for SG in SS5, the analysis of information was carried out based on 21 settlements, since heritability in Carlosama 12A was lower than 0.5. As a result the values for $H^2$ for the SG character ranged between 0.38 and 0.93. Superior values matched the ones reported by Ticona-Benavente and Silva (2015).

GAM values show no meaningful advancement within the selective states, indicating that for the SG variable performing familiar selection, a greater advancement was achieved in the early stages of selection by proposing to decrease the selective pressure to values of 50%. This would negate the need for exhaustive selection in later stages, indicating that predicted values might enable the increase of GG, so long as pressure decreases to 30% (Ticona-Benavente and Silva, 2015).

**Selection index**

Using as criterion a selection pressure near 10% for a population susceptible to improvement, based on the analysis of specific values for SS3, SS4 and SS5, the top 10 genotypes are obtained (Tab. 3).
Table 3. Selection index for selection stages three, four and five.

| Genotype     | SI     | Genotype     | SI     | Genotype     | SI     |
|--------------|--------|--------------|--------|--------------|--------|
| 08-058-65    | 2.548224 | 08-048-86    | 1.148919 | 08-004-16    | 1.252889 |
| 08-058-12    | 1.892389 | 08-051-64    | 1.136598 | 08-051-90    | 0.707345 |
| 08-056-69    | 1.871687 | 08-058-69    | 1.105712 | 08-051-64    | 0.503355 |
| 08-053-77    | 1.820245 | 08-040-120   | 1.08126 | Galeras      | 0.44831 |
| 08-051-53    | 1.70215  | 08-048-79    | 1.039077 | 08-046-191   | -0.10097 |
| 08-056-15    | 1.604584 | 08-051-68    | 1.03866 | 08-046-187   | -0.16004 |
| Guaneña      | 1.490208 | 08-046-191   | 0.982446 | Colombia     | -0.35929 |
| 08-053-57    | 1.40364  | 08-042-7     | 0.918086 | 08-051-68    | -0.43807 |
| 08-055-2     | 1.334886 | 08-004-16    | 0.857351 | 08-051-70    | -0.7391 |
| 08-053-53    | 1.320219 | 08-051-70    | 0.468743 | 08-004-59    | -1.11443 |

Families that provided the individuals selected were 08-051 (Criolla Latina × Criolla Colombia), 08-046 (Criolla Guaneña × Criolla Colombia), 08-004 (Criolla Guaneña × Criolla Galeras). Criolla Galeras and Criolla Colombia were highlighted as parents that enabled the selection of individuals that became new cultivars, implying that they had a high, unexplored potential for improvement leading to an increase in efficiency or even the improvement of complex characters.

The reduction of families presented as superior occurred mainly because phenotypical resemblance is a tendency that genetically related individuals have towards sharing a greater number of genes with each other than with the general population, because of the variation for efficiency potential among and within families in a population of diploid potatoes. They are thus grouped according to the principle of phenotypic resemblance among related individuals increase in efficiency or even the improvement of complex characters.

The reduction of families presented as superior occurred mainly because phenotypical resemblance is a tendency that genetically related individuals have towards sharing a greater number of genes with each other than with the general population, because of the variation for efficiency potential among and within families in a population of diploid potatoes. They are thus grouped according to the principle of phenotypic resemblance among related individuals. The main particularity of genetic improvement in potato lies in vegetative multiplication, which guarantees homogeneity in the tubers obtained with an identical genetic base. Therefore, when a desirable
A genotype is identified, it can be multiplied and maintained generation after generation without genetic segregation, offering a great advantage over crops that only multiply through botanic cuttings or sexual seeds.

In order to establish the effect of GXE on advanced genotypes on SS5, it was initially proven that its effect was statistically meaningful via ANOVA analysis. In order to classify settlements by the variable TY, a grouping method was applied (Fig. 1.) resulting in similarities among them and thus creating four major groups: San Ramon 12A and Zipaquirá 12B which correspond to group 1, presented as an external group; Subachoque 12 A, Mosquera 12 A and 12B, Cumbal 12 A e Ipialpud 12B corresponding to group 2; Zipaquirá 12A, Subachoque 12B, Santa Barbara 12B, Ipialpud 12 A and Obonuco 12 A correspond to group 3, and Jamondino 12A, Santa Barbara 12B, Obonuco 12B, Carlosama 12B and Jamondino 12B in group 4. This grouping indicated similarities among the settlements and, therefore, the conditions in some of them.

Figure 1. Dendogram for settlements, Ward’s distance , variance clustering method.
Francis and Kanenberg’s (1978) quadrant method enabled the identification of superior genotypes as those possessing a high mean and low CV, for RT variable (Fig. 2).

![Diagram](image)

**Figure 2.** Evaluation of advanced genotypes SS5. Quadrant method.

Volpato *et al.* (2019) indicate that BLUP values enable an accurate estimation of the genetic parameters in multi-trait, multi-environment evaluations (MTME), that, under the quadrant method, enabled the identification of genotypes 08-051-90, 08-004-16, 08-053-57, that, besides showing high mean for TY variable and acceptable CV, also showed round, yellow tubers with shallow buds, good flavor and texture. All these conditions are appreciated in the improvement of the yellow diploid potato, making them suitable phenotypes for registry as new cultivars for
BLUE vs. BLUP contrast

TY y SG variables for SS3, SS4 and SS5, showed a high degree of correlation between the values BLUP vs BLUE, and were highly meaningful (α=0.05) for the response variables (Tab. 4).

Table 4. Correlations for SG and TY for the different stages of selection.

|       | SS3       |       |       |       |
|-------|----------|-------|-------|-------|
|       | BLUP_TY  | BLUE_TY | BLUP_SG | BLUE_SG |
| BLUP_TY | 1.00   |       |       |       |
| BLUE_TY | 0.994 (<.0001) | 1.00 |       |       |
| BLUP_SG | 0.160 (0.1027) | 0.170 (0.0835) | 1.00 |       |
| BLUE_SG | 0.169 (0.0861) | 0.188 (0.0563) | 0.992 (<.0001) | 1.00 |

|       | SS4       |       |       |       |
|-------|----------|-------|-------|-------|
|       | BLUP_TY  |       |       |       |
| BLUE_TY | 1.00   |       |       |       |
| BLUP_SG | -0.344 (0.0535) | -0.366 (0.0395) | 1.00 |       |
| BLUE_SG | -0.351 (0.0490) | -0.385 (0.0298) | 0.977 (<.0001) | 1.00 |

|       | SS5       |       |       |       |
|-------|----------|-------|-------|-------|
|       | BLUP_TY  |       |       |       |
| BLUE_TY | 1.00   |       |       |       |
| BLUP_SG | -0.481 (0.1591) | -0.481 (0.1591) | 1.00 |       |
| BLUE_SG | -0.481 (0.1591) | -0.481 (0.1591) | 1.00 (<.0001) | 1.00 |

Correlation above, meaningfulness aside.

High correlations for advanced stages of the associated variable responses, indicated that there is no higher relevance if the effects are treated as fixed or random. This is the reason why a BLUP methodology is advised, as it provides more modest responses, which have a low tolerance effect on extreme genotypic responses; and it provides a vision of possible behaviors in a further essay, as expressed by Vittorazzi et al. (2017), who indicate that the application of BLUP results in a higher estimated gain than those applied from classic biometric selection index methodologies, and thus BLUP should be incorporated in the progenie section.
CONCLUSION

The implementation of BLUP values and ESIM in advanced selection stages become tools that can improve the selection methodology, as it facilitates the integration of responded variables that are corrected and organized within an index allowing discrimination of the best genotypes.

For selection stage five, an efficient statistical support was achieved. It corroborated the description for obtaining some genotypes as registered varieties, indicating that the technique has a high potential for discriminating between genotypes and discriminating among them to select superior genotypes.

GXE analysis facilitated the characterization of settlements and the distinction of the best ones, in order to turn this analysis into an additional tool that leads to an even more restrictive discrimination, associating its superior behavior to a better environment.

$H^2$ is a genetic parameter that, once obtained from the BLUP values, can be used in advanced selection stages for the variables TY and SG.

Genetic improvement in diploid potatoes becomes an option for developing genotypes with a high agronomic value, high efficiency potential and superior characteristics in color, texture, flavor and early blooming, taking advantage of heterotic values present in diploid populations, and, thus, showing a seldom-explored road for world improvement programs.

DEDICATION

This paper and my whole life as a researcher is dedicated to the loving memory of Dr. José C. Pacheco Maldonado (1950-2019).

My father devoted his whole life to education. He started his career as a high school teacher and subsequently dedicated 40 years to his beloved Universidad Pedagógica y Tecnológica de Colombia- “UPTC” as a professor of genetics.

During the 1980s, he founded the research group BIOPLASMA-UPTC, where his main research area was plant tissue culture. His contributions left a lasting impact on this field that carried on through the following decades.

His work focused on the protection of endangered species such as frailejones ($Espeletia sp.$) and the use of biotechnology in the propagation and improvement of species with agricultural potential.
The best dad and the best professor. Your light still guides my way. Mom and I will always remember you. Thanks for all your love “Papío”

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Conflict of interests: The manuscript was prepared and reviewed with the participation of the authors, who declare that there exists no conflict of interest that puts at risk the validity of the presented results.

BIBLIOGRAPHIC REFERENCES

Araujo, F.F., M.N.S. Santos, N.O. Araújo, T.P. Silva, L.C. Costa, and F.L. Finger. 2020. Growth and dry matter partitioning of potato influenced by paclobutrazol applied to seed tuber. Rev. Colomb. Cienc. Hortic. 14(1). Doi: https://doi.org/10.17584/rcch.2020v14i1.10357

Barbosa, M.H.P., A. Ferreira, L.A. Peixoto, M.D.V. Resende, M. Nascimento, and F.F. Silva. 2014. Selection of sugar cane families by using BLUP and multi-diverse analyses for planting in the Brazilian savannah. Genet. Mol. Res. 13(1), 1619-1626. Doi: https://doi.org/10.4238/2014.March.12.14

Benavente, C.A.T., C.A.B.P. Pinto, I.C.R. Figueiredo, and G.H.M.R. Ribeiro. 2011. Repeatability of family means in early generations of potato under heat stress. Crop Breed. Appl. Biotechnol. 11, 330-337. Doi: https://doi.org/10.1590/S1984-70332011000400006

Bernardo, R. 1995. Best linear unbiased prediction of maize single-cross performance. Crop Sci. 36, 50-56. Doi: https://doi.org/10.2135/cropsci1996.0011183X003600010009x
Bernardo, R. 1996. Testcross additive and dominance effects in best linear unbiased prediction of maize single-cross performance. Theor. Appl. Genet. 93(7), 1098-1102. Doi: https://doi.org/10.1007/BF00230131

Bonierbale, M., W. Amoros, E. Espinoza, E. Mihovilovich, W. Roca, and R. Gómez. 2004. Recursos genéticos de la papa: don del pasado, legado para el futuro. Rev. Latinoam. Papa 12 (Suppl.) 3-14.

Borges, V., P.V. Ferreira, L. Soares, G.M. Santos, and A.M.M. Santos. 2010. Selección de clones de batata-doce pelo procedimento REML/BLUP. Acta Sci. Agron. 32(4), 643-649. Doi: https://doi.org/10.4025/actasciagron.v32i4.4837

Burgos, G., W. Amoros, M. Morote, J. Stangoulis, and M. Bonierbale. 2007. Iron and zinc concentration of native Andean potato cultivars from a human nutrition perspective. J. Sci. Food Agric. 87, 668-675. Doi: https://doi.org/10.1002/jsfa.2765

Ceballos, H., J.C. Pérez, O. Joaqui Barandica, J.I. Lenis, N. Morante, F. Calle, and C.H. Hershey 2016. Cassava breeding I: the value of breeding value. Front. Plant Sci. 7, 1227. Doi: https://doi.org/10.3389/fpls.2016.01227

Cerón-Rojas, J.J., F. Castillo-González, J. Sahagún-Castellanos, A. Santacruz-Varela, I. Benítez-Riquelme, and J. Crossa. 2008. A molecular selection index method based on eigen analysis. Genetics 180(1), 547-557. Doi: https://doi.org/10.1534/genetics.108.087387

Cerón-Rojas, J.J., J. Crossa, J. Sahagún-Castellanos, F. Castillo-González y A. Santacruz-Varela, 2006. A selection index method based on eigenanalysis. Crop Sci. 46(4), 1711-1721. Doi: https://doi.org/10.2135/cropsci2005.11-0420
Cerón-Rojas, J.J., J. Crossa, F.H. Toledo, and J. Sahagún-Castellanos. 2016. A predetermined proportional gains eigen selection index method. Crop Sci. 56(5), 2436-2447. Doi: https://doi.org/10.2135/cropsci2015.11.0718

Cotes, J.M., C.E. Ñustez, R. Martínez, and N. Estrada. 2000. Análisis de la interacción genotipo por ambiente en papa (Solanum tuberosum spp. andigena), a través de una metodología no paramétrica. Agron. Colomb. 17, 43-56.

Federer, W.T. 1998. Recovery of interblock, intergradient, and intervariety information in incomplete block and lattice rectangle. Des. Exp. 54(2), 471-481. Doi: https://doi.org/10.2307/3109756

Federer, W. and D. Raghavarao. 1975. On augmented designs. Biometrics 31(1), 29-35. Doi: https://doi.org/10.2307/2529707

Ferreira, A.D.C., R. Fritsche Neto, and I.O. Geraldi. 2008. Estimation and prediction of parameters and breeding values in soybean using REML/BLUP and Least Squares. Crop Breed. Appl. Biotechnol. 8(3), 219-224. Doi: https://doi.org/10.12702/1984-7033.v08n03a06

Flori, A.R.P.A. and L.B.S. Hamon. 2001. Prediction of oil palm (Elaeis guineensis, Jacq.) agronomic performances using the best linear unbiased predictor (BLUP), 787-792. Doi: https://doi.org/10.1007/s001220051711

Francis, T.R. and L.W. Kannenberg. 1978. Yield stability studies in short-season maize. I. A descriptive method for grouping genotypes. Can. J. Plant Sci. 62(I), 105-111.

Gómez, M.I., H. Restrepo, L.E. Rodríguez, S. Magnitskiy, L. Manrique, and A. Garzón. 2018. Abiotic stress caused by foliar applications of boron to the yellow diploid potato (Solanum tuberosum, Group Phureja) cultivar Criolla Galeras. Rev. Colomb. Cienc. Hortic. 12(3), 582-591. Doi: https://doi.org/10.17584/rcch.2018v12i3.9520
Hammond, J.P., M.R. Broadley, H.C. Bowen, W.P. Spracklen, R.M. Hayden, and P.J. White. 2011. Gene expression changes in phosphorus deficient potato (Solanum tuberosum L.) leaves and the potential for diagnostic gene expression markers. PLoS ONE 6(9). e24606. Doi: https://doi.org/10.1371/journal.pone.0024606

Henderson, C. 1953. Estimation of variance and covariance components. Biometrics 9(2), 226-252. Doi: https://doi.org/10.2307/3001853

Henderson, C. 1984. Applications of linear models in animal breeding models. University of Guelph, Guelph, Ontario, Canada.

Henderson, C.R. 2012. Best linear unbiased prediction (BLUP) of random effects in the normal linear mixed effects model. Statistics, Iowa State University, Ames, IA.

Huamán, Z. and D.M. Spooner. 2002. Reclassification of landrace populations of cultivated potatoes (Solanum sect. Petota). Am. J. Bot. 89(6), 947-965. Doi: https://doi.org/10.3732/ajb.89.6.947

Littell, R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. 2nd ed. SAS Press, Cary, NC.

Olivoto, T., M. Nardino, I.R. Carvalho, D.N. Follmann, M. Ferrari, V.J. Szareski de Pelegrin, and V.Q. de Souza. 2017. REML/BLUP and sequential path analysis in estimating genotypic values and interrelationships among simple maize grain yield-related traits. Genet. Mol. Res. 16(1), gmr16019525. Doi: https://doi.org/10.4238/gmr16019525

Patterson, H. and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. Biometrika 58(3), 545-554. Doi: https://doi.org/10.1093/biomet/58.3.545
Peña, C., L.-P. Restrepo-Sánchez, A. Kushalappa, L.-E. Rodríguez-Molano, T. Mosquera, and C.-E. Narváez-Cuenca. 2015. Nutritional contents of advanced breeding clones of *Solanum tuberosum* group Phureja. LWT - Food Sci. Technol. 62(1), 76-82. Doi: https://doi.org/10.1016/j.lwt.2015.01.038

Piepho, H.P. 1994. Best linear unbiased prediction (BLUP) for regional yield trials: a comparison to additive main effects and multiplicative interaction (AMMI) analysis. Theor. Appl. Genet. 89(5). Doi: https://doi.org/10.1007/BF00222462

Piepho, H.P., J. Möhring, A.E. Melchinger, and A. Büchse. 2008. BLUP for phenotypic selection in plant breeding and variety testing. Euphytica 161(1-2), 209-228. Doi: https://doi.org/10.1007/s10681-007-9449-8

PGSC, Potato Genome Sequencing Consortium. 2011. Genome sequence and analysis of the tuber crop potato. Nature 475, 189-195. Doi: https://doi.org/10.1038/nature10158

Poehlman, J. and D. Allen. 2003. Mejoramiento genético de las cosechas. 2nd ed. Limusa, Mexico D.F.

Rivadeneira, J., D. Ortega, V. Morales, C. Moneros, and X. Cuesta. 2016. Efecto de la interacción genotipo por ambiente sobre los contenidos de hierro, zinc y vitamina C en genotipos de papa (*Solanum* sp.). Rev. Latinoam. Papa 20(1), 32-45.

Rivera, J.E., A.O. Herrera, and L.E. Rodríguez. 2011. Assessment of the processing profile of six "creole potato" genotypes (*Solanum tuberosum* Phureja Group). Agron. Colomb. 29(1), 73-81.

Robinson, G.K. 1991. That BLUP is a good thing: the estimation of random effects. Stat. Sci. 6(1), 15-32. Doi: https://doi.org/10.1214/ss/1177011926
Rodríguez, L.E. 2013. Análisis genético y molecular para rendimiento y período de reposo de tubérculo en papa a nivel diploide (S. bukasovii x S. tuberosum grupo Phureja). PhD thesis. Universidad Nacional de Colombia, Bogota.

Rodríguez-Pérez, L. 2010. Ecofisiología del cultivo de la papa (Solanum tuberosum L.). Rev. Colomb. Cienc. Hortic. 4(1), 97-108. Doi: https://doi.org/10.17584/rcch.2010v4i1.1229

Slater, A.T., G.M. Wilson, N.O.I. Cogan, J.W. Forster, and B.J. Hayes. 2014. Improving the analysis of low heritability complex traits for enhanced genetic gain in potato. Theor. Appl. Genet. 127(4), 809-820. Doi: https://doi.org/10.1007/s00122-013-2258-7

Smith, H.F. 1936. A discriminant function for plant selection. pp. 466-476. In: Papers on Quantitative Genetics and Related Topics. Department of Genetics, North Carolina State College, Raleigh, CN.

Ticona-Benavente, C.A. and C.A.B.P. Pinto. 2012. Selection intensities of families and clones in potato breeding. Ciênc. Agrotecnol. 36(1), 60-68. Doi: https://doi.org/10.1590/S1413-70542012000100008

Ticona-Benavente, C.A. and D.F. da Silva Filho 2015. Comparison of BLUE and BLUP/REML in the selection of clones and families of potato (Solanum tuberosum). Genet. Mol. Res. 14(4), 18421-18430. Doi: https://doi.org/10.4238/2015.December.23.30

Vittorazzi, C.A.T., A.G. Amaral Junior, A.P. Guimarães, F.H.L. Viana, G.F. Silva Pena, R.F. Daher, I.F.S. Gerhardt, G.H.F. Oliveira, and M.G. Pereira. 2017. Indices estimated using REML/BLUP and introduction of a super-trait for the selection of progenies in popcorn. Genet. Mol. Res. 16(3), gmr16039769. Doi: https://doi.org/10.4238/gmr16039769

Volpato, L., R.S. Alves, P.E. Teodoro, M.D. Vilela de Resende, M. Nascimento, A.C.C. Nascimento, W.H. Ludke, F. Lopes da Silva, and A. Borém. 2019. Multi-trait multi-environment
models in the genetic selection of segregating soybean progeny. PLoS One. 14(4), e0215315. Doi: https://doi.org/10.1371/journal.pone.0215315