

Nikolai Ivanovich Vavilov (1887–1943) and the definition of the center of origin of corn (*Zea mays* L.): implications for current Reciprocal Recurrent Selection (RRS)

Nikolai Ivanovich Vavilov (1887-1943) e a definição do centro de origem do milho (*Zea mays* L.): implicações para a atual Seleção Recorrente Recíproca (SRR)

Nikolai Ivanovich Vavilov (1887–1943) y la definición del centro de origen del Maíz (*Zea mays* L.): implicaciones para la actual Selección Recurrente Recíproca (SRR)

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ABSTRACT

Nikolai Ivanovich Vavilov (1887-1943) developed the theory of centers of origin and diversity, identifying eight primary hotspots like the south Mexican/Mesoamerican center for maize (*Zea mays* L.), where maximum genetic variability arises from environmental heterogeneity and human coevolution. Reciprocal Recurrent Selection (RRS), formalized by Comstock et al. (1949), improves divergent heterotic groups (A/B) via hybrid evaluation cycles. This article integrates Vavilov's spatiotemporal concepts with maize domestication, variability structure, RRS applications, and conservation strategies to reconcile breeding efficiency with biodiversity preservation in origin centers. The review was based on a narrative and comparative analysis of classical and contemporary literature retrieved from indexed scientific databases and institutional sources, including Web of Science, Scopus, SciELO, Google Scholar, and relevant technical portals. The selected publications were used to synthesize Vavilov's concepts of centers of origin and diversity, maize domestication, and their implications for the early stages of Reciprocal Recurrent Selection (RRS). Mesoamerican center exemplifies Vavilov's model, providing teosinte-derived landraces (Tuxpeño, Cónico) for RRS heterotic groups, yielding 1-3.5% per-cycle gains via additive/dominance effects. In addition, the best intervarietal and intravarietal crosses involving adapted Tuxpeño and local Chalqueño germplasm yielded competitively with commercial checks, suggesting the presence of heterosis and the breeding value of adapted exotic maize. Vavilov's principles are most relevant in the initial phase of RRS, particularly for defining base populations and generating interpopulation progenies, because centers of origin and diversity help identify contrasting genotypes with adaptive complementarity, thereby strengthening the foundation of recurrent improvement.

Keywords: centers of origin, hybrid evaluation cycles, maize, plant breeding, Vavilov's model

RESUMO

Nikolai Ivanovich Vavilov (1887-1943) desenvolveu a teoria dos centros de origem e diversidade, identificando oito hotspots primários como o centro mexicano/mesoamericano sul para o milho (*Zea mays* L.), onde a máxima variabilidade genética surge da heterogeneidade ambiental e coevolução humana. A Seleção Recorrente Recíproca (SRR), formalizada por Comstock et al. (1949), melhora grupos heteróticos divergentes (A/B) via ciclos de avaliação de híbridos. Este artigo integra os conceitos espaciotemporais de Vavilov com a domesticação do milho, estrutura de variabilidade, aplicações de SRR e estratégias de conservação para reconciliar eficiência de melhoramento com preservação da biodiversidade em centros de origem. A revisão foi baseada em uma análise narrativa e comparativa da literatura clássica e contemporânea, recuperada em bases científicas indexadas e fontes institucionais, incluindo Web of Science, Scopus, SciELO, Google Scholar e portais técnicos relevantes. As publicações selecionadas foram utilizadas para sintetizar os conceitos de Vavilov sobre centros de origem e diversidade, domesticação do milho e suas implicações para as fases iniciais da Seleção Recorrente Recíproca (RRS). O centro mesoamericano exemplifica o modelo de Vavilov, fornecendo variedades locais derivadas de teosinte (Tuxpeño, Cónico) para grupos heteróticos de SRR, gerando ganhos de 1-3,5% por ciclo via efeitos aditivos/dominância. Além disso, os melhores cruzamentos intervarietais e intravarietais envolvendo germoplasma adaptado de Tuxpeño e de Chalqueño local apresentaram rendimentos competitivos com as variedades comerciais de referência, sugerindo a presença de heterose e o valor de melhoramento do milho exótico adaptado. Os princípios de Vavilov são mais relevantes na fase inicial da RRS, particularmente para definir as populações base e gerar progênies interpopulacionais, porque os centros de origem e de diversidade ajudam a identificar genótipos contrastantes com complementaridade adaptativa, fortalecendo assim a base do melhoramento recorrente.

Palavras-chave: centros de origem, ciclos de avaliação de híbridos, milho, melhoramento vegetal, Modelo de Vavilov

RESUMEN

Nikolai Ivanovich Vavilov (1887-1943) desarrolló la teoría de centros de origen y diversidad, identificando ocho hotspots primarios como el centro sur mexicano/mesoamericano para el maíz (*Zea mays* L.), donde surge máxima variabilidad genética por heterogeneidad ambiental y coevolución humana. La Selección Recurrente Recíproca (SRR), formalizada por Comstock et al. (1949), mejora grupos heteróticos divergentes (A/B) mediante ciclos de evaluación de híbridos. Este artículo integra conceptos espaciotemporales de Vavilov con domesticación del maíz, estructura de variabilidad, aplicaciones de SRR y estrategias de conservación para reconciliar eficiencia de mejoramiento con preservación de biodiversidad en centros de origen. La revisión se basó en un análisis narrativo y comparativo de la literatura clásica y contemporánea, recuperada de bases de datos científicas indexadas y fuentes institucionales, incluidas Web of Science, Scopus, SciELO, Google Scholar y portales técnicos relevantes. Las publicaciones seleccionadas se utilizaron para sintetizar los conceptos de Vavilov sobre los centros de origen y diversidad, la domesticación del maíz y sus implicaciones para las fases iniciales de la Selección Recurrente Recíproca (RRS). El centro mesoamericano ejemplifica el modelo de Vavilov, proporcionando landraces derivadas de teosinte (Tuxpeño, Cónico) para grupos heteróticos de SRR, generando ganancias de 1-3,5% por ciclo vía efectos aditivos/dominancia. Además, los mejores cruces intervarietales e intravarietales que involucraron germoplasma adaptado de Tuxpeño y germoplasma local de Chalqueño produjeron resultados competitivos con los testigos comerciales, lo que sugiere la presencia de heterosis y el valor de mejoramiento del maíz exótico adaptado. Los principios de Vavilov son más relevantes en la fase inicial de la RRS, particularmente para definir las poblaciones base y generar progenies interpopulacionales, porque los centros de origen y de diversidad ayudan a identificar genotipos contrastantes con complementariedad adaptativa, fortaleciendo así la base del mejoramiento recurrente.

Palabras clave: centros de origen, ciclos de evaluación de híbridos, maíz, mejoramiento vegetal, modelo de Vavilov

1 INTRODUCTION

Nikolai Ivanovich Vavilov (1887-1943), a pioneering Russian botanist and geneticist, developed the theory of centers of origin and diversity through extensive global expeditions (Cohen; Loskutov, 2016; Corinto, 2014; Huerga Melcón, 2026; Plachetka, 2020). As a major achievement, he identified eight primary centers of origin for cultivated species., including the south Mexican/Mesoamerican center for maize (*Zea mays* L.) (Costa *et al.*, 2024), where cultivated plants exhibit maximum genetic variability due to environmental heterogeneity, human coevolution, and evolutionary laws like homologous series in variation (Kistler *et al.*, 2018; Levina; Yesakov; Kisselev, 2005a; Ruiz *et al.*, 2024; Yali, 2021).

The Reciprocal Recurrent Selection (RRS), formalized by Comstock, Robinson, and Harvey in 1949 (Comstock; Robinson; Harvey, 1949), that simultaneously improves two divergent heterotic populations (A and B) by selecting based on the performance of their interpopulation hybrids, exploiting both general combining ability (GCA) and specific combining ability (SCA) to enhance crossbred performance in crops like maize (Cui *et al.*, 2024; Ledesma *et al.*, 2023; Ramalho; Souza; Junior, 2023). The RRS cycle comprises four main phases repeated across generations: (1) *Evaluation phase*, where progeny from interpopulation crosses ($A \times B$ and $B \times A$, often full-sib or half-sib families) are grown and assessed for target traits like yield; (2) *Selection phase*, identifying superior families based on hybrid means; (3) *Recombination phase*, intercrossing selected individuals within their original population (A with A, B with B) to restore variability; and (4) *Random mating phase*, bulking seed from recombinants to form the next cycle's improved populations (Covarrubias-Pazarán; Werner; Gemenet, 2023; Ramalho; Souza; Junior, 2023). Vavilov's principles are most relevant in the initial phase of RRS, especially in defining the base populations and obtaining interpopulation progenies, since centers of origin and diversity guide the choice of contrasting and adaptively complementary genotypes.

This article aims to integrate, within a historical-evolutionary and applied approach, Nikolai I. Vavilov's theoretical foundations on centers of origin and centers of diversity with current knowledge on the origin, domestication, and structure of variability in maize (*Zea mays* L.), linking them to the development and application of Reciprocal Recurrent Selection (RRS) and to contemporary strategies for the conservation and use of genetic resources. It first seeks to explicate and critically examine Vavilov's concepts of species as a spatiotemporal system, centers of origin/diversity, and the law of homologous series in variation, discussing their relevance for interpreting the evolutionary history of maize. Next, it aims to synthesize archaeological, genetic, and genomic evidence on the domestication of *Zea mays* and the formation of its major racial groups, connecting these patterns to the structuring of variability exploited in breeding programs.

The article also intends to provide a critical analysis of the role of RRS in maize, considering its genetic underpinnings, its implementation in divergent populations, and its relationship with heterotic groups. Finally, it seeks to discuss the implications of this theoretical framework for the conservation of genetic resources and for the delineation of heterotic groups in maize, from a perspective that reconciles breeding efficiency with the preservation of diversity in centers of origin and centers of diversity.

2 METHODOLOGY

The methodology of this study was based on a narrative literature review with systematized elements, focused on the relationship between Nikolai Vavilov's theory of centers of origin, the origin and diversification of *Zea mays*, and the application of reciprocal recurrent selection in breeding programs (Snyder, 2019; Torracco, 2005). The guiding question was established through the inquiry: "How does the definition of the center of origin of corn, within Vavilov's theoretical framework, support and influence modern strategies of reciprocal recurrent selection?"

The bibliographic search was carried out in international and specialized databases, including Web of Science, Scopus, SciELO, PubMed, ScienceDirect, and Google Scholar, as well as in specific portals related to genetic resources and plant breeding, such as the N.I. Vavilov Research Institute of Plant Industry (VIR), journals in the field of plant breeding (e.g., *Crop Breeding and Applied Biotechnology*), and repositories from maize research institutions (Palmatier; Houston; Hulland, 2018; Snyder, 2019). Descriptors combined terms in Portuguese and English, such as "Nikolai Vavilov," "centers of origin," "crop centers of diversity," "*Zea mays* origin," "maize domestication," "reciprocal recurrent selection," and "heterotic groups in maize," using Boolean operators (AND, OR) and subject filters (Agricultural Sciences, Botany, Genetics, and Plant Breeding) (Tiah et al., 2026; Wang; Shaw; Fan, 2025).

The inclusion criteria comprised publications addressing: (1) Vavilov's theory of centers of origin/diversity; (2) Archaeological, genetic, and phylogeographic evidence on the origin and domestication of maize; (3) Conceptual and applied studies on reciprocal recurrent selection in maize; and (4) Discussions on genetic resource conservation and centers of diversity related to *Zea mays* (Igamberdiev, 2025a; Levina; Yesakov; Kisselev, 2005a). Priority was given to works published in journals indexed in the aforementioned databases and books. Excluded materials included non-peer-reviewed texts (except institutional reference documents), studies focusing exclusively on other species, and works with no explicit relationship to at least one of the central axes of the study (Torraco, 2005).

The selection of studies was carried out in two stages: an initial screening through the reading of titles and abstracts, followed by a full-text review of potentially relevant works. Extracted information was organized into thematic matrices, categorizing studies into four main axes: (1) theoretical foundations of Vavilov and centers of origin/diversity; (2) origin, domestication, and structure of variability in *Zea mays*; (3) development and application of reciprocal recurrent selection in maize; and (4) implications for genetic resource conservation and formation of heterotic groups (Palmatier; Houston; Hulland, 2018; Snyder, 2019). This organization enabled the identification of convergences, controversies, knowledge gaps, and conceptual and applied implications for maize breeding in light of Vavilov's theory.

3 RESULTS AND DISCUSSIONS

3.1 THEORETICAL FOUNDATIONS OF VAVILOV AND CENTERS OF ORIGIN/DIVERSITY

Nikolai Vavilov's theoretical framework on centers of origin and centers of diversity represents an innovative synthesis of evolutionary botany, agricultural geography, and the history of civilizations (Igamberdiev, 2025a; Janick, 2015; Plachetka, 2020). Vavilov is portrayed as the architect of a systematic program of expeditions that culminated in the identification of eight global centers of origin of cultivated plants, concentrated in mountainous regions of Asia, Africa, and the Americas, where cultivated forms, traditional varieties, and wild relatives accumulate (Igamberdiev, 2025a; Janick, 2015). This approach extends beyond a mere geographic description by postulating that such centers represent focus of maximum genetic variability, driven by environmental heterogeneity and long-term coevolution with human societies (Cohen, 2021a).

The conceptual distinction between the center of origin (the probable site of initial domestication) and the center of diversity (the area of greatest current accumulation of variants) is central to this theory, allowing the interpretation of crop diffusion patterns from primary to secondary regions (Igamberdiev, 2025a; Solberg *et al.*, 2022). By characterizing these centers as agricultural biodiversity "hotspots", Vavilov highlighted the genetic structure of species, typically with dominant alleles concentrated in the core and recessive alleles toward the periphery, overlapping with historical processes such as the Neolithic Revolution and the emergence of autonomous civilizations (Levina; Yesakov; Kisselev, 2005b; Plachetka, 2020). For Vavilov, this spatial structuring reflects evolutionary laws shared between nature and cultivation, with direct implications for germplasm exploration (Cohen, 2021b; Janick, 2015).

This theory is further articulated with the law of homologous series in variation, which postulates the recurrence of phenotypic patterns across phylogenetically related species and genera (Bulatova, 2020; Igamberdiev, 2025a; Plachetka, 2020). By examining parallel variations in cereals

such as wheat and barley, Vavilov developed this law from observations conducted in centers of diversity, enabling the prediction of useful forms in less-studied crops (Corinto, 2014; Plachetka, 2020). This perspective aligns with molecular evidence suggesting that parallel amino acid substitutions in orthologous genes underpin the observed homology, reinforcing the utility of these centers for tracing domestication trajectories (Bulatova, 2020; Igamberdiev, 2025a).

In the case of maize, analyses indicate that the south Mexican/Mesoamerican center perfectly exemplifies these foundations, functioning as a region of high diversity where teosintes and landraces coexist, serving as a reservoir of adaptive alleles (Cohen, 2021b; Janick, 2015; Kistler *et al.*, 2018). The centers of origin are intimately linked to the logic underlying the formation of civilizations, as Vavilov argued that crop centers of origin delineate early ethnographic nuclei in mountain valleys, later spreading to river plains and shaping cultural dialogues and agricultural world-systems (Igamberdiev, 2025a; Plachetka, 2020; Solberg *et al.*, 2022). Moreover, Vavilov's collections at the VIR (N.I. Vavilov All-Russian Institute of Plant Genetic Resources), established with botanical material collected from these centers of origin, materialized this vision in the form of a global germplasm bank that remains relevant today (Igamberdiev, 2025b; Janick, 2015).

Vavilov's emphasis on centers of origin/diversity as "natural laboratories" of variability not only validates the theory in light of modern phylogeographic data but also underpins conservation and breeding strategies, such as the formation of heterotic groups in maize derived from divergent Mesoamerican materials (Bulatova, 2020; Kistler *et al.*, 2018). Thus, Vavilov provides not only a historical key to the origin of maize but also a paradigm for the sustainable use of its diversity in both evolutionary and applied contexts.

3.2 ORIGIN, DOMESTICATION, AND STRUCTURE OF VARIABILITY IN CORN (*Zea mays* L.)

The origin and domestication of maize (*Zea mays* L.) are closely associated with the south Mexican/Mesoamerican center identified by Nikolai Vavilov, a region characterized by high diversity of native races and wild relatives such as the teosintes (*Zea mays* ssp. *Parviglumis* and *Zea mays* ssp. *Mexicana*) (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024; Corinto, 2014; Cui *et al.*, 2024; Kistler *et al.*, 2018; Ruiz *et al.*, 2024). Archaeological evidence points to the Balsas River Valley in southern Mexico as the main focus of domestication around 9,000 years ago, when human populations selected key mutations in the TBC Complex (teosinte branched¹, teosinte glume architecture¹, and sugary¹) that transformed the branched, non-shattering inflorescence of teosinte into compact ears with accessible kernels (Ai *et al.*, 2025; Igamberdiev, 2025a). This transition, corroborated by genomic studies, resulted in a typical domestication syndrome, with the loss of wild

alleles and an initial reduction in genetic diversity, but with the maintenance of reservoirs of variability in local ecotypes (genetically distinct populations within the same species) adapted to different altitudes, photoperiods, and stress conditions (Cui *et al.*, 2024; Melkikh, 2025; Salami *et al.*, 2015; Shah *et al.*, 2005).

The structure of variability in *Zea mays* reflects both the primary domestication event and secondary processes of dispersal and anthropic selection across the Americas (Corinto, 2014; Kistler *et al.*, 2018; Ruiz *et al.*, 2024). Following the Mesoamerican Core, maize diversified into roughly 300 native races, grouped into sets such as “Racial Complexes” (e.g., Cónicas, Chapalote, Nal-Tel), with latitudinal and altitudinal gradients that generated adaptive contrasts: Lowland Tropical Races (e.g., Tuxpeño); Highland Races (e.g., Cónico); Andean Races (e.g., Chileno), and Caribbean races (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024; Kistler *et al.*, 2018; Ruiz *et al.*, 2024; Sanchez-Porras *et al.*, 2025). Phylogeographic analyses reveal that this diversity is not uniform but stratified into partially isolated genetic pools, separated by geographic and cultural barriers, with teosintes acting as continuous sources of gene introgression (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024). This structuring, aligned with Vavilov’s view of centers of diversity as “evolutionary laboratories,” supports the exploitation of heterosis in breeding (Cohen, 2021a; Corinto, 2014; Janick, 2015).

From the perspective of Vavilov’s centers of origin, Mesoamerican maize variability constitutes a strategic reservoir for Reciprocal Recurrent Selection (RRS), as it provides divergent populations with a broad genetic base for the formation of heterotic groups (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024; Ramalho; Souza; Junior, 2023; Reis *et al.*, 2009). The concentration of adaptive alleles in the primary center enables the recombination of contrasting materials, maximizing per-cycle gains in RRS by exploiting both additive and nonadditive effects in intergroup crosses (Corinto, 2014; Plachetka, 2020; Ramalho; Souza; Junior, 2023). Thus, the evolutionary history of maize validates Vavilov’s model, in which diversity structured in centers of origin provides germplasm of interest for species improvement programs.

3.3 DEVELOPMENT AND APPLICATION OF RECIPROCAL RECURRENT SELECTION (RRS) IN CORN

Reciprocal Recurrent Selection (RRS) in maize was formalized by Comstock, Robinson, and Harvey (1949) as a diallel method for simultaneously improving two divergent heterotic populations, selecting individuals on the basis of the mean performance of their reciprocal hybrids (Comstock; Robinson; Harvey, 1949).

“The most important aspect of the comparisons made above is the fact that reciprocal selection appears about as effective as either of the other two methods in all of the genetic situations considered. Further, it is clearly superior to selection for general combining ability for loci at which there is over-dominance and to the method proposed by Hull "for loci at which there is partial dominance. Hence, in the event of partial dominance at some loci and over-dominance at others reciprocal selection would be more effective than either of the other methods. In addition, assuming no over-dominance, there appears a strong possibility that reciprocal selection would be superior to selection for general combining ability as a consequence of either interactions of nonallelic genes or repulsion phase linkages between certain loci, or both” (Comstock; Robinson; Harvey, 1949, p.366).

Unlike Simple Recurrent Selection, which maximizes additive variance within a population, RRS jointly exploits additive and dominance effects between populations, accumulating favorable alleles in both the parental lines and their crosses (Comstock; Robinson; Harvey, 1949; Ramalho; Souza; Junior, 2023). These results indicate that, using the selection cycle as the temporal reference, the progress from cycle 1 to cycle 7 was associated with a clear improvement in yield (Comstock; Robinson; Harvey, 1949; Ramalho; Souza; Junior, 2023; Shah *et al.*, 2005; Wang; Shaw; Fan, 2025). Although the cycle 7, materials did not fully match all commercial controls, they clearly outperformed their original versions, so the change between cycles should be interpreted as an accumulated genetic gain derived from selection for adaptation and yield.

Practical implementation requires broad-based and genetically contrasting base populations, often structured as heterotic groups A and B, with selection criteria weighted by indices that integrate hybrid vigor (F1), *per se* performance, and phenotypic stability (Seledes; Ogliari; Souza, 2022; Tiah *et al.*, 2026). The combined analysis of variance detected significant differences among environments for grain yield, ear length, ear diameter, and prolificacy index, as well as for female flowering, male flowering, and ear height, indicating a differential response of the genotypes according to the evaluation conditions (Seledes; Ogliari; Souza, 2022).

The conceptual link between Vavilov’s centers of origin and RRS lies in the geographic structuring of maize diversity, particularly in the Mesoamerican center, which provides germplasm for divergent populations rich in contrasting adaptive alleles (Plekhanova *et al.*, 2017). Landraces from tropical lowlands (e.g., Tuxpeño Norte) versus high-altitude ecotypes (e.g., Cónico Chalqueño) or materials with teosinte introgressions (*Zea mays ssp. Parviglumis* and *Zea mays ssp. Mexicana*) exemplify genetic pools with high gene complementarity, maximizing σ_D^2 in interpopulation crosses (Kistler *et al.*, 2018; Ruiz *et al.*, 2024; Yali, 2021). This historical divergence, aligned with Vavilov’s law of homologous series of variation, supports the formation

of stable heterotic groups in which RRS can recombine favorable alleles without excessive homogenization (Bulatova, 2020; Plachetka, 2020).

The development and application of RRS in maize critically depend on identifying genetically complementary populations whose origin traces back to the centers of diversity defined by Vavilov (Igamberdiev, 2025b; Levina; Yesakov; Kisselev, 2005b). The concentration of adaptive variability in the Mesoamerican core makes it possible to structure programs that combine sustainable genetic gains with resilience to emerging stresses, confirming the continuing relevance of Vavilov's theoretical framework for quantitative breeding in cross-pollinated species.

3.4 IMPLICATIONS FOR GENETIC RESOURCE CONSERVATION AND FORMATION OF HETEROTIC GROUPS

The conservation of maize genetic resources in the centers of origin and diversity defined by Vavilov, particularly the south Mexican/Mesoamerican core, is strategic for sustaining reciprocal recurrent selection (RRS) programs, as it preserves divergent genetic pools essential for the formation of heterotic groups (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024; Kistler *et al.*, 2018; Levina; Yesakov; Kisselev, 2005a). The structuring of variability in ecotypes adapted to altitudinal gradients (lowlands vs. highlands), photoperiods, and edaphoclimatic conditions, including teosinte and landraces such as Tuxpeño and Cónico, provides rare alleles for tolerance to abiotic stress, pathogen resistance, and grain quality, whose controlled introgression into RRS base populations maximizes dominance variance in intergroup hybrids (Díaz-Ceniceros *et al.*, 2020; Santiago-López *et al.*, 2017). The Vavilov-RRS integration recovers “genomic islands” (chromosome 4) for adaptation to high densities and emerging stresses, turning conservation into a driver of agronomic innovation (Plekhanova *et al.*, 2017).

The formation of A and B heterotic groups in maize, grounded in the historical genetic divergence mapped by Vavilov, exploits evolutionary contrasts from the Mesoamerican center to optimize heterosis via RRS, using populations derived from lowland tropical races (e.g., materials with gene flow from *Z. mays* ssp. *Parviglumis*) versus highland ecotypes with mexicana introgressions (Acosta-Bayona; León-Martínez; Vielle-Calzada, 2024; Ruiz *et al.*, 2024). This approach ensures per-cycle gains of 2–3.5% in yield and resilience, while preserving gene complementarity between groups by selecting simultaneously for per se performance and hybrid vigor (Ramalho; Souza; Junior, 2023; Santiago-López *et al.*, 2017). Thus, integrating Vavilov's ideas with RRS promotes dynamic conservation through composite populations (e.g., biparental 2255A × 2276A), increasing heterosis from 12.3% to 24.9% in three cycles, and on-farm strategies to maintain variability against modern uniformization (Ledesma *et al.*, 2023; Ramalho; Souza;

Junior, 2023; Santiago-López *et al.*, 2017). Vavilov's model not only legitimizes targeted prospecting in centers of diversity, but also guides conservation protocols that reconcile breeding use with genetic sustainability, positioning RRS as an evolutionarily applied tool.

4 CONCLUSION

Vavilov's principles remain especially relevant in the initial phase of Reciprocal Recurrent Selection (RRS), when the choice of base populations and the development of interpopulation progenies determine the efficiency of the entire breeding program. By prioritizing centers of origin and diversity, breeders can identify contrasting genotypes with complementary adaptive attributes, thereby increasing the probability of capturing favorable allelic combinations and strengthening the genetic foundation required for sustained recurrent improvement. In this sense, Vavilov's geographic-genetic framework is not only historically important, but also strategically useful for guiding the early stages of maize population improvement.

The evidence discussed here supports the view that germplasm collected from regions of origin and diversity can broaden the genetic base, enhance adaptive complementarity, and improve the long-term response to selection in RRS schemes. For maize, especially, the integration of Vavilov's concepts into breeding strategy helps connect biodiversity, domestication history, and genetic improvement, offering a robust rationale for assembling divergent yet complementary populations. Thus, the legacy of Vavilov continues to inform modern breeding by reinforcing the importance of diversity as the starting point for population improvement and the generation of superior interpopulation hybrids.

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