improvement research, this method has been widely used to elucidate the intrinsic relationships among yield, stress resistance, and quality traits, and it shows particular advantages in identifying potential trade-offs between traits (Derbyshire et al., 2024).

In practical applications, bivariate GREML models are highly sensitive to data quality and model specification. On the one hand, phenotypic measurement error can directly interfere with the estimation of variance and covariance components, thereby increasing the uncertainty of genetic correlation estimates. On the other hand, insufficient sample overlap or limited information on the covariance structure may also lead to unstable parameter estimation. Therefore, when interpreting results, particular attention should be paid to the standard errors and confidence intervals of genetic correlation coefficients, so as to avoid overinterpreting genetic correlations in situations where sample size is limited or trait correlations are mainly driven by environmental factors.

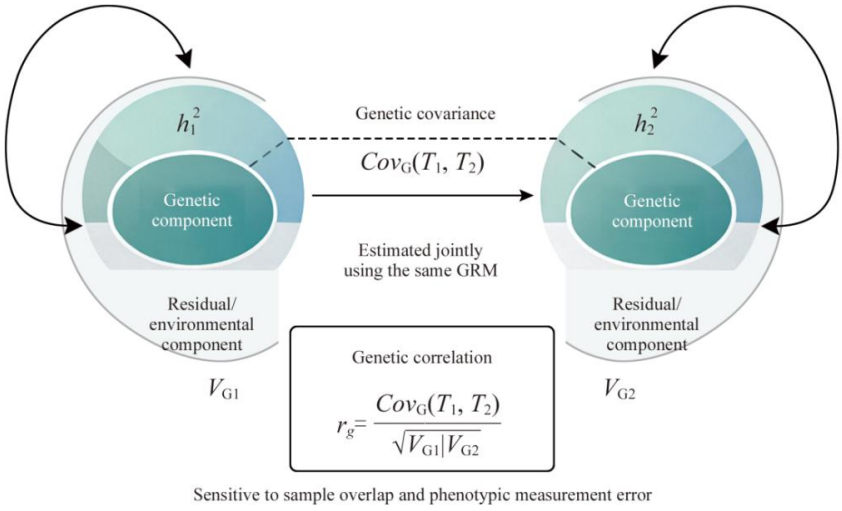

Figure 2 Schematic illustration of genetic covariance and genetic correlation in a bivariate GREML model

Note: Each trait is decomposed into a genetic component and a residual component. The bivariate GREML framework jointly estimates the additive genetic variances of Trait 1 and Trait 2, as well as their genetic covariance, using a common genome-wide relationship matrix (GRM). The genetic correlation r_g is derived from the estimated genetic covariance standardized by the square roots of the trait-specific genetic variances. This schematic emphasizes that genetic correlation reflects shared genetic architecture rather than phenotypic correlation, and its estimation is sensitive to sample overlap and phenotypic measurement error. The figure is illustrative and based on published GREML applications

6 Interpretation of Results and Common Pitfalls

6.1 Proper interpretation of "missing heritability"

This section clarifies the concept of "missing heritability" by focusing on the statistical comparability between SNP-based and pedigree-based heritability estimates. In studies based on GREML (genomic-relatedness-based restricted maximum likelihood) or SNP-derived heritability, a commonly observed phenomenon is that the proportion of phenotypic variance explained by genotyped SNPs is often substantially lower than heritability estimates derived from pedigree or twin studies (Speed et al., 2016; Evans et al., 2017; Yang et al., 2017; Wainschtein et al., 2022). This discrepancy should not be interpreted as evidence that the trait itself is weakly heritable, but rather as a reflection of differences in the identifiability of genetic variance under distinct statistical frameworks.

From a statistical genetics perspective, the systematic downward bias of SNP-based heritability primarily arises from the capturability constraints imposed by genotyping platforms, including marker coverage boundaries, heterogeneity in linkage disequilibrium (LD) structure, and the allele frequency (AF) spectrum of variants included in the analysis (Speed et al., 2016; Yang et al., 2017; Génin, 2019). Common SNP arrays provide strong tagging of common variants but have limited coverage of low-frequency, rare, and structural variants, which may contribute non-negligibly to total genetic variance (Speed et al., 2016; Wainschtein et al., 2022).