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EVALUACIÓN DE SELECCIÓN TEMPRANA EN EL PROGRAMA DE MEJORAMIENTO DE ARROZ DE INIA

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Magíster en Ciencias Agrarias
opción Bioestadística

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RESUMEN

El programa de mejoramiento genético de arroz de INIA (PMGA) lidera desde hace décadas la oferta varietal nacional, necesitando dar respuesta rápida y eficiente a las necesidades varietales del sector. Seleccionar con buena precisión en el primer año de evaluación fenotípica de rendimiento (E1) puede tener un gran impacto en mejorar la eficiencia de un programa de mejoramiento. En esta tesis se evaluó el impacto de incorporar análisis multiambientales en la selección de líneas del PMGA en E1, empleando una estrategia de validación que contempla el momento en el que los datos fenotípicos se hacen disponibles. Se estudiaron cinco escenarios de predicción (PS) considerando diferentes niveles de disponibilidad y agregación de datos, y la inclusión o no del término interacción genotipo por ambiente (GA). Identificamos el mejor PS para implementar de forma rutinaria en el PMGA teniendo en cuenta la partición de la varianza fenotípica de rendimiento de grano, la habilidad predictiva y el porcentaje de las mejores líneas en E1 que alcanzaron etapas de evaluación avanzadas. La estrategia de validación fue efectiva y recreó en forma realista la selección en E1 considerando la estructura del PMGA. El análisis conjunto de múltiples ensayos y ambientes estimó mejor los componentes de la varianza y generó una alta habilidad predictiva respecto a análisis parciales, para la selección de padres y avance de líneas en E1. La inclusión de un término GA en los modelos correspondientes a PS no tuvo una mejora clara y consistente en la habilidad predictiva. Esta tesis generó evidencia para la toma de decisiones en la distribución de recursos del PMGA, contribuyendo a que pueda lograr sus objetivos en forma más eficiente y rápida.

Palabras clave: mejoramiento genético, selección temprana, análisis multiambientales

EVALUATION OF EARLY SELECTION STRATEGIES IN RICE LINES FROM INIA'S RICE BREEDING PROGRAM

SUMMARY

INIA's rice breeding program (PMGA) has led the national varietal offer for decades, needing to respond quickly and efficiently to the varietal needs of the sector. Selecting with good precision in the first year of phenotypic yield evaluation (E1) can have a great impact on improving the efficiency of a breeding program. In this thesis, the impact of incorporating multi-environmental analyses in the selection of PMGA lines in E1 was evaluated, using a validation strategy that contemplates the moment in which the phenotypic data becomes available. Five prediction scenarios (PS) were studied considering different levels of data availability and aggregation, and the inclusion or not of a genotype by environment (GA) interaction term. We identified the best PS to implement routinely in the PMGA considering the phenotypic variance partition of grain yield, the predictive ability and the percentage of the best lines in E1 that reached advanced evaluation stages. The validation strategy was effective and realistically recreated the selection in E1 considering the PMGA structure. The joint analysis of multiple trials and environments estimated the variance components better and generated a high predictive ability with respect to partial analyses, for the selection of parents and advancement of lines in E1. The inclusion of a GA term in the models corresponding to PS did not have a clear and consistent improvement in predictive ability. This thesis generated evidence for decision-making in the distribution of PMGA resources, helping it to achieve its objectives more efficiently and quickly.

Keywords: plant breeding, early selection, multi-environmental trials

1 INTRODUCCIÓN

El arroz está entre los primeros rubros de exportación de nuestro país: se exporta un 95 % de la producción (MGAP-DIEA, 2021a). La producción arrocerana nacional se caracteriza por altos niveles de rendimiento y calidad, localizada en tres zonas. La zona norte está conformada por Artigas y Salto y se caracteriza por sus altos rendimientos. En la zafra 2020/21 tuvo un rendimiento promedio de 9,7 ton ha⁻¹, el más alto de las tres zonas, con 25.000 ha sembradas. La zona centro, conformada por Rivera, Tacuarembó y Cerro Largo, tuvo niveles de rendimiento similares a la zona norte y contó con 12.700 ha sembradas. La zona este es la más tradicional en producción arrocerana, con 100.000 ha sembradas, y niveles de rendimiento más bajos que en las demás, debido a sus características climáticas y ambientales. Además de estas características, las zonas se diferencian por su perfil de adopción de cultivares, tenencia de tierra y costos de tierra y agua, lo que las hace muy distinguibles (MGAP-DIEA, 2021b).

Para mantener su competitividad y sustentabilidad ambiental y económica, el sector arrocerano debe enfrentar escenarios cambiantes en distintos frentes: condiciones climáticas y ambientales que generan inestabilidad en la producción y la necesidad de mantener la rentabilidad de los emprendimientos arroceranos de forma sustentable, con menor uso de insumos y huella ambiental (Uruguay XXI, 2018, Saldías et al., 2016, Pérez de Vida y Macedo, 2013, Ferraro y Lanfranco, 2016, Pittelkow et al., 2016, Zorrilla de San Martín et al., 2018).

El programa de mejoramiento genético de arroz de INIA (PMGA) lidera desde hace décadas la oferta varietal a nivel nacional (MGAP-DIEA, 2021a) mediante el desarrollo de variedades de alto rendimiento, calidad molinera y resistencia genética a enfermedades fúngicas, para los diferentes tipos de calidad y mercados objetivo de la industria molinera uruguaya, y adaptadas a las zonas de

producción. Esto implica cuatro subpoblaciones de arroz (Kovach et al., 2007) y calidades diferentes: índica de grano largo (IND); japónica tropical de grano largo (JTR); japónica templada de grano corto, medio y pesado; y variedades IND y JTR resistentes a herbicidas para el sistema de producción Clearfield; así como tres unidades experimentales representativas de las zonas de producción en las que se evalúan las líneas del programa. La Unidad Experimental Paso de La Laguna (PL), ubicada en Treinta y Tres (33.27 S, 54.17 W), es la principal localidad del programa, en donde se evalúan líneas en todas las etapas de evaluación. En los campos experimentales Paso Farías (PF) en Artigas (30.54 S, 57.26 W) y en Tacuarembó (PB) (31.93 S, 55.38 W) se evalúan etapas avanzadas y finales, para lograr estimar con mayor precisión la performance de las líneas en los diferentes ambientes objetivo y estimar el efecto de la localidad e interacción genotipo por localidad.

La variedad INIA Merín (Pérez de Vida et al., 2016), liberada en los últimos años, es el cultivar más sembrado en el país, y es uno de los principales factores que explican el récord de rendimiento promedio nacional de superior a 9 t ha⁻¹ en las zafas 2020/21 y 2021/22 (MGAP-DIEA, 2021a, MGAP-DIEA, 2022). Para continuar cumpliendo este rol de liderazgo, el PMGA debe ser capaz de dar respuesta en forma rápida a las necesidades varietales del sector, además de hacerlo de la manera más eficiente posible, considerando la relación entre el logro de objetivos de mejoramiento con el tiempo y costos insumidos.

En cultivos autógamos como el arroz, el desarrollo de nuevas variedades implica, normalmente, la generación de diversidad mediante cruzamientos, el avance generacional hasta obtención de líneas fijas y la selección de las mejores líneas en ensayos de evaluación fenotípica. Particularmente en el PMGA, el proceso de mejoramiento consiste en generar alrededor de 100 cruzamientos anualmente, seguido por una combinación de *bulk* modificado y métodos de avance de generaciones de autofecundación por pedigrí, con selección fenotípica por altura y

arquitectura de planta, así como largo de ciclo, hasta las generaciones F₅ o F₆. El avance generacional se acelera con *shuttle-breeding* y avance rápido generacional en poblaciones seleccionadas. Se evalúan y seleccionan líneas fijas por *culling* independiente para rendimiento en grano, calidad molinera y resistencia a enfermedades, en cuatro años consecutivos de ensayos a campo (E1 a E4) seguidos por una etapa de evaluación final (EF). En la EF se replican los ensayos en diferentes épocas de siembra y en las localidades PF y PB.

Los programas de mejoramiento genético deben seleccionar padres para cruzamientos, cuya progenie va a constituir el nuevo ciclo de mejoramiento, los cuales se evalúan según su valor de cría (VC); también deben seleccionar líneas para avanzar hasta la siguiente etapa de evaluación fenotípica, cuyo objetivo final es la liberación de cultivares comerciales, seleccionados por su valor genotípico (VG) (Piepho et al., 2008). Falconer y Mackay (1996) definen al VG como el efecto aleatorio que expresa la combinación específica y única de genes de un individuo, y al VC como el efecto aleatorio aditivo que expresa la proporción del VG transmitido de padres a progenie. Para seleccionar padres, los mejoradores generalmente ordenan los candidatos en base a su VC y seleccionan una cierta cantidad de los mejores, mientras que para decidir qué línea avanzar basan su decisión en el VG de los candidatos.

La ecuación de ganancia genética (ΔG) (Lush, 1937, Eberhart, 1970), también conocida como la ecuación del mejorador, fue propuesta por Cobb et al. (2019) como un indicador de la eficiencia de los programas de mejoramiento genético, ya que articula los parámetros cruciales que los equipos de mejoramiento genético pueden usar en la optimización de los programas. El número de años por ciclo de mejoramiento (L) es inversamente proporcional a ΔG , por lo tanto algunas de las estrategias con mayor impacto en la eficiencia de mejoramiento involucran

decisiones tomadas en selección fenotípica temprana (Rutkoski, 2019a, Cobb et al., 2019).

Seleccionar con una precisión de selección alta en el primer año de evaluación fenotípica (E1) puede tener un alto impacto en mejorar la eficiencia de un programa de mejoramiento ya que: *i*) con padres seleccionados en base a su VC en E1, L disminuye significativamente, incrementando ΔG linealmente; ΔG se incrementa directamente aumentando la precisión de selección; *ii*) y seleccionado líneas candidatas para liberación de cultivares comerciales con estimaciones precisas tiene un alto impacto en la eficiencia de un programa de mejoramiento, asegurando una alta oferta de variedades mejoradas con mejor distribución de recursos (Werner, 2022).

Para explotar el potencial de la selección temprana y precisa en aumentar la eficiencia de los programas de mejoramiento, se deben superar algunos desafíos que pueden limitar la viabilidad de su implementación. El primer desafío es generado por el desequilibrio de los datos y la representación limitada de los ambientes en los que se evalúan los genotipos, lo que dificulta la estimación de los efectos y los componentes de varianza del ambiente y de la interacción genotipo por ambiente (GA) (Malosetti et al., 2016). GA es la respuesta diferencial de genotipos en diferentes ambientes, la cual afecta la heredabilidad de una característica y el ranking de líneas en diferentes ambientes, y por lo tanto afecta frecuentemente la toma de decisiones de mejoramiento (Romagosa y Fox, 1993). Tener en cuenta la interacción genotipo por ambiente permite desarrollar genotipos adaptados a ambientes específicos o seleccionar los más estables en la población de posibles ambientes objetivo (Yan et al. 2007). La GA puede ser tratada como una manifestación de la variación en la adaptación de genotipos a ambientes, los cuales deben ser identificados e incorporados a las decisiones de selección y recomendación de variedades (Mackay et al. 2019). El desafío planteado por la

limitada representación de ambientes en evaluación temprana se puede superar utilizando modelos mixtos multiambiente, ya que éstos toman prestada información de ensayos conectados que representan distintos ambientes dentro de un mismo año o en años anteriores (Piepho et al. 2008). Por otra parte, este análisis suele requerir altas capacidades computacionales, por lo cual se debe tener en cuenta la relación entre (i) el volumen de datos, la complejidad del modelo y la cantidad de parámetros a estimar; y (ii) la facilidad de cómputo, dada por el acceso a software adecuado, el tiempo de cómputo requerido y la capacidad de convergencia del modelo (Rogers y Taylor, 2019, Covarrubias-Pazaran et al., 2021).

Otra consideración necesaria a la hora de implementar un cambio en la estrategia de selección de un programa en funcionamiento es su validación, comparando la nueva con la estrategia convencional o de referencia (Heffner et al., 2011, Resende et al., 2012, Krchov et al., 2015), que debe contemplar y recrear en forma realista la situación en la que la nueva estrategia de selección se va a aplicar. Las métricas de comparación de estrategias de selección de uso común son la precisión de predicción (ρ) (Lorenzana y Bernardo, 2009, de los Campos et al., 2013, Desta y Ortiz, 2014) y la habilidad predictiva (PA) (Crossa et al., 2010, 2011). La definición más frecuente de ρ es la correlación entre valores predichos por el modelo el verdadero valor, y de PA, la correlación entre valores predichos por el modelo y un valor de referencia (Ould Estaghvirou et al., 2013).

Uno de los métodos de validación de estrategias de selección más comunes es la validación cruzada, que consiste en dividir el conjunto de datos en varios grupos o *fold*s, entrenando el modelo de predicción con cierto número de *fold*s y validándolo con el o los *fold*s restantes (Utz et al., 2000, Zhao et al., 2012, Ly et al., 2013), la asignación de los datos a cada *fold* no tiene en cuenta la estructura de los programas de mejoramiento, ya que divide aleatoriamente todo el conjunto de datos sin considerar ensayos, años ni localidades. Krchov et al. (2015) y Michel et

al. (2017) utilizaron validaciones cruzadas estructuradas en las que los *folds* corresponden a años de evaluación, pero para lograr poder cruzar los datos en *folds* de predicción y validación a lo largo de las iteraciones, deben ignorar el orden cronológico de los años. Aleatorizar datos correspondientes a años posteriores a E1 y usarlos como *folds* para predecir el comportamiento en E1 generaría artificialmente una conectividad entre datos de diferentes años que no recrea en forma realista la estructura de datos más habitual en un programa de mejoramiento vegetal. Un método de validación que respete la estructura en la que se generan datos y la conectividad de estos permitiría una evaluación realista de estrategias de selección.

En este trabajo evaluamos diferentes escenarios de predicción con un uso creciente de información de ensayos y ambientes y complejidad de su modelación, para la selección en E1 de padres y para avance de líneas en el PMGA. Esta comparación de escenarios se hace en base a la partición de varianzas y la PA calculada mediante una estrategia de validación que recrea en forma realista la conectividad y el orden cronológico de los datos de mejoramiento.

1.1 HIPÓTESIS

- a) La precisión de la estimación de los componentes de varianza en el análisis de ensayos en E1 se incrementa con la incorporación de datos de ensayos del mismo año y de años anteriores.
- b) La precisión de las estimaciones de los componentes de varianza en el análisis de ensayos en E1 se incrementa con el modelado del ambiente y la interacción genotipo por ambiente.
- c) La habilidad predictiva de los valores de cría y genético de líneas evaluadas en E1 se incrementa con la incorporación de datos de ensayos del mismo año y de años anteriores.

d) La habilidad predictiva de los valores de cría y genético de líneas evaluadas en E1 se incrementa con el modelado del ambiente y la interacción genotipo por ambiente.

e) Los escenarios que recrean la selección realizada históricamente por el PMGA tienen mayor número de líneas de mayor valor genotípico predicho que coinciden con las líneas históricamente seleccionadas por el PMGA, que aquellos escenarios que plantean criterios de selección alternativos.

1.2 OBJETIVOS

1.2.1 Objetivo general

Evaluar la selección en E1 de padres y para avance de líneas en el PMGA para contribuir al aumento de su eficiencia.

1.2.2 Objetivos específicos

- a) Comparar la precisión de estimación de componentes de varianza y la habilidad predictiva de valores de cría y genético obtenidas en escenarios de selección en E1 con niveles crecientes de incorporación de datos de otros ensayos del mismo año y de años anteriores.
- b) Comparar la precisión de estimación de componentes de varianza y la habilidad predictiva de valores de cría y genético obtenidas en escenarios de selección en E1 con datos de múltiples ambientes que se diferencien en modelar o no la interacción genotipo por ambiente.
- c) Evaluar la correspondencia entre el criterio de selección aplicado históricamente por el PMGA y el de escenarios de predicción alternativos.

2 EVALUATION OF STRATEGIES FOR EARLY SELECTION IN RICE LINES¹

2.1 RESUMEN

Seleccionar con buena precisión en el primer año de evaluación del rendimiento (E1) puede tener un gran impacto en la mejora de la eficiencia de un programa de mejoramiento. En este trabajo evaluamos el impacto de incorporar análisis multiambientales en la selección en etapas tempranas de evaluación en un programa de fitomejoramiento público, utilizando una estrategia de validación que contempla el momento en que se dispone de los datos fenotípicos. Se estudiaron cinco escenarios de predicción (PS) donde se predijeron valores con modelos considerando diferentes niveles de disponibilidad y agregación de datos para los análisis y la inclusión o no un término de interacción genotipo por ambiente (GE). Estudiamos el mejor PS para implementar de forma rutinaria en un programa público de fitomejoramiento considerando la partición de la varianza fenotípica del rendimiento de grano, la habilidad predictiva de los valores de cría y genéticos y el porcentaje de las líneas superiores en E1 que alcanzaron etapas de evaluación avanzadas. Propusimos una estrategia de validación efectiva y realista para la estructura de los programas de mejoramiento. Encontramos que el análisis conjunto de múltiples ensayos y ambientes resultó en una mejor estimación de los componentes de la varianza que cuando se realizaron análisis parciales, así como una alta habilidad predictiva para la selección temprana de padres y avance de líneas, con el uso de datos correspondientes a múltiples ensayos y ambientes. Otro hallazgo de este trabajo es que la inclusión de un término GE en los modelos

¹ Artículo para someter a revisión en *Crop Science*.

correspondientes a escenarios de predicción no tuvo una respuesta clara y consistente en la habilidad predictiva.

2.2 SUMMARY

Selecting with good precision in the first year of yield evaluation (E1) can have a great impact on improving the efficiency of a breeding program. In this work, we evaluated the impact of incorporating multi-environmental analyses in selection on early evaluation stages in a public plant breeding, using a validation strategy that contemplates the moment in which the phenotypic data becomes available. Five prediction scenarios (PS) were studied where values were predicted with models considering different levels of data availability and aggregation for analyses, and the inclusion or not of a genotype by environment interaction (GE) term. We studied the best PS to implement routinely in a public plant breeding program considering phenotypic variance partition of grain yield, predictive ability and percentage of the top lines on E1 that reached advanced evaluation stages. We proposed an effective and realistic validation strategy for breeding programs' structure. We found that the joint analysis of multiple trials and environments resulted in a better estimation of variance components than when partial analyses were carried out, as well as a high predictive ability for early selection of parents and line advancement, with the use of data corresponding to multiple trials and environments. Another finding of this work is that the inclusion of a GE term in the models corresponding to PS did not have a clear and consistent response in predictive ability.

2.3 INTRODUCTION

Public breeding program optimization is an area of active research (Cobb et al., 2019; Santantonio et al., 2020; Ceballos et al., 2021). Optimization strategies usually differentiate the two major selection activities addressed by breeding programs: parent selection and selection for line advancement (Heffner et al., 2010; Gorjanc et al., 2018).

Breeding programs must address both parent selection and line advancement. Parent selection is the selection of lines for crossing to generate the progenies that will be the base population for the next breeding cycle. Line advancement is the selection of lines to be advanced to the following evaluation stage, with the final goal of releasing commercial varieties. Candidates for parent selection should be evaluated by their breeding values (BV, i.e. the random additive effect that expresses the portion of the genotypic value that is transmitted from parents to offspring), while candidates for line advancement and commercial varieties development should be evaluated by their genotypic values (GV, the random effect that expresses the particular assemblage of genes possessed by the individual, including additive and non-additive genotypic effects) (Piepho et al., 2008). Falconer and Mackay (1996) define BV as the random additive effect that expresses the portion of the genotypic value that is transmitted from parents to offspring. BV's variance-covariance structure is $\mathbf{A}\sigma_a^2$, where σ_a^2 is the additive variance and \mathbf{A} is the numerator relationship matrix, computed from the coefficient of coancestry between individuals. GV are described as the random effect that expresses the particular assemblage of genes possessed by the individual. GV's variance-covariance structure, when there is no genomic data available, is usually considered as $\mathbf{I}\sigma_g^2$, where σ_g^2 is the genotypic variance and \mathbf{I} is an identity matrix, denoting that covariance between individuals is underestimated. To decide what parents to select, breeders usually rank candidates based on the lines' BV and select

a certain number of them, while to decide what lines to advance onto the next evaluation stage, breeders make decisions based on lines' GV.

Genetic gain is the improvement in average genetic value in a population or the improvement in average phenotypic value due to selection within a population over cycles of breeding (Rutkoski, 2019b). The genetic gain equation, also known as the breeders' equation, described by Lush (1937) and complemented by Eberhart (1970) has been proposed as a measure of plant breeding programs' efficiency (Cobb et al., 2019) as it articulates the crucial parameters of the plant breeding process. In the equation, the genetic gain per unit of time (ΔG) is given by $\Delta G = \frac{r_{xa}\sigma_a k}{L}$, where r_{xa} is the selection accuracy, σ_a is the additive genetic standard deviation, k is the selection intensity and L is the time required to complete one breeding cycle (Rutkoski, 2019b). Given the importance of L in determining ΔR , some of the strategies with a higher potential impact on breeding efficiency involve decisions taken in early phenotypic evaluation (Rutkoski, 2019b; Cobb et al., 2019). Selecting with high accuracy in the first year of phenotypic evaluation (E1) can have a great impact on improving the efficiency of a breeding program, as: *i*) when parents are selected for new crosses based on their BV in E1, L decreases significantly, therefore ΔG increases linearly; and ΔG is directly increased when r_{xa} increases; and *ii*) selecting candidate lines for product development with accurate estimates ensuring a high offer of improved varieties with better resource allocation (Werner, 2022).

To exploit the great potential that accurate early selection has on increasing breeding programs' efficiency, some challenges that might limit the viability of its implementation must be overcome. The first challenge is due to the unbalance of data and the limited representation of environments in which genotypes are evaluated, which makes it difficult to estimate the effect and variance components of the environment and of the genotype by environment interaction (GE)

(Malosetti et al., 2016). GE is the differential response of genotypes in different environments, and it affects the heritability of a trait and the ranking of lines in different environments, and thus strongly affects decision-making in breeding programs (Romagosa and Fox, 1993). Accounting for GE allows for developing environment-specific adapted genotypes or for selecting the most stable ones in the population of target environments (Yan et al., 2007). GE can be treated as a source of noise that reduces selection accuracy and thus the genetic gain; or as a manifestation of the variation in the adaptability of genotypes to environments that must be identified and incorporated into parental and line advance selection decisions (Mackay et al., 2019). The challenge caused by the limited representation of environments in early evaluation stages can be overcome using mixed models for multi-trial analysis that borrow information from connected trials representing environments in the same year or in previous years (Piepho et al., 2008). However, this analysis often requires high computational capabilities, which may not be compatible with the fast and accurate selection decisions that daily practice in annual crop breeding programs requires. There is a trade-off between, (i) the volume of data, model complexity and the number of parameters to estimate; and (ii) ease of computing, given by access to suitable software, computational time, and model convergence ability (Rogers and Taylor, 2019; Covarrubias-Pazaran et al., 2021).

Another challenge for implementing new selection strategies in a running breeding program is its validation, i.e., how to realistically compare the performances of alternative strategies contemplating the situation in which they are to be applied. Usually, this is done by comparing the strategy being studied to a reference strategy (Heffner et al., 2011; Resende et al., 2012; Krchov et al., 2015). The most common validation metrics are accuracy (ρ) (Lorenzana and Bernardo, 2009; de los Campos et al., 2013; Desta and Ortiz, 2014) and predictive ability (PA)

(Crossa et al., 2010, 2011). There are several definitions for both ρ and PA, although the most frequent definition for ρ is the correlation between values predicted by the model under evaluation and the true value, and for PA, the correlation between values predicted by the model under evaluation and a reference value, e.g., the values predicted by an alternative strategy (Ould Estaghvirou et al., 2013).

One of the most common validation methods for selection strategy is cross-validation, which consists of dividing the data set into several groups or folds, training the prediction model with a certain number of folds and validating it with the remaining fold(s). This process is repeated in a high number of iterations, each one with a different distribution of the data in folds. This causes data to be crossed that in some iterations will be in the prediction folds and in others in the validation folds. In the case of random cross-validation (Utz et al., 2000; Zhao et al., 2012; Ly et al., 2013), the assignment of the data to each fold does not consider the structure of breeding programs, since it randomly divides the entire data set without considering trials, years or locations. Krchov et al. (2015) and Michel et al. (2017) used structured cross validations in which the folds correspond to evaluation years, but in order to be able to cross the data in prediction and validation folds throughout the iterations, they must ignore the chronological order of the years. This is possible when the same genotypes are replicated in several years, but frequently in selection for E1 lines, breeders have phenotypic evaluations of these lines in a single year. Therefore, randomizing data corresponding to years after E1 and using them as folds to predict behavior in E1 would artificially generate a connectivity between data from different years that does not realistically recreate the most common data structure in a plant breeding program. A validation method that respects the structure in which data is generated and its connectivity would allow a realistic evaluation of selection strategies.

Another extensively used validation method for evaluating selection strategies are simulations (Wong and Bernardo, 2008; Iwata and Jannink, 2011; Gorjanc et al., 2018b; Chris Gaynor et al., 2021). This method has the advantage that true BV is known (Meuwissen et al., 2001; Ceron-Rojas et al., 2015), which allows for directly calculating selection accuracy. Therefore, selection strategies can be compared in terms of genetic gain easily (Sun et al., 2011; Rutkoski, 2019a). However, to apply this method, a series of assumptions are made, on which the results are strongly dependent (Johnsson et al., 2019; Gaynor et al., 2021). This can make the results of the comparisons less convincing, which can be a disadvantage when making real decisions in a real breeding program.

Generally, breeding programs recombine elite parents in crossing stages, followed by progeny multiplication or progeny derivatives generation (e.g., test crosses or inbred derivatives, including inbred lines) and testing stages to evaluate the potential of progeny derivatives as parents or products to release as commercial varieties (Covarrubias-Pazaran et al., 2022). This process generates a recurrent selection scheme, by the cyclical repetition of the process, that increases the population mean of quantitative traits under selection (Rutkoski, 2019b; Covarrubias-Pazaran et al., 2022). A key feature of breeding program's process is that several generations run in parallel, not waiting for a cycle to be completed to start a new one, which leads to highly unbalanced datasets (Piepho et al., 2008). Covarrubias-Pazaran et al. (2022) define a cohort as a set of genotypes at a given stage within a given cycle, where generations are discrete when parents are selected from a unique cohort or overlapping when parents are selected from multiple cohorts. Overlapping generations are the most common and lead to higher genetic connectivity between cohorts.

To explore methodological strategies for early selection that contemplate breeding programs' structure, as well as their data generating process, this work focuses on a small-size national public program from Uruguay as a case study.

The Uruguayan National Institute of Agricultural Research's rice breeding program (IRBP) has led the Uruguayan rice cultivar variety market for decades. In 2020-2021, more than 60% of the rice area was sown with varieties developed by IRBP (DIEA MGAP, 2021). IRBP's goal is to develop high-yielding, high-quality and disease-resistant inbred varieties (lines) for two major rice subpopulations (Kovach et al., 2007) and grain quality types: long-grain indica (IND), long-grain tropical japonica (TRJ) (Quero et al., 2018). In IRBP's breeding process, around 100 crosses are generated every year, followed by a combination of modified bulk and pedigree selfing generation advance methods, with phenotypic selection for plant height, architecture and cycle length until F₅ or F₆. Phenotypic evaluation and selection are applied to one new cohort of around 489 fixed lines per year by independent culling for grain yield, milling quality and blast resistance during four consecutive years of phenotypic yield trials (E1 to E4) followed by a final evaluation stage (FE). Trials are conducted in three locations representing the major production regions (Tseng et al., 2021). IRBP has a consolidated database (Rebollo et al., 2023), with historic records from more than 20 years of phenotypic trials, with the typical unbalanced structure of breeding programs.

In this work, we evaluated different prediction scenarios with increasing use of information corresponding to trials and environments, as well as increasing complexity of the model, for parent selection and line advancement in E1. The prediction scenario comparison is based on variance partition and predictive ability calculated through a validation strategy that recreates connectivity and chronological order of breeding programs data in a realistic way.

2.4 MATERIALS AND METHODS

2.4.1 Phenotypic and Pedigree Data

The dataset used in this study was a subset from the IRBP's database (Rebollo et al., 2023), which corresponded to grain yield records and pedigree information of 9888 inbred lines distributed in 14 cohorts, evaluated in 527 field trials from evaluation stages E1 to FE conducted from 2003 to 2019. Trials had a randomized complete block design with two replicates in E1 and E2, three replicates in E3 and E4 and four replicates in FE. Trials in E1 to E3 were conducted at Paso de la Laguna Experimental Unit (PL) (33.27 S, 54.17 W), trials in E4 to FE were conducted in PL and a second location at Paso Farías Experimental Unit (PF) (30.54 S, 57.26 W), while FE trials were conducted in two contrasting sowing dates at PL, and one sowing date at PF and Pueblo del Barro Experimental Unit (31.93 S, 55.38 W).

2.4.1.1 Field Trial Quality

We evaluated trial quality through the study of heritability on a per-trial basis by fitting the following model for each trial: $y_{ij} = \mu + g_i + b_j + \varepsilon_{ij}$, where y_{ij} is the grain yield score (kg ha^{-1}), μ is the trial overall mean, g_i is the i^{th} random genotype effect with $g_i \sim N(0, \mathbf{I}\sigma_g^2)$, where σ_g^2 is the genetic variance, b_j is the fixed effect of the j^{th} block and ε_{ij} is the random residual, with $\varepsilon_{ij} \sim N(0, \mathbf{I}\sigma_\varepsilon^2)$, where σ_ε^2 is the error variance. Models were fitted using the *ASReml-R* R package (Butler, 2021) and variance components were estimated via REML. Broad sense heritability (H^2) was calculated as: $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_\varepsilon^2 / r)$, where r is the number of replicates. Only trials with heritability higher than 0.3 were used in subsequent analyses.

2.4.1.2 Reference Lines

Reference lines (RL) were defined as the lines under selection in IRBP that were evaluated in field trials for at least 3 years. Trials with at least one reference line were included in the analyses described below.

2.4.1.3 Environments and Environmental Connectivity

We defined environment as combinations of year, location and planting time. Planting time was a categorical variable based on the trial's planting date: early planting time corresponded to trials planted before October 15th, intermediate-early to trials planted between October 16th and 31st, intermediate-late between November 1st and 15th and late after November 16th. We computed inter-environment connectivity through lines as the number of evaluated lines shared between environments and the number of evaluated lines within each environment. To facilitate model convergence, we applied filters to the datasets to increase connectivity. First, only environments with mean connectivity higher than 20 and minimum connectivity higher than 3 were kept. Secondly, only trials in which at least one line was evaluated for 3 years or more in the full dataset were kept. The resulting dataset was defined as the reference (REF) dataset.

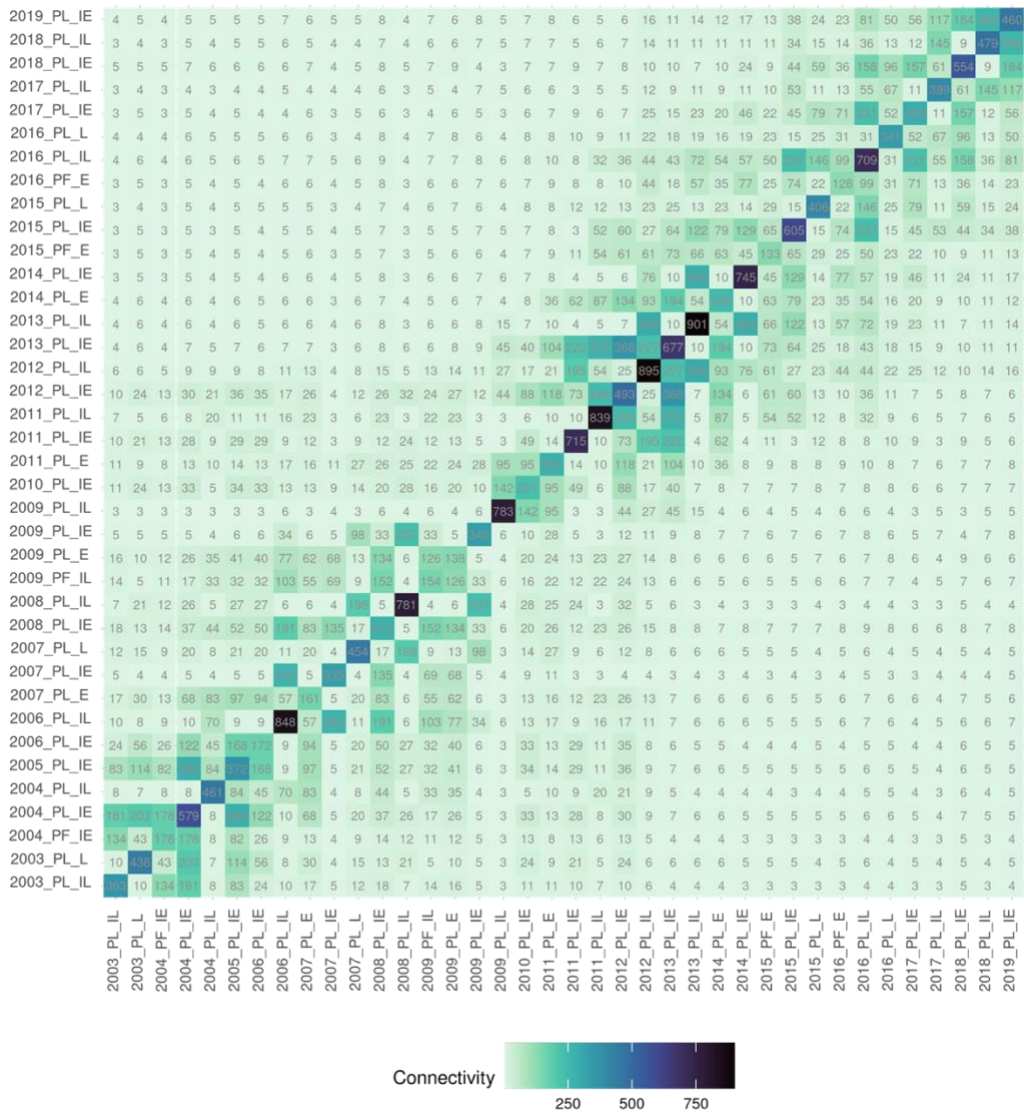


Figure 1. Inter-environment connectivity through phenotyped lines measured as the number of shared lines is shown in the non-diagonal and the total number of lines in the diagonal.

2.4.1.4 Reference Dataset Characterization

The inter-environment connectivity through shared lines of the REF dataset (non-diagonal, Figure 1) had a minimum, mean and maximum of 3, 26 and 368 lines, respectively. The number of lines evaluated by environment for the REF dataset (diagonal, Figure 1) had a minimum, mean, and maximum of 128, 457 and 901 lines, respectively.

The REF dataset used for analysis consisted of 48,850 field plot records of grain yield phenotypic evaluation, corresponding to 17 years, 527 field trials, 38 environments and 9888 breeding lines, and their corresponding pedigree information. Cohorts from years 2003 to 2018 had at least three evaluation stages (E1 to E3) in the dataset. Data unbalance was found across years, planting times and locations (Figure 2). The average number of lines evaluated by year was 1,125, with a maximum number of 1,853 evaluated lines in 2011 and a minimum of 200 lines in 2010. PL was the most important location, with all the lines evaluated, whereas 551 lines were evaluated in PF.

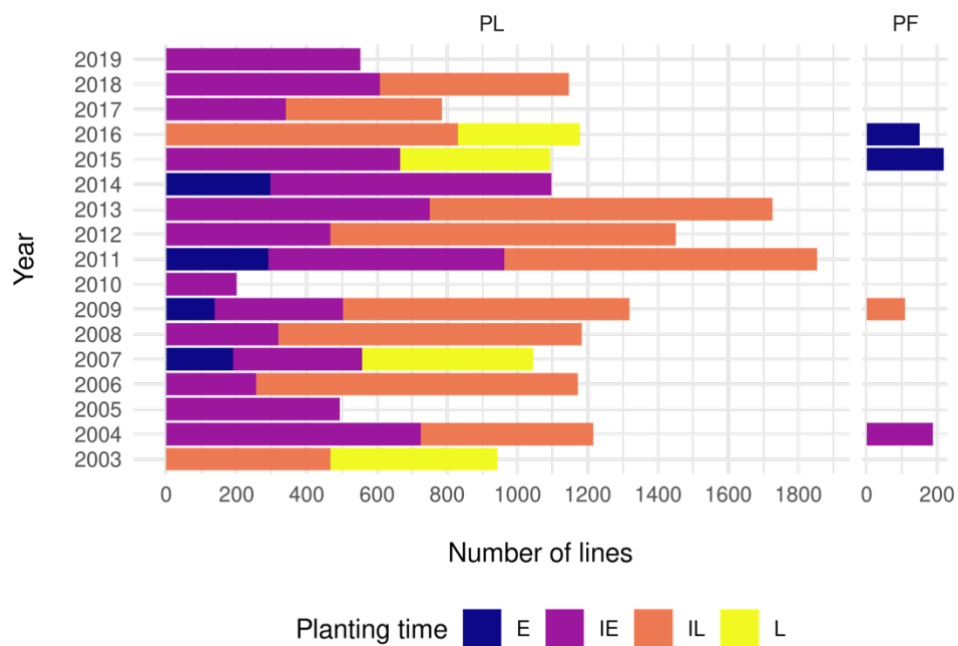


Figure 2. Number of evaluated lines by year, location and planting time. Locations: PL, Paso de la Laguna; PF, Paso Farías. Planting times: E, early; IE, intermediate-early; IL, intermediate-late; L, late.

We characterized IRBP's process through the number of lines evaluated by year, cohort and evaluation stage (Figure 3). Cohorts from one to 14 correspond to the group of lines that started being evaluated in the years 2003 to 2018, respectively. The cohort corresponding to year 2005 was missing due to operative

issues, while the cohort for year 2010 had to be reseeded in 2011 together with the following cohort, due to severe adverse climatic conditions. Thus, cohort 7 is the combination of the cohorts corresponding to years 2010 and 2011. Eleven cohorts were evaluated in all the evaluation stages in the period included in the dataset. The minimum, mean and maximum number of lines in E1 was 139, 489 and 776, respectively. The average percentage of lines advanced from E1 to E2, from E2 to E3, from E3 to E4 and from E4 to FE were 35, 66, 49 and 42 %, respectively.

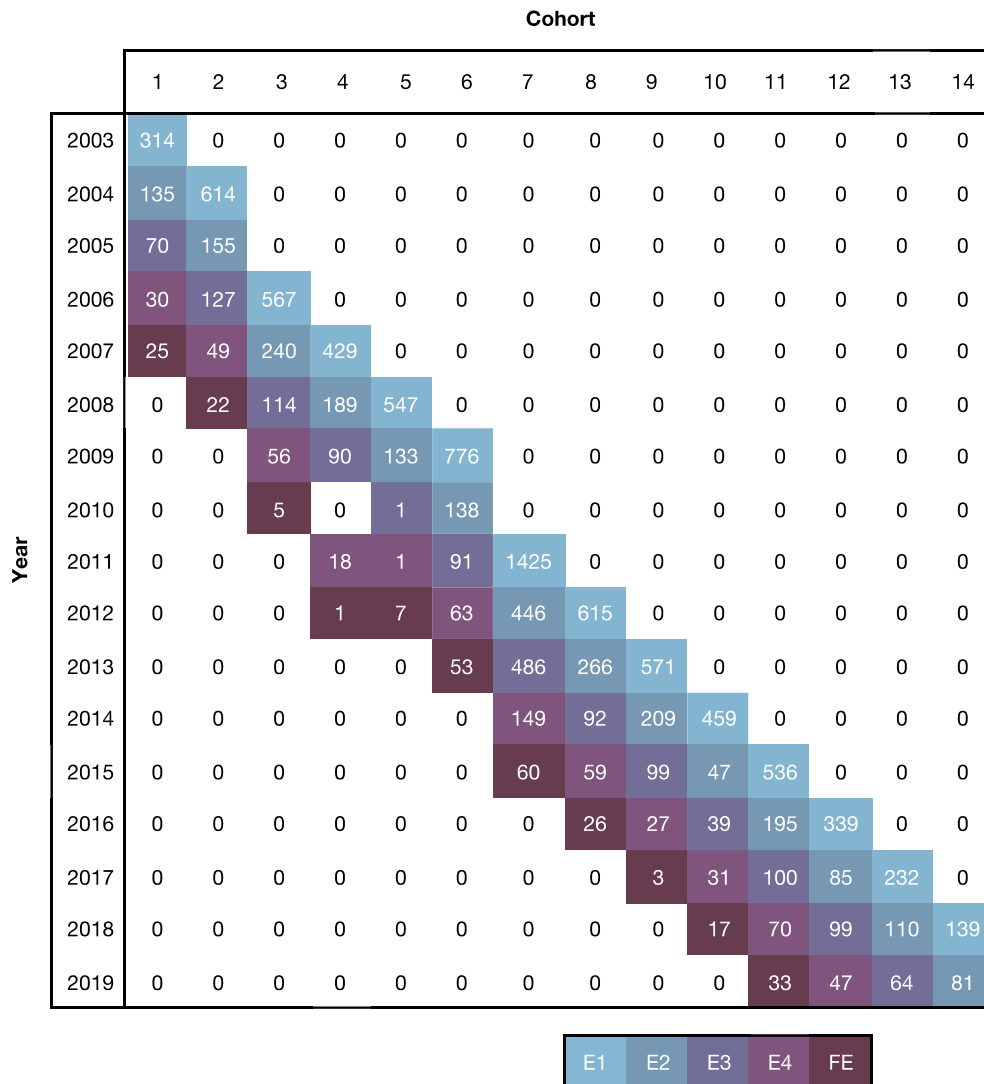


Figure 3. Number of lines by cohort, year and evaluation stage.

The size of cohorts and their connectivity as shared parents were computed (Figure 3). Minimum, mean and maximum number of parents were 10, 30 and 70, respectively. Parent connectivity between cohorts had a minimum, mean and maximum of 0, 2 and 22, respectively. Three groups of cohorts were observed based on their parent connectedness, which denoted parent change over time and cohorts. The first group with cohorts 1 to 7 shared an average of 5 parents, the second group with cohorts 8 to 11 shared an average of 6 parents and the third

group with cohorts 12 to 14 shared an average of 4 parents. Average connectivity between the first and second groups was 1.5 parents, between the second and third group was 1 parent, and between the first and third group was 0.7 parents.

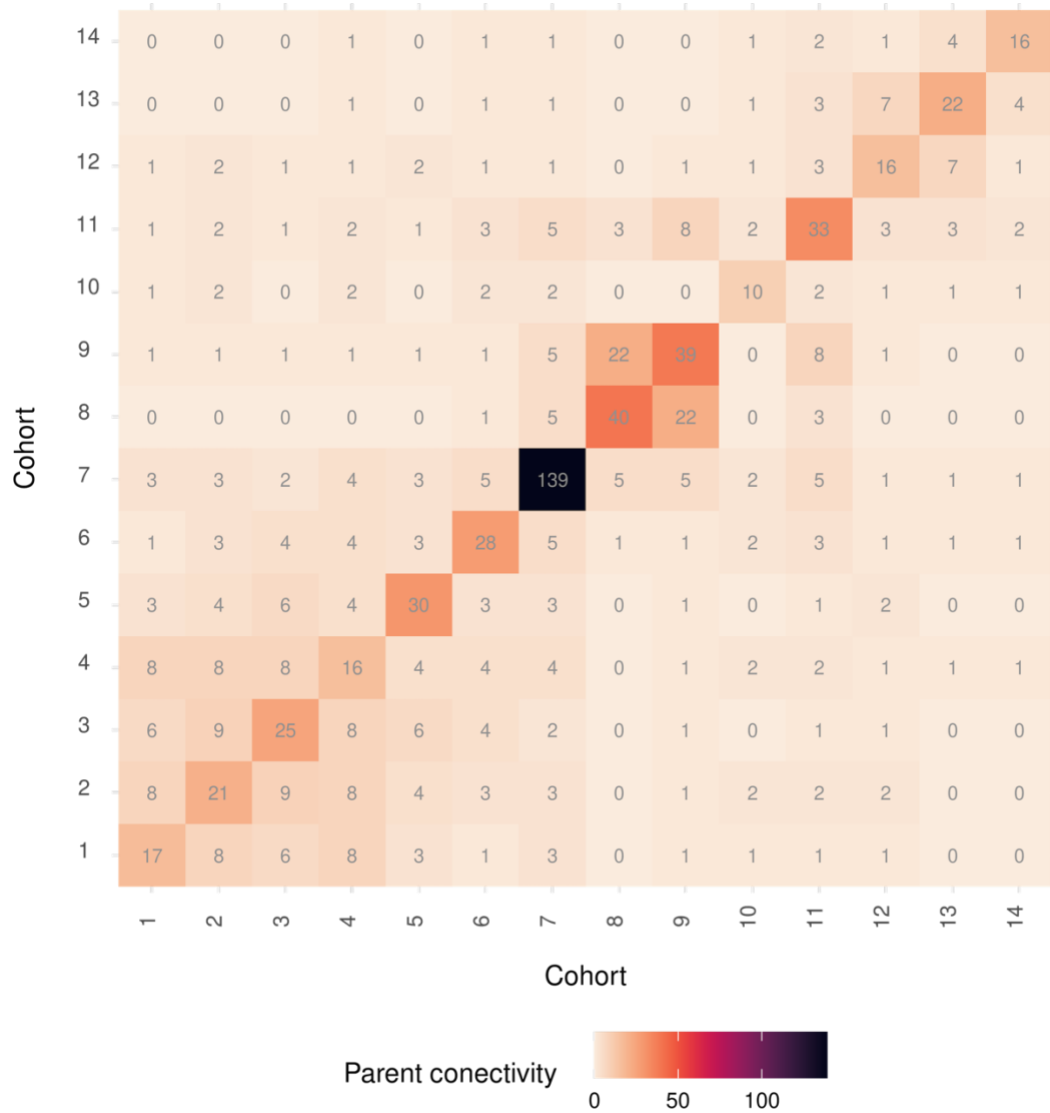


Figure 4. Number of parents by cohort (diagonal) and parent connectivity between cohorts (off-diagonal)

2.4.2 Prediction Scenarios

Five prediction scenarios (PS) were studied for parent selection and line advancement, where BV and GV were predicted fitting models with varying terms

and different subsets of the REF dataset (Figure 4). PS were defined to recreate different levels of data availability and data aggregation for analyses and the inclusion or not of the GE term.

PS0 represented the lowest level of data availability and data aggregation for analysis, as values were predicted using data from every single trial separately. A model was fitted for each of the 527 trials (models PS0_{M1} to PS0_{M527}) as: $y_{ij} = \mu + g_i + b_j + \varepsilon_{ij}$, where y_{ij} is the grain yield score (kg ha⁻¹), μ is the trial overall mean, g_i is the i^{th} random genotypic effect with $g_i \sim N(0, \mathbf{A}\sigma_a^2)$ for BV and $g_i \sim N(0, \mathbf{I}\sigma_g^2)$ for GV, where σ_a^2 is the additive variance, \mathbf{A} is the numerator relationship matrix, σ_g^2 is the genotypic variance and \mathbf{I} is an identity matrix; b_j is the fixed effect of the j^{th} block and ε_{ij} is the random residual effect, with $\varepsilon_{ij} \sim N(0, \mathbf{I}\sigma_\varepsilon^2)$, where σ_ε^2 is the error variance.

PS1 used all the data generated in the year of evaluation, as values were predicted fitting a model to all the trials (E1 to FE) of the same year jointly. PS5 used all data available from five consecutive years. For PS5, values were predicted fitting the data from the year when selection decisions were recreated, plus the previous four consecutive years. A model was fitted for each of 14 years for PS1 (years 2003, 2004, 2006 to 2009, and 2011 to 2018, models PS1_{M2003}, PS1_{M2004}, PS1_{M2006} to PS1_{M2009}, and PS1_{M2011} to PS1_{M2018}) and for the 13 5-year windows available for PS5 (5-year windows ending in 2007 to 2019, models PS5_{M2007} to PS5_{M2019}) as: $y_{ijkl} = \mu + g_i + e_j + b_{k(l)} + \varepsilon_{ijkl}$, where y_{ijkl} is the grain yield score (kg ha⁻¹), μ is the PS overall mean, g_i is the i^{th} random genotype effect with $g_i \sim N(0, \mathbf{A}\sigma_a^2)$ for BV and $g_i \sim N(0, \mathbf{I}\sigma_g^2)$ for GV, where σ_a^2 is the additive variance, \mathbf{A} is the numerator relationship matrix, σ_g^2 is the genotypic variance and \mathbf{I} is an identity matrix; e_j is the j^{th} random environment effect with $e_j \sim N(0, \mathbf{I}\sigma_e^2)$, where σ_e^2 is the environmental variance; $b_{k(l)}$ is the random effect of the k^{th} block nested within the l^{th} trial with $b_{k(l)} \sim N(0, \mathbf{I}\sigma_b^2)$, where σ_b^2 is the

block variance; and ε_{ijkl} is the random residual effect with $\varepsilon_{ijkl} \sim N(0, I\sigma_\varepsilon^2)$, where σ_ε^2 is the error variance.

Finally, PS1GE and PS5GE predicted values with the same data subsets as PS1 and PS5, respectively, but with the addition of a GE interaction term in the models, as: $y_{ijkl} = \mu + g_i + e_j + ge_{ij} + b_{k(l)} + \varepsilon_{ijkl}$, where all the terms are the same described in the previous paragraph, and in addition ge_{ij} is the random effect of the interaction between the i^{th} genotype and the j^{th} environment, with $ge_{ij} \sim N(0, I\sigma_{ge}^2)$, where σ_{ge}^2 is the genotype by environment interaction variance.

The numerator relationship matrix (\mathbf{A}) was computed from the pedigree information for the individuals evaluated in each of the data subsets of each PS and their parents from up to five crossbred generations back using the coefficient of coancestry between individuals (Falconer and Mackay, 1996). \mathbf{A} was calculated considering the number of inbreeding generations with the *pedigreeTools* R package (Vazquez et al., 2018).

2.4.3 Prediction Scenario Comparison

To compare the studied PS and identify the best one, we computed phenotypic variance components of grain yield and their standard errors, predictive ability (PA) and the percentage of the top performing lines on E1 according to each PS that advanced to E4 or beyond (PTLA).

To analyze the phenotypic variance partition of grain yield, variance components and their standard errors were obtained from each model and averaged by PS.

To compute PA, we defined a reference BV (RBV) and reference GV (RGV) as the ones produced with a reference PS (termed REF) that used the most complete model we could fit to the whole REF dataset (Figure 5). The model fitted to the REF dataset to obtain the RBV and RGV was: $y_{ijkl} = \mu + g_i + e_j + ge_{ij} +$

$b_{k(l)} + \varepsilon_{ijkl}$, where y_{ijkl} is the grain yield score (kg ha⁻¹), μ is the overall mean, g_i is the i^{th} random genotype effect with $g_i \sim N(0, \mathbf{A}\sigma_a^2)$ for RBV and $g_i \sim N(0, \mathbf{I}\sigma_g^2)$ for RGV, where σ_a^2 is the additive variance, \mathbf{A} is the numerator relationship matrix, computed as described above, σ_g^2 is the genotypic variance and \mathbf{I} is an identity matrix; e_j is the j^{th} random environment effect with $e_j \sim N(0, \mathbf{I}\sigma_e^2)$, where σ_e^2 is the environmental variance; ge_{ij} is the random effect of the interaction between the i^{th} genotype and the j^{th} environment, with $ge_{ij} \sim N(0, \mathbf{I}\sigma_{ge}^2)$, where σ_{ge}^2 is the genotype by environment interaction variance; $b_{k(l)}$ is the random effect of the k^{th} block nested within the l^{th} trial with $b_{k(l)} \sim N(0, \mathbf{I}\sigma_b^2)$, where σ_b^2 is the block variance; and ε_{ijkl} is the random residual effect with $\varepsilon_{ijkl} \sim N(0, \mathbf{I}\sigma_\varepsilon^2)$, where σ_ε^2 is the error variance.

PA for parent selection was computed as the Spearman's correlation between the rankings based on BV obtained with the studied PS and the ranking based on RBV. PA for line advancement was computed as the Pearson's correlation between the GV obtained with the studied PS and the RGV.

For validation of the studied PS the two TRJ and IND germplasm groups were studied separately, as they correspond to separate breeding targets and are selected independently from each other in IRBP. We computed PA for parent selection and PA and PTLA for line advancement across several iterations within each PS using a validation scheme (Figure 5 **Error! Reference source not found.**) that recreated the availability of data in the breeding program for each year.

The workflow of the validation scheme is depicted in Figure 5. Firstly, models were fitted with REF dataset to obtain RGV and RBV. Subsequently, for each PS and year, considered as a fold of the validation scheme, we fitted the corresponding models to obtain the GV and BV. The GV and BV corresponding to lines in E1 in that year formed the PS_{year} dataset. Only datasets with more than 30 lines were used in further analyses. Pearson correlation between GV and RGV was

calculated to obtain the PA for line advancement. We ranked the lines in each PS_{year} dataset based on BV and RBV and calculated the Spearman correlation between these two ranks, obtaining the PA for parent selection.

As our validation strategy implied folds with different sizes, and to rule out the effect of the fold size on the estimation of PA, we analyzed the relationship between the number of folds and the number of lines per fold by fitting a linear model of predictive ability in function of number of lines per fold, for each PS.

PTLA was calculated for each PS to assess the correspondence between each PS and the realized line advancement criteria applied historically by IRBP. To that end, we used the same validation scheme as for calculating PA (Figure 5**Error! Reference source not found.**). For each PS and year, we calculated the number of RL (N_{RL}) in that PS and year. Lines were ranked by their GV in that PS and year, and PTLA was computed as the percentage of the RL that were on the top N_{RL} lines.

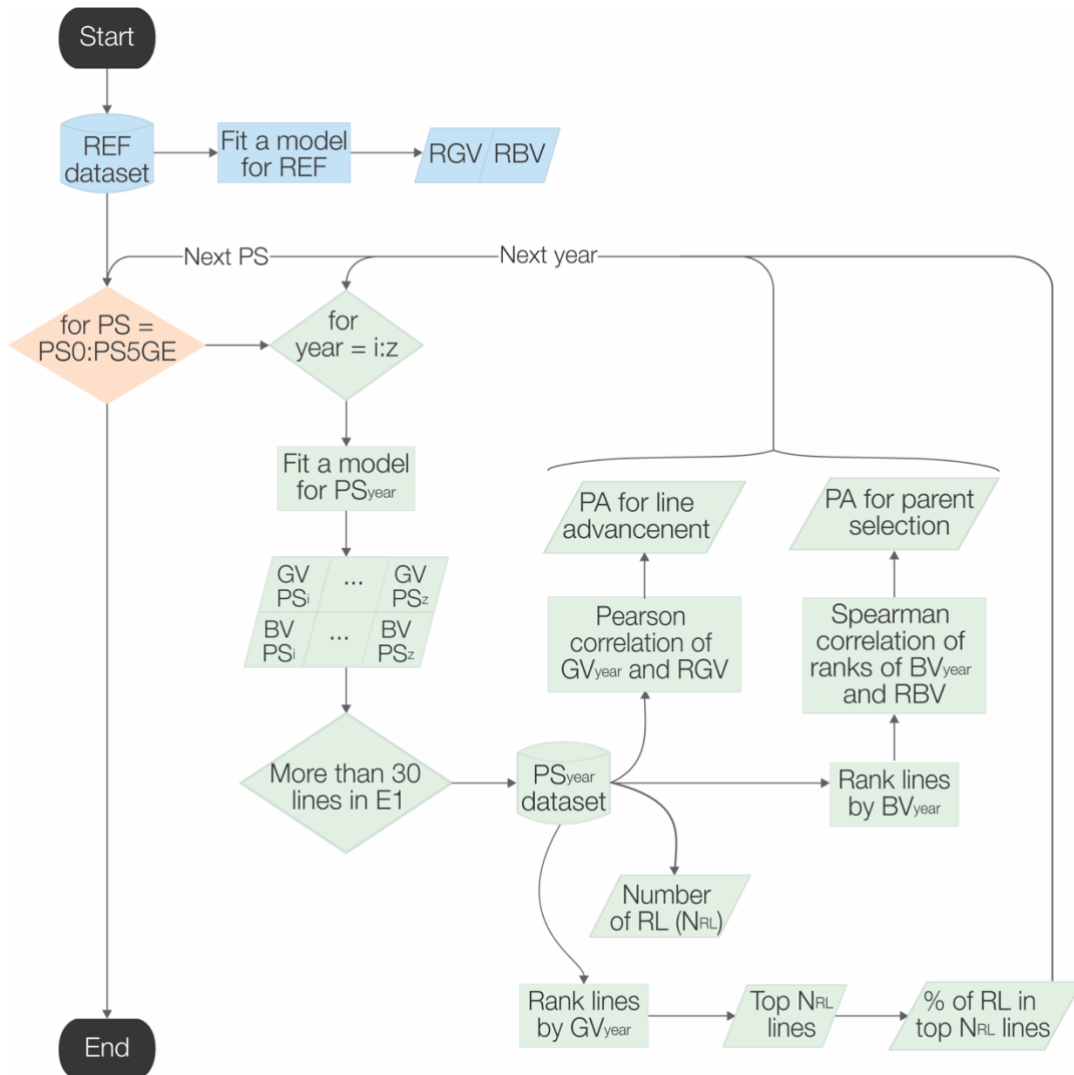


Figure 5. Workflow of the validation scheme. Elements of the workflow are coded by shape: cylinder, data; rectangle, action; parallelogram, results; diamonds, decisions. REF dataset: reference dataset; RGV: reference genotypic value; RBV: reference breeding value; PS: prediction scenario; PS0:PS5GE: list of all PS; GV: genotypic value; BV: breeding value; E1: first year of phenotypic evaluation trial; PA: predictive ability; RL: reference lines; N_{RL} : number of RL.

2.5 RESULTS

2.5.1 Variance Partition

We studied how the phenotypic variance was partitioned across model terms in each PS for parent selection and line advancement, and its standard error. The PS that estimated variance components with the lower standard error and the second lower residual variance was REF (Figure 6), and it was the PS with the higher number of observations. Furthermore, REF captured almost all environmental variance, since its residual variance was almost the same as the one captured by PS0, where only one trial and environment are modeled. REF had the lower line evaluation trials, genotype and block variances.

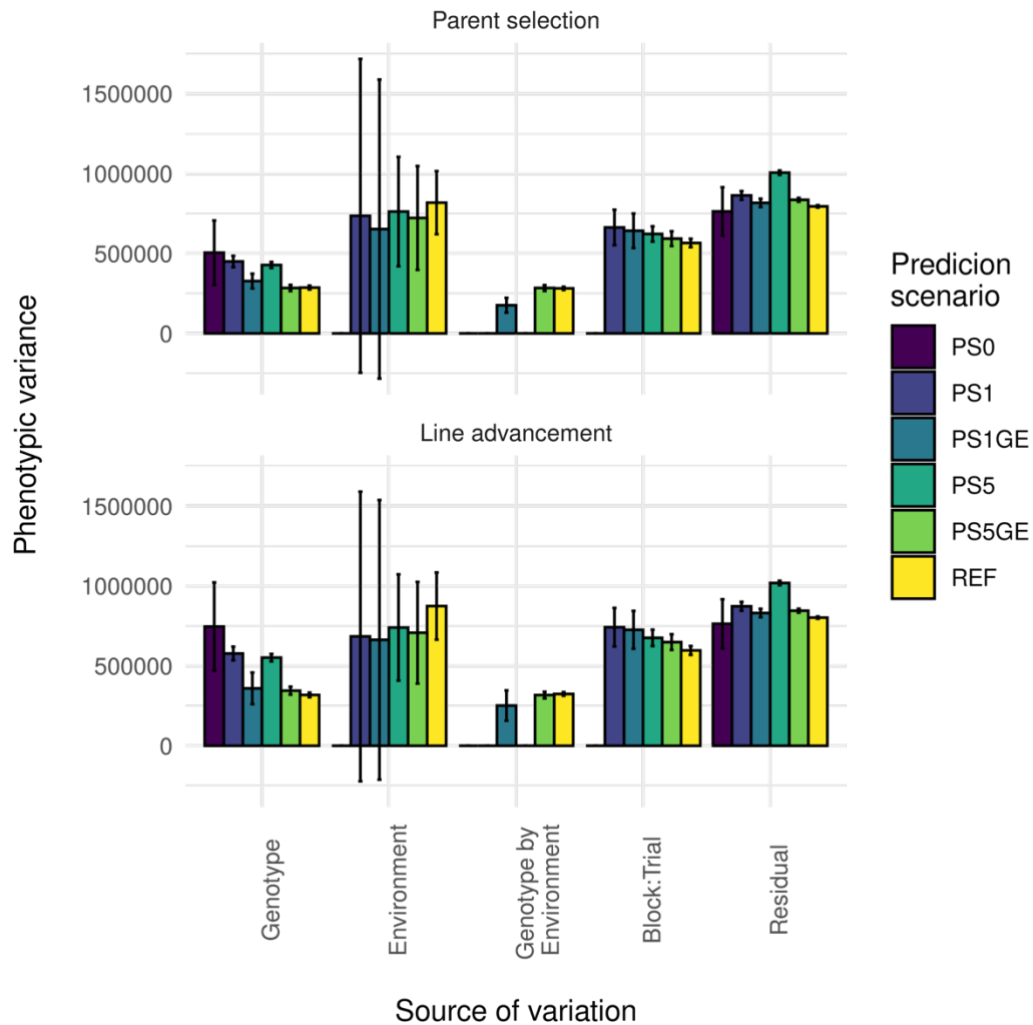


Figure 6. Phenotypic variance partition of grain yield for each prediction scenario (PS) evaluated in this study, for parent selection and line advancement in early phenotypic evaluation. Error bars represent the standard error of the variance estimation. PS0: each trial was analyzed separately; PS1: all the trials from the year in which selection occurs were analyzed together; PS1GE: same as PS1, including a genotype by environment interaction term; PS5: all the trials from the selection year and the four previous years were analyzed together; PS5GE: same as PS5, including a genotype by environment interaction term; REF: all the available trials were analyzed together, including a genotype by environment interaction term.

For both parent selection and line advancement, the genotypic variance was higher in PS0, followed by the PS, PS1 and PS5. PS1GE, PS5GE and REF, in which GE was modeled, were the PS with lower genotypic variance. As genotypic

variances were estimated with more data corresponding to more trials and environments, genotypic variances were lower, and their estimations had a lower standard error. Furthermore, genotypic variances for parent selection were lower than the ones for line advancement, which might be attributable to the A matrix modelling inbreeding for parent selection, contrarily to the identity matrix used for line advancement. The environmental variance was in general, the second higher variance component. In PS0 it was not estimated, because the PS contemplated only one environment, therefore, an environmental term was not included in the PS0 models. As the PS used more data including more trials and environments, environmental variance was higher, and its standard error was lower. GE variance was, in general, the lower variance component. It was not estimated for PS0, PS1 and PS5, where the models did not include a GE term. With more data used, GE variance increased and its standard errors decreased. Block nested in trial variance encompassed trial variance, and, as the PS used more data, variance and the estimation standard error were lower. The residual variance was the higher variance component in all PS, suggesting an important role for additional sources of variance not modelled in our PS.

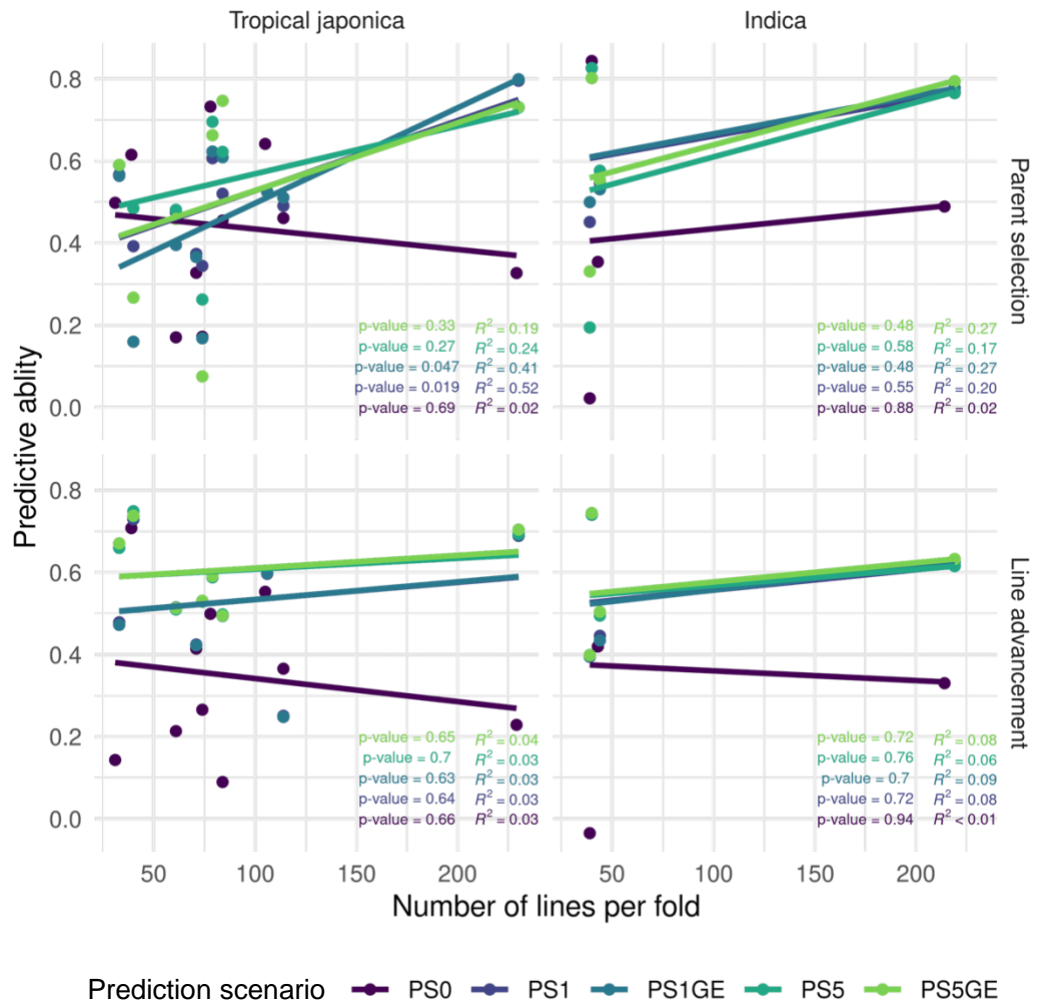
The more the data availability included in a PS, the lower the standard error obtained for the estimated variance components. Estimations of environmental variance were not possible in PS0 since all the data for each analysis is restricted to a single environment. Furthermore, estimation of environmental variance in PS with lower environmental representation (i.e., PS1 and PS1GE) had a high standard error, whereas joint analyses that include a higher number of environments (PS5, PS5GE, REF) achieve a more precise estimation of this variance.

Joint analyses that include a higher number of environments and do not model GE (PS5) had a higher residual variance than PS with lower environmental

representation (PS1 and PS1GE), but when GE is accounted for (PS5GE), the residual variance is close to the ones of PS with lower environmental representation. Additionally, all PS where GE was modeled had a lower residual variance than the time-correspondent PS without GE.

With lesser environmental representation, genotypic, environmental and GE variance are confounded. As data comes from trials in a higher number of environments, estimating environmental variance components is more precise. Environmental variance gets confounded with genotypic, GE and block nested in trial variances, when environmental variance is better estimated (in PS with more environmental representation) the other mentioned variance components are lower.

2.5.2 Predictive Ability



Supplemental Fig. S1. Predictive ability by number of lines, in each fold, colored by prediction scenario. PS0: each trial was analyzed separately; PS1: all the trials from the year in which selection occurs were analyzed together; PS1GE: same as PS1, including a genotype by environment interaction term; PS5: all the trials from the selection year and the four previous years were analyzed together; PS5GE: same as PS5, including a genotype by environment interaction term.

We analyzed the relationship between the number of folds and the number of lines per fold, with the estimated PA. In our validation scheme for estimating PA, the number of folds (Figure 7) and the number of lines on each fold (Supplemental Fig. S1) varied depending on data availability, structure and unbalance. TRJ

had more records in more years, therefore, it had more folds than IND, with seven to ten folds in TRJ and 4 folds in IND. The number lines on each fold ranged from 31 to 230, with an average of 87. PA was not affected by the number of lines on each fold, except for parent selection in TRJ in PS1 and PS1GE, where the regression was significant (p -value < 0.05). This significance may have been leveraged due to the low number of points with more than 200 lines per fold. There was no significant interaction between the number of lines, PA and PS (Supplemental Fig. S1), which indicated that the association between the number of lines and predictive ability on each fold did not affect the comparison between PS based on their predictive ability (Figure 7).

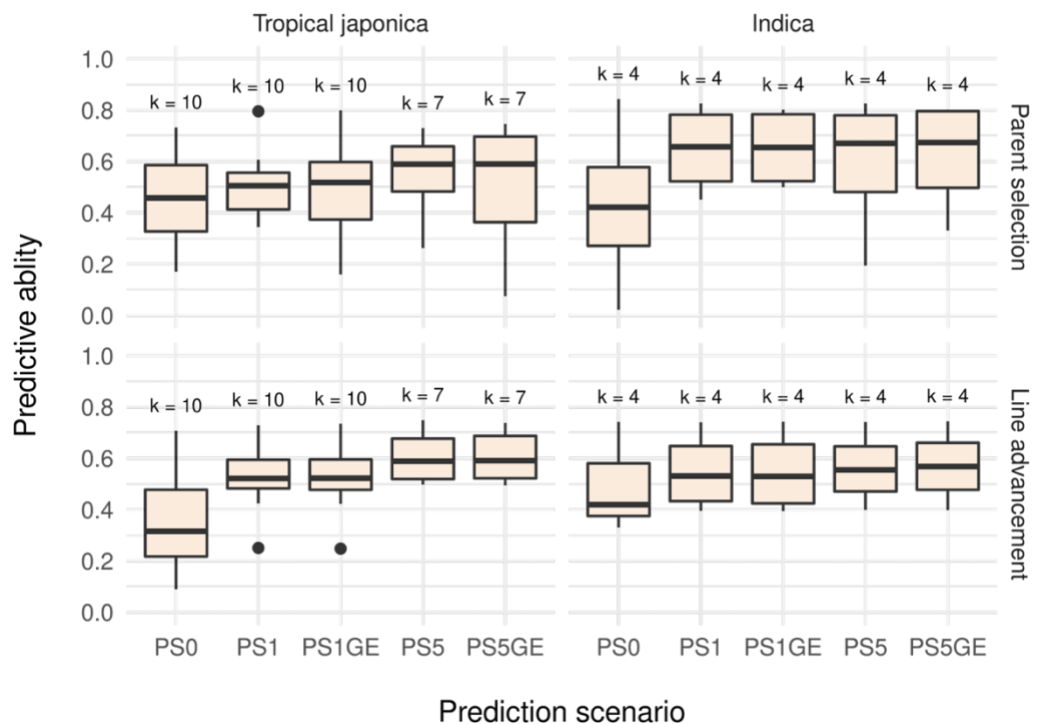


Figure 7. Predictive ability for each prediction scenario (PS) in Tropical Japonica and Indica germplasm groups for parent selection and line advancement in early phenotypic evaluation. PS0: each trial was analyzed separately; PS1: all the trials from the year in which selection occurs were analyzed together; PS1GE: same as PS1, including a genotype by environment interaction term; PS5: all the trials from the selection year and the four previous years were analyzed together;

PS5GE: same as PS5, including a genotype by environment interaction term; k: number of folds on each PS.

We studied PS ability to predict *i)* the ranking based on BV for parent selection, and *ii)* GV for line advancement, both in the first phenotypic evaluation stage, for TRJ and IND germplasm groups. For parent selection in TRJ, the mean PA values were 0.44, 0.51, 0.47, 0.55 and 0.5 for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. Mean PA was higher when the GE term was not included in PS within the same level of data availability. Furthermore, the highest mean PA was reached in the PS with the highest data availability and without GE modeling (PS5). Consequently, the lowest mean PA was obtained in the PS with the lowest data availability and aggregation (PS0).

For parent selection in IND, the mean PA values were 0.43, 0.65, 0.65, 0.59 and 0.62, for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. Mean PA increased with the inclusion of the GE term in PS with data from five consecutive years (PS5GE). The highest mean PA was reached in the PS with data from all trials in one year, regardless of GE modeling (PS1 and PS1GE) and the lower mean PA was obtained in the PS with the lowest data availability and aggregation (PS0).

For line advancement in TRJ, the mean PA values were 0.35, 0.53, 0.53, 0.6 and 0.61 for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. Mean PA was not affected by the inclusion of a GE term in the model irrespective of the number of years included in the PS, as PS1 and PS1GE had similar mean PA, and the same was observed for PS5 and PS5GE. The highest mean PA was reached in the PS with more data availability, regardless of GE modeling (PS5 and PS5GE) and the lower mean PA was obtained in the PS with the lowest data availability and aggregation (PS0).

For line advancement in IND, the mean PA values were 0.36, 0.55, 0.55, 0.56 and 0.57 for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. The inclusion of the

GE term did not affect the mean PA when data from a single year was used (PS1 and PS1GE), while in PS that gathered data from five consecutive years (PS5 and PS5GE) an increase of the mean PA was achieved with the inclusion of the GE term. The highest mean PA was reached in the PS with data from five consecutive years when GE was modeled (PS5GE), although values from all PS that included data from more than one trial were almost identical (the difference in mean PA among them was 0.2). The lower mean PA was obtained in the PS with the lowest data availability and aggregation (PS0).

In general, a PA plateau was reached with data from fewer environments in IND than in TRJ, as in IND the plateau was reached with PS1 and PS1GE, while in TRJ it was reached with PS5 and PS5GE. The inclusion of the GE term in the models did not have a consistent response, in most of the cases the means are similar but the dispersion changes when adding the GE term. The highest difference between PS that included or not a GE term in their models was 0.05 difference in mean PA found between PS5 and PS5GE for parent selection in TRJ.

2.5.3 Percentage of the Top Lines on E1 that Reached E4

Finally, to evaluate the correspondence between the PS studied in this work and the line advancement criteria historically applied by IRBP, we calculated PTLA (Figure 8). In TRJ, mean PTLA was 35, 49, 46, 48 and 43 % for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. The highest mean PTLA was reached when data from trials in one year was used and without modeling GE (PS1), though the percentage was similar to the ones reached in PS1GE and PS5. Additionally, the lowest mean PTLA was reached when data from only one trial was used (PS0). In IND, mean PTLA was 25, 42, 40, 40 and 37 % for PS0, PS1, PS1GE, PS5 and PS5GE, respectively. Hence, a higher mean PTLA was reached with data from one year and no GE modeling. With the same data availability, GE modeling had a consistently negative effect on PTLA. In both genetic groups, higher PTLA was reached with

data from one year and no GE modelling; in addition, PTLA was consistently lower than in TRJ, meaning that PS were more distant from IRBP selection criteria.

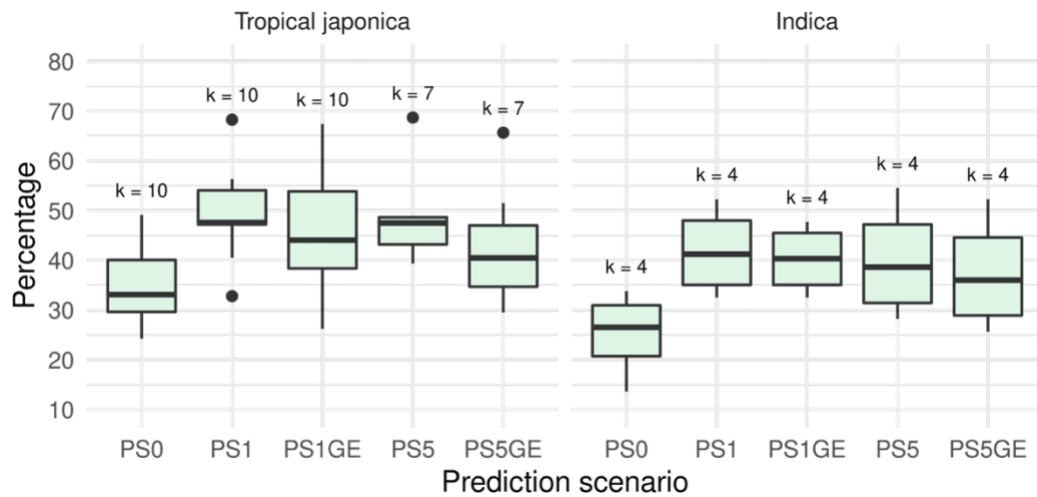


Figure 8: Percentage of the top $NEIR$ lines in early phenotypic evaluation that advanced at least 3 years, by the ranking based on their GV obtained with each prediction scenario, in Tropical Japonica and Indica germplasm groups. PS0: each trial was analyzed separately; PS1: all the trials from the year in which selection occurs were analyzed together; PS1GE: same as PS1, including a genotype by environment interaction term; PS5: all the trials from the selection year and the four previous years were analyzed together; PS5GE: same as PS5, including a genotype by environment interaction term; k: number of folds on each PS.

2.6 DISCUSSION

In this work, we studied strategies for early selection of parents and line advancement in the first year of phenotypic evaluation, proposing a validation strategy that realistically accounts for breeding programs' structure. We found that the joint analysis of multiple trials and environments resulted in a better estimation of variance components than when partial analyzes with a limited environmental representation were carried out. Furthermore, joint analyses with data from multiple trials and environments had a higher predictive ability for early selection of parents and line advancement for both IND and TRJ genetic groups. Another finding was that the inclusion of a GE term in the analysis of multiple trials and environments did not have a clear and consistent response in predictive ability with the dataset and models used in this work.

The validation scheme used was effective and allowed for a realistic approximation to the performance of each selection strategy, recreating the data availability from lines and parent selection in early evaluation under usual breeding program conditions, using only the phenotypic data that breeders would have access to in real circumstances. To our understanding, this provides a more useful estimation of PA than the most used validation schemes such as cross-validation, in which future and present data are used without considering the structure and timing of data generation (Michel et al., 2016; Covarrubias-Pazaran et al., 2022).

Our results show that as data from more trials and environments is analyzed jointly, a better estimation of variance components is achieved. We found that the residual error in the fitted model with all available environments (REF) was very similar to that obtained with models fitted to single-trial data in which no environment nor genotype by environment variance is present. This suggests that our REF PS adequately accounts for environment and genotype by environment

terms as sources of phenotypic variance. In the same way, REF estimated the genotypic effect, which is classically the focus of study in plant breeding programs (Lorenzana and Bernardo, 2009), with the lowest standard error. Nevertheless, the residual variance for PS0 was high, which could be solved by modelling other sources of variation not included in model used, as intra-block variance, that can be corrected using models with spatial correction (Lado et al., 2013; Bernal-Vasquez et al., 2014; Elias et al., 2018).

The convenience of correctly modeling the interaction between genotypes and environments has been extensively studied (Malosetti et al., 2013; Tolhurst et al., 2019, 2021). In our study, the inclusion of the GE term in the models in PS that encompassed multi-environment analyses (PS1 and PS5) led to a better estimate of all the other terms and a reduction of the residual variance.

In our study, environmental connectivity as the absolute number of lines in the dataset was comparable to that in the dataset used by Aoun et al. (2021), which allowed for diverse GE analysis. However, the ratio of shared lines to total lines was much lower in our work, which may hinder the multi-environment analyses. Furthermore, connectivity in our dataset was significantly lower than the ones used by Lado et al. (2016), Ukrainetz et al. (2018) and Tolhurst et al. (2019). In our case, given the high total number of lines and relatively low environmental connectivity through lines, models with complex GE variance-covariance structures did not converge. Therefore, multi-environmental data might have been under-used, as information from correlated environments was not properly borrowed (Jarquín et al., 2017).

Notwithstanding, with the use of multi-environmental information, high PA for selection was achieved at early stages of phenotypic evaluation, both in TRJ and IND. These values are superior to those reported for phenotypic selection of unreplicated lines in preliminary yield trials (Michel et al., 2017) and comparable

to those achieved with early phenotypic selection (Matei et al., 2018) and genomic selection (Heslot et al., 2012; Michel et al., 2017; Matei et al., 2018). We also found that the inclusion of a GE term in models did not have a consistent effect on the predictive abilities, although given the partition of variances and the best estimation of the effects when a GE term was included, the use of multi-environment models that include a GE term is recommended. Furthermore, the model that encompassed all the available environments had a residual variance similar to the one achieved in models that used information from individual trials. Therefore, we concluded that the model that uses all environments managed to capture all the environmental and GE variance.

The PS that correlated the best with IRBP's selection criteria, indicated by a higher PTLA, was also the one that used the same level of data aggregation for analysis as IRBP did.

This work focuses on analyzing grain yield. However, breeding programs in general evaluate and select lines considering other traits of interest, such as resistance to diseases and quality attributes. Those additional breeding targets are often complex and low heritability traits. The strategy used in this work could be applied to evaluate early multi-trait selection, which also would allow to exploit the genetic covariance between traits to further improve the efficiency of multi-environment analysis (Malosetti et al., 2013; Lado et al., 2018).

The breeding and genotypic values obtained, as well as the partition of variances between the models that predicted them, are remarkably similar, which suggests that modeling the relationship between individuals does not have an important effect on the estimation of values and variances. This can be attributed to the lack of depth and connectivity in the pedigree data, generating a sparse matrix \mathbf{A} , or to, as Ahmad et al. (1986) suggest, non-additive genetic variance not

being relevant in rice, although there is no consensus on the subject (Zhuang et al., 2002)

This work demonstrates that an early and accurate selection of parents is possible in early stages of phenotypic evaluation. The impact of its measure has been extensively studied. Gorjanc et al. (2018), Rutkoski (2019b) and Cobb et al. (2019) show that shortening the breeding cycle directly increases genetic gain in breeding programs and that, in fact, it is the component of the breeders' equation that is easiest to understand, cheapest to manipulate and the most powerful parameter to measure. The possibility of having precise predictions for line advancement would allow breeding programs to directly increase genetic gain, as well as to make use of that precision to increase selection intensity, advancing fewer lines to the next stages of evaluation, which would allow reducing the number of field phenotypic evaluation trials.

2.6.1 Conclusions

Joint analysis of multiple trials and environments, as well as GE modeling, improves the estimation of variance components, as it reduces the residual error of the model and the standard error of variance estimations in all model terms.

Under the conditions of our study, incorporating a GE term did not substantially and consistently improve the predictive ability for selection in the first stage of phenotypic evaluation.

With an adequate use of multi-environment data, sufficiently good predictive abilities are achieved so the efficiency of the breeding programs can be improved.

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3 DISCUSIÓN GENERAL

En este trabajo se evaluaron estrategias para la selección temprana de padres y el avance de líneas en el primer año de evaluación fenotípica. Se propuso una estrategia de validación efectiva y realista para las condiciones del PMGA. Se encontró que el análisis conjunto de múltiples ensayos y ambientes resultó en una mejor estimación de componentes de varianza que cuando se realizaron análisis parciales. A su vez, se reportó una alta habilidad predictiva para la selección temprana de padres y el avance de líneas, con el uso de datos correspondientes a múltiples ensayos y ambientes, tanto en el grupo genético IND como en JTR. Otro hallazgo de este trabajo es que la inclusión de un término GA en los modelos correspondientes a los escenarios de predicción no generó una respuesta clara y consistente en la habilidad predictiva de estos.

La estrategia de validación utilizada fue efectiva y permitió tener una aproximación recreando en forma realista las situaciones de selección de líneas y padres en evaluación temprana en las condiciones del PMGA, ya que no hace uso de datos fenotípicos que el mejorador no tendría en circunstancias reales. La estrategia de validación más comúnmente usada es la validación cruzada, en la cual datos futuros y presentes se utilizan sin considerar la estructura y temporalidad de la generación de los datos (Michel et al., 2016, Covarrubias-Pazaran et al., 2022).

Los resultados muestran que, a medida que los análisis contienen datos de más ensayos y ambientes, se logra una mejor estimación de componentes de varianza, indicado por un error residual en el modelo ajustado con todos los ambientes disponibles (REF) muy similar al obtenido con datos de ensayos individuales, así como una estimación con menor error estándar de los demás términos del modelo, incluyendo el efecto genotípico, el cual es clásicamente el foco de estudio en programas de mejoramiento genético de plantas (Lorenzana y Bernardo, 2009). Sin

embargo, la varianza residual para PS0 fue alta, lo que podría solucionarse modelando otras fuentes de variación no incluidas en el modelo utilizado, como la varianza intrabloque, que puede corregirse utilizando modelos con corrección especial (Lado et al., 2013, Bernal-Vásquez et al., 2014, Elias et al., 2018).

La conveniencia de modelar correctamente la interacción entre genotipos y ambientes ha sido ampliamente estudiada (Malosetti et al., 2013, Tolhurst et al., 2019, 2021). En nuestro estudio, la inclusión del término GA en los modelos en PS que incluían análisis de múltiples ambientes (PS1 y PS5) condujo a una mejor estimación de todos los demás términos y una reducción de la varianza residual.

En nuestro estudio, la conectividad ambiental como número absoluto de líneas en el conjunto de datos, fue comparable a la del conjunto de datos utilizado por Aoun et al. (2021), el cual les permitió diversos análisis de GA. Sin embargo, la proporción de líneas compartidas con respecto al total de líneas fue mucho más baja en nuestro trabajo, lo que dificultó los análisis de múltiples ambientes. Además, la conectividad en nuestro conjunto de datos fue significativamente menor que la utilizada por Lado et al. (2016), Ukrainetz et al. (2019) y Tolhurst et al. (2019). En nuestro caso, dado el alto número total de líneas y la conectividad ambiental relativamente baja a través de las líneas, los modelos con estructuras complejas de varianza-covarianza de GA no convergieron. Por lo tanto, los datos multiambientales podrían haber sido infrautilizados, ya que la información de ambientes correlacionados no se tomó prestada (Jarquín et al., 2017).

Con el uso de información multiambiental, se lograron habilidades predictivas altas para selección en etapas tempranas de evaluación fenotípica, tanto en TRJ como en IND. Estos valores fueron superiores a los reportados para la selección de líneas no replicadas en ensayos preliminares de evaluación de rendimiento (Michel et al., 2017) y comparables a los hayados en selección fenotípica (Matei et al., 2018) y genómica (Heslot et al., 2012, Michel et al., 2017,

Matei et al., 2018). También se encontró que la inclusión de un término GA en los modelos no tuvo un efecto consistente sobre las habilidades predictivas, aunque, dada la partición de varianzas y la mejor estimación de los efectos cuando se incluye término GA, se sugiere el uso de modelos multiambiente que incluyan un término GA.

Se encontró que el escenario de predicción que más se asemeja al criterio de selección históricamente aplicado por el PMGA fue en el que se usaron datos pertenecientes a todos los ensayos de un año, sin modelar GA. Esto se corresponde con la estrategia que históricamente y con más frecuencia ha utilizado el PMGA, en la cual la selección se basa en el análisis de ensayos de un mismo año en forma conjunta. Esto sugiere que la estrategia de validación reconstruye con fidelidad la dinámica de selección del PMGA.

Se estudió solamente rendimiento, pero el PMGA evalúa y selecciona considerando, además, otros rasgos de interés, como resistencia a enfermedades (Rosas et al., 2020), calidad de grano y molinera (estos últimos son caracteres complejos y de baja heredabilidad). La selección temprana multirrasgo permitiría explotar la covarianza genética entre los rasgos (Malosetti et al., 2013, Lado et al., 2018).

Al estudiar el efecto ambiental y de GA, se asume independencia entre ambientes, un supuesto que, dada la complejidad ambiental en nuestro país, es difícil de sostener (Carracelas et al., 2019). Asimismo, en el modelo que usó todos los ambientes disponibles, se llegó a una varianza residual similar a la lograda en los modelos que usaron información de un ensayo, de lo que se concluye que el primero logró capturar toda la varianza ambiental y de GA.

Los valores genéticos y de cría obtenidos, así como la partición de varianzas entre los modelos que los predijeron, son marcadamente similares, lo cual sugiere que modelar el parentesco entre individuos no tiene un efecto importante en la

estimación de valores y de varianzas. Esto se puede atribuir a la falta de profundidad en el pedigrí, generando una matriz A dispersa, o a que, como lo sugieren Ahmad et al. (1986), la varianza genética no aditiva no es relevante en arroz, aunque no hay consenso en el tema (Zhuang et al., 2002).

Este trabajo demuestra y motiva que es posible una selección temprana y precisa de padres en etapas tempranas de evaluación fenotípica. Esta medida ha sido ampliamente estudiada, y en Gorjanc et al. (2018), Rutkoski (2019b) y Cobb et al. (2019) muestran que acortar el ciclo de mejoramiento logra aumentar de manera directa la ganancia genética en programas de mejoramiento, y que, de hecho, es el componente de la ecuación del mejorador más fácil de entender, más barato de manipular y el parámetro más poderoso para incrementar la ganancia genética. La posibilidad de tener predicciones precisas para el avance de línea permitiría al PMGA incrementar directamente la ganancia genética, así como aumentar la intensidad de selección, avanzando un menor número de líneas a las próximas etapas de evaluación, lo que permitiría disminuir el número de ensayos de evaluación fenotípica a campo.

4 CONCLUSIONES

El análisis conjunto de múltiples ensayos y ambientes y el modelado de la GA genera una mejor estimación de componentes de varianza y reduce el error residual, así como el error estándar de estimaciones de varianzas de todos los términos del modelo.

Con un adecuado uso de datos multiambiente, se logran habilidades predictivas suficientemente buenas que pueden mejorar la eficiencia del PMGA.

Con el conjunto de datos y forma de modelar GA estudiados, incorporar un término de GA no mejora de forma sustancial y consistente la habilidad predictiva para selección en la primera etapa de evaluación fenotípica en el PMGA.

La selección histórica en el PMGA se basa en múltiples rasgos, lo cual no coincide con la selección exclusiva por rendimiento estudiada en este trabajo. A pesar de eso, se logra una moderada coincidencia entre líneas seleccionadas en el escenario de selección que más se asemeja al uso de datos histórico del programa.

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