

PLANTCOM meeting, Dijon

# Quantitative genetics of plant–plant interactions: case of varietal mixtures and crop mixtures

Jemay Salomon, Maxence Remerand

UMR GQE Le Moulon  
Université Paris-Saclay, INRAE, CNRS, AgroParisTech

# Outline

Context and motivation

Case of varietal mixtures

Case of crop mixtures

Material and methods

Results

Conclusions and perspectives

# Outline

Context and motivation

Case of varietal mixtures

Case of crop mixtures

Material and methods

Results

Conclusions and perspectives

Intra-plot diversification: major agroecological lever

- ▶ caveat: not used in breeding

Intra-plot diversification: major agroecological lever

- ▶ caveat: not used in breeding

Challenge: combinatorial explosion

- ▶ strategy (here): quantitative genetics model to predict unobserved mixtures
- ▶ *joint* analysis of monovarietal and mixed stands to *gradually* introduce mixing ability in breeding programs

Intra-plot diversification: major agroecological lever

- ▶ caveat: not used in breeding

Challenge: combinatorial explosion

- ▶ strategy (here): quantitative genetics model to predict unobserved mixtures
- ▶ *joint* analysis of monovarietal and mixed stands to *gradually* introduce mixing ability in breeding programs

Gaps of knowledge:

- ▶ Which experimental designs?
- ▶ Which magnitude of genetic (co)variances?
- ▶ Which genetic architectures?

# Outline

Context and motivation

Case of varietal mixtures

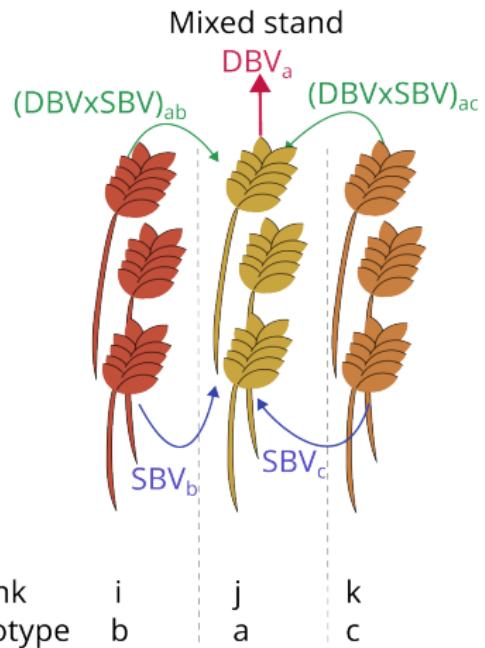
Case of crop mixtures

Material and methods

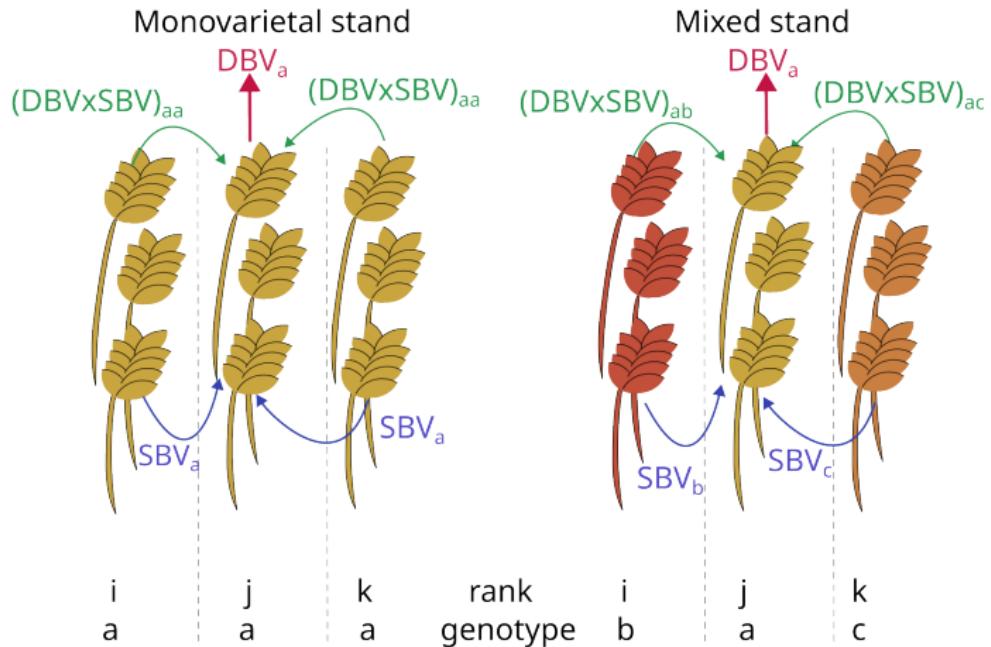
Results

Conclusions and perspectives

# Design and model



# Design and model



$(DBVxSBV)_{aa}$  corresponds to  $SMA_{aa}$  from Forst et al (2019)

# Design and model



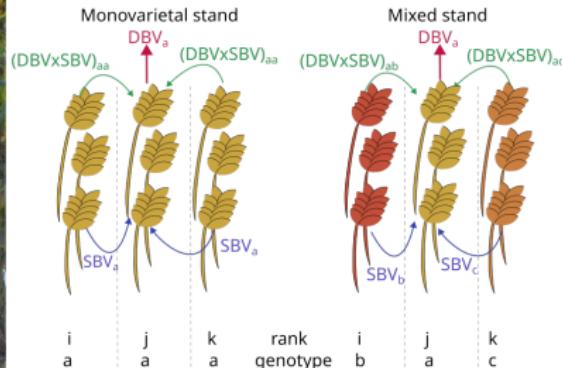
$$y_j = \mu + \alpha_{fix}$$

$$+ DBV_{g_j} + \frac{1}{2}(SBV_{g_i} + SBV_{g_k})$$

$$+ \frac{1}{2}(DBV \times (1/2)SBV)_{g_j g_i}$$

$$+ \frac{1}{2}(DBV \times (1/2)SBV)_{g_j g_k}$$

$$+ \epsilon_j$$



## Design and model



- ▶ Genotyping : TaBW420k chip (200k polymorphic SNPs) of 100 lines from a MAGIC population
- ▶ Phenotyping : Yield component for each row (central for monovarietal stands)
- ▶ Use of alternate rank in early selection trials: **can we accurately estimate DBV, SBV and interaction variances?**

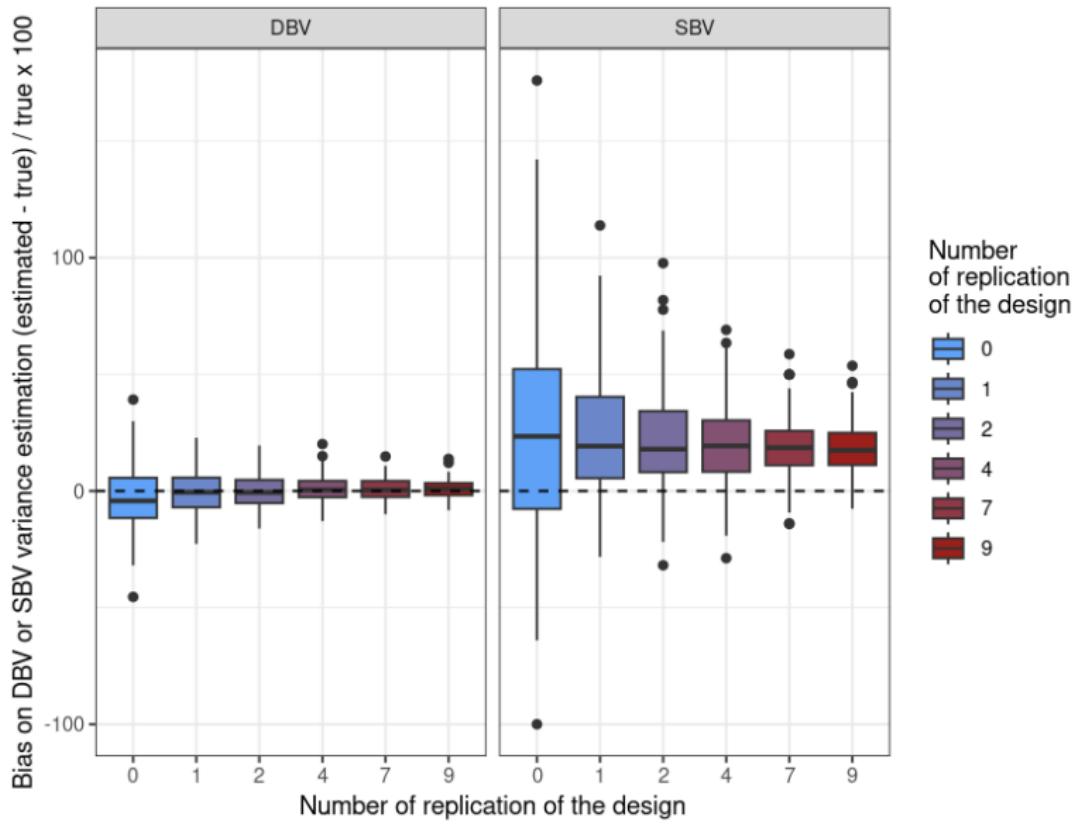
# Simulations

- ▶ Simulations based on experimental design
  - ▶ 3-way component mixtures (alternate rows)
  - ▶ per line: 2 monovarietal stands + 4 mixed stands
  - ▶ Total of around 1000 rows (no replicates)
  - ▶ Parameter values: Montazeaud et al. 2023 + our data
- ▶ Test of design accuracy: addition of replicates (0 to 9)

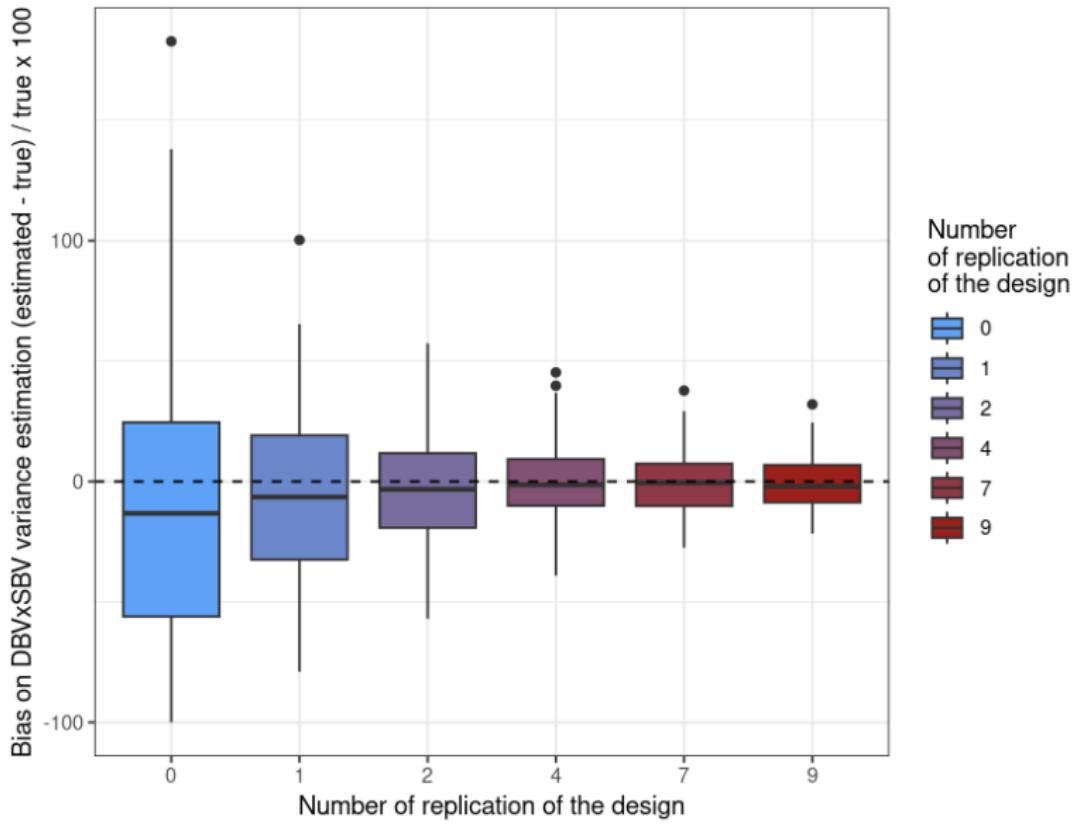
$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + Z_{DS} \mathbf{BV}_{DS} + Z_{DxS} \mathbf{DBVxSBV} + Z_e \boldsymbol{\epsilon}$$

- ▶  $\boldsymbol{\beta}$ : fixed effects
- ▶  $\mathbf{BV}_{DS}$ : correlated DBV and SBV effects
- ▶  $\mathbf{DBVxSBV}$ : uncorrelated interactions between DBV and SBV

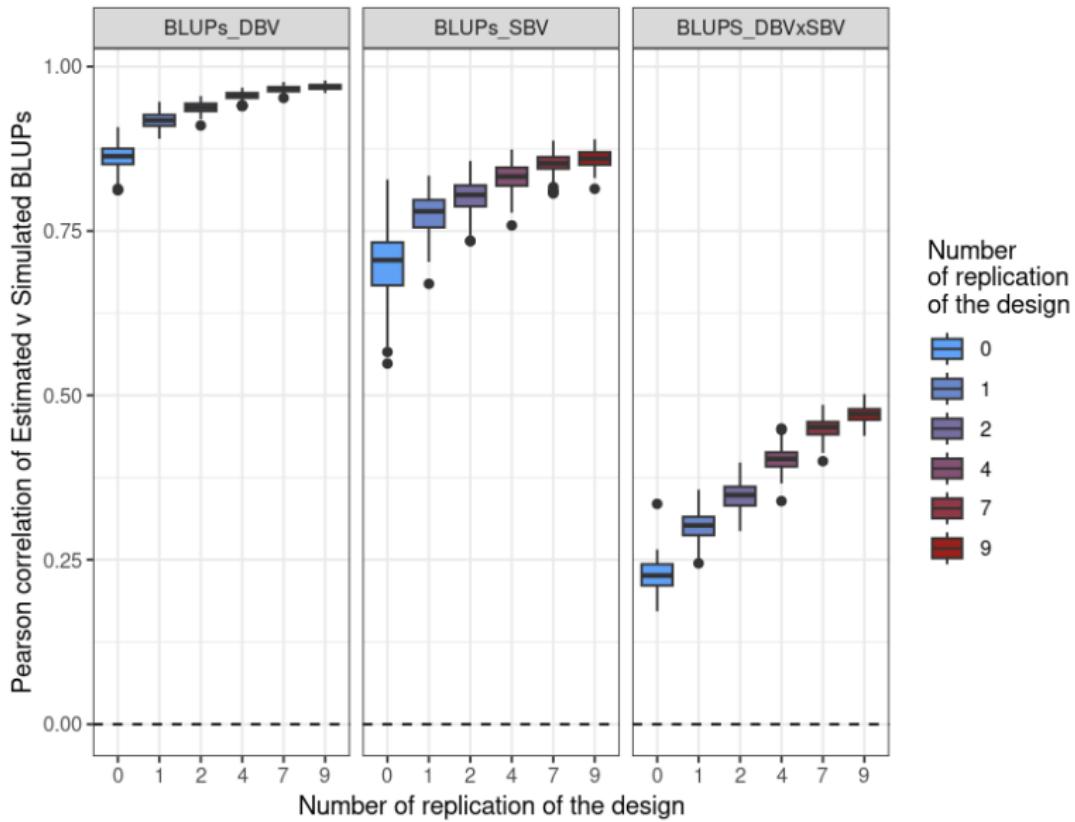
# Results



# Results



# Results



# Outline

Context and motivation

Case of varietal mixtures

Case of crop mixtures

Material and methods

Results

Conclusions and perspectives

# Outline

Context and motivation

Case of varietal mixtures

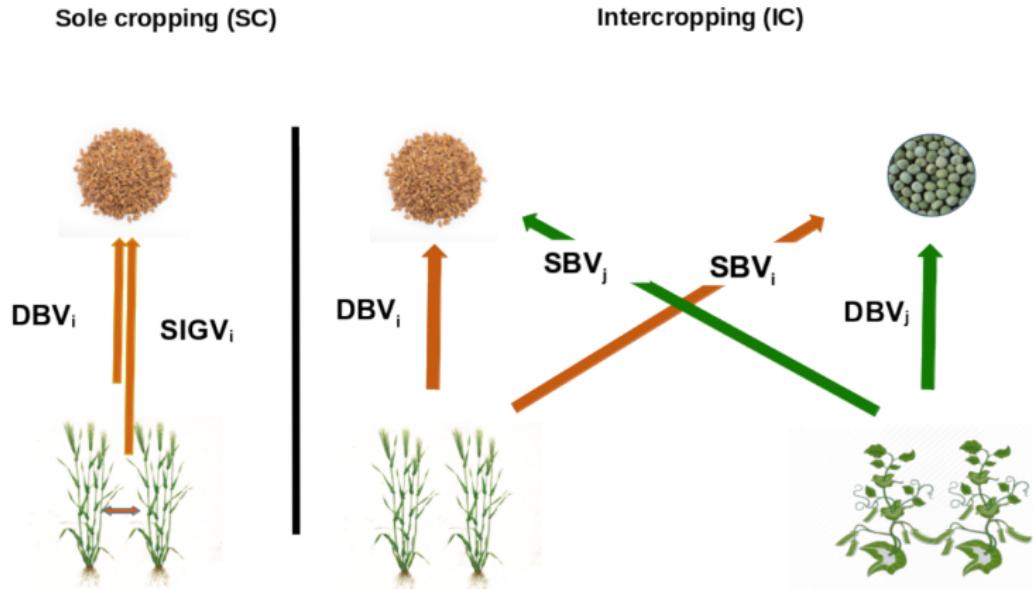
Case of crop mixtures

Material and methods

Results

Conclusions and perspectives

# Genetic model



Social intra-genotypic value:  $SIGV := SBV^{SC} + (DBV \times SBV)^{SC}$

# Genetic model

Intercrop of  $i$  (species  $s_1$ ) and  $j$  (species  $s_2$ ):

$$Y_{i(j)} = \mu^{s_1, IC} + DBV_i + SBV_j^{IC} + (DBV \times SBV)_{ij}^{IC}$$
$$Y_{j(i)} = \mu^{s_2, IC} + DBV_j + SBV_i^{IC} + (DBV \times SBV)_{ji}^{IC}$$

Sole crop of  $i$  and sole crop of  $j$ :

- ▶  $Y_i = \mu^{s_1, SC} + DBV_i + SIGV_i$
- ▶  $Y_j = \mu^{s_2, SC} + DBV_j + SIGV_j$

## Simulation and inference

- ▶ 200 wheat genotypes + 2 pea genotypes (testers)

## Simulation and inference

- ▶ 200 wheat genotypes + 2 pea genotypes (testers)
- ▶ 3 experimental designs of 400 plots each:
  - Sole\_only (complete): sole cropping system (SC)
  - Inter\_only (sparse): intercropping system (IC)
  - Sole\_inter\_50 (sparse): combination of SC and IC

## Simulation and inference

- ▶ 200 wheat genotypes + 2 pea genotypes (testers)
- ▶ 3 experimental designs of 400 plots each:
  - Sole\_only (complete): sole cropping system (SC)
  - Inter\_only (sparse): intercropping system (IC)
  - Sole\_inter\_50 (sparse): combination of SC and IC
- ▶ Parameter values: Moutier et al. (2022); Haug et al. (2023)

## Simulation and inference

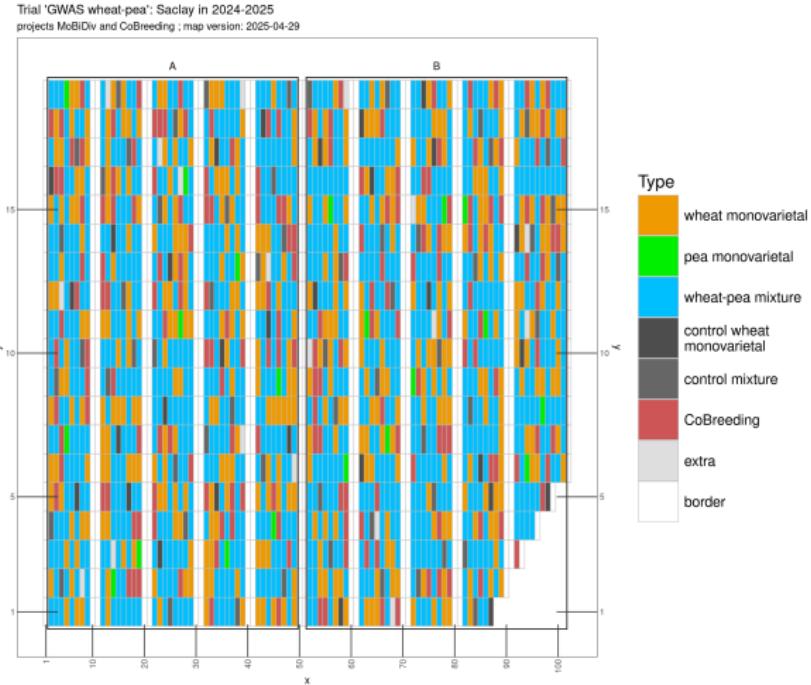
- ▶ 200 wheat genotypes + 2 pea genotypes (testers)
- ▶ 3 experimental designs of 400 plots each:
  - Sole\_only (complete): sole cropping system (SC)
  - Inter\_only (sparse): intercropping system (IC)
  - Sole\_inter\_50 (sparse): combination of SC and IC
- ▶ Parameter values: Moutier et al. (2022); Haug et al. (2023)
- ▶ Varying proportions of  $\text{var}(\text{SIGV})$  relative to  $\text{var}(\text{DBV})$

## Simulation and inference

- ▶ 200 wheat genotypes + 2 pea genotypes (testers)
- ▶ 3 experimental designs of 400 plots each:
  - Sole\_only (complete): sole cropping system (SC)
  - Inter\_only (sparse): intercropping system (IC)
  - Sole\_inter\_50 (sparse): combination of SC and IC
- ▶ Parameter values: Moutier et al. (2022); Haug et al. (2023)
- ▶ Varying proportions of  $\text{var}(\text{SIGV})$  relative to  $\text{var}(\text{DBV})$
- ▶ Software implementation: plantmix (R package)

# Panel and field trial

- 200 wheat varieties
  - ▶ 395k SNPs
- 2 pea varieties (testers)
- All sole and intercrops in 2 complete blocks
- Traits per species: grain yield, TKW, final height, SLA, soil cover



# Panel and field trial



Le Moulon, Saclay, 2025

# Outline

Context and motivation

Case of varietal mixtures

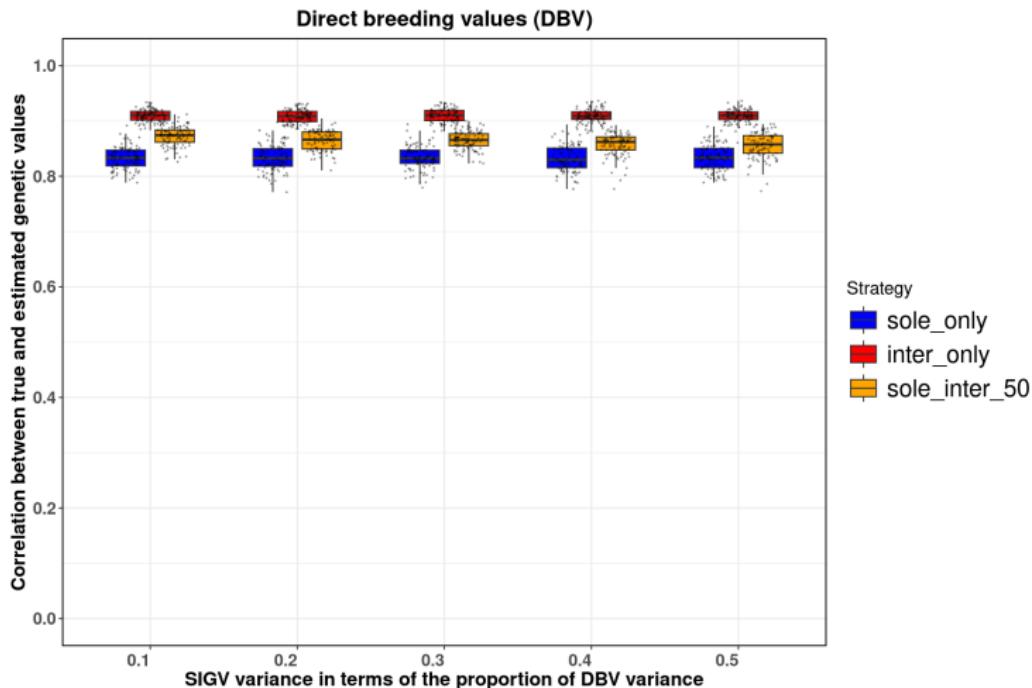
Case of crop mixtures

Material and methods

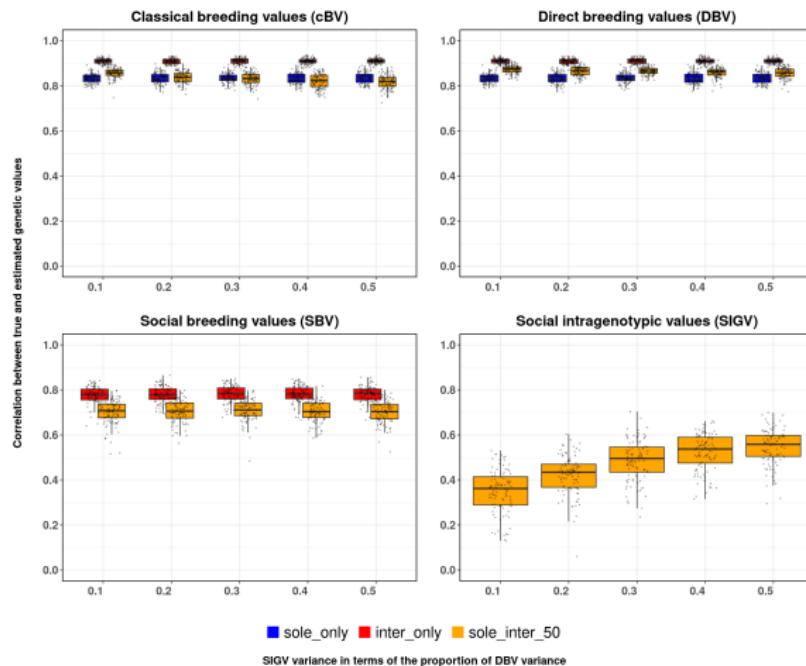
Results

Conclusions and perspectives

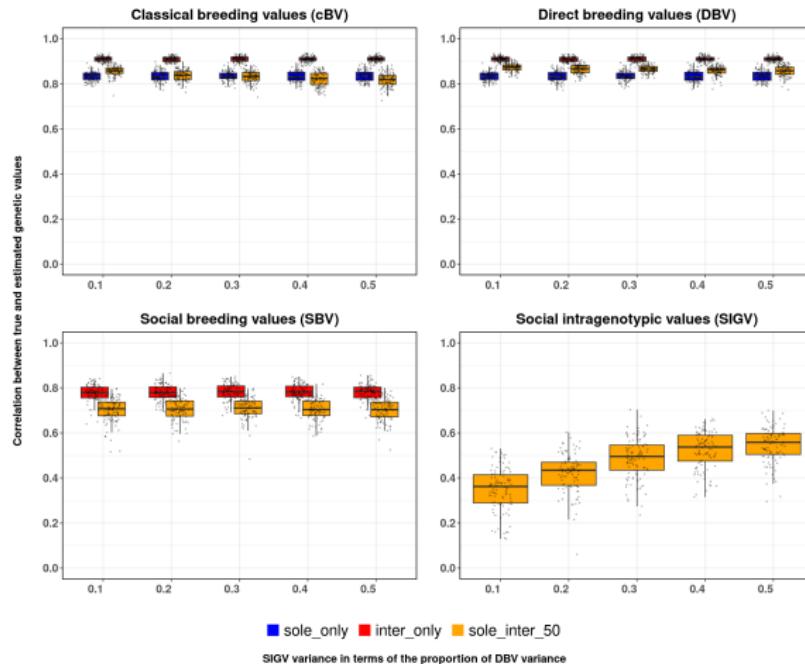
# Accuracy of parameter estimation



# Accuracy of parameter estimation

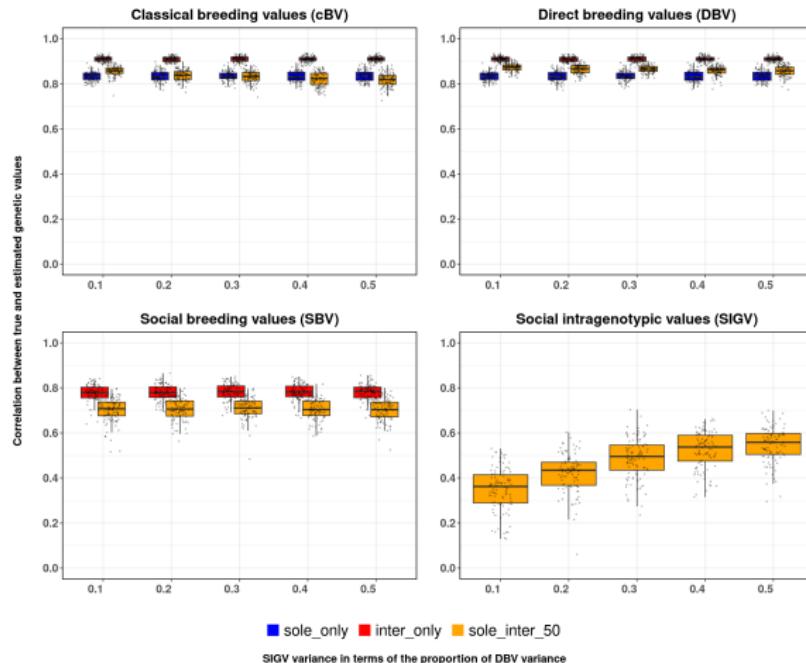


# Accuracy of parameter estimation



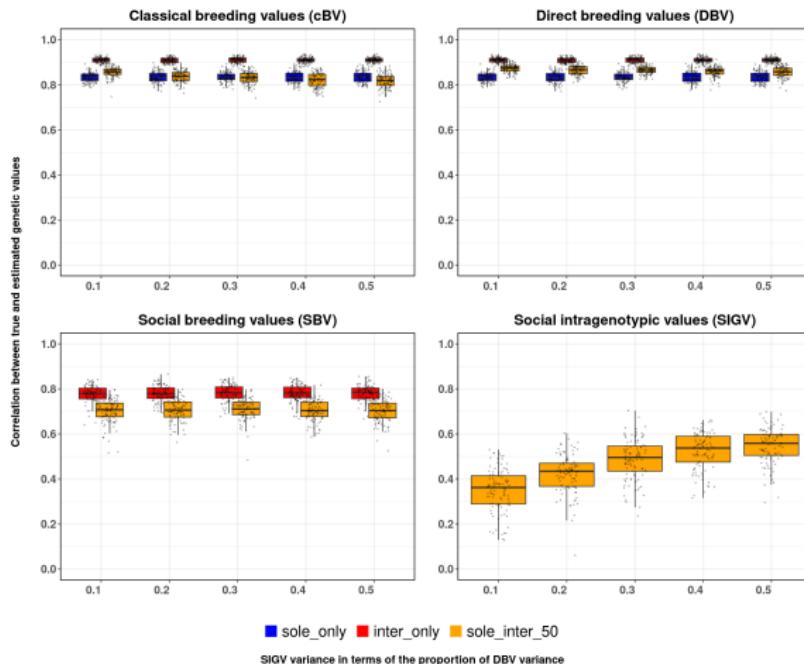
- **Experimental design, genetic effects, and the ratio  $\sigma_{SIGV}^2/\sigma_{DBV}^2$  influence accuracy.**

# Accuracy of parameter estimation



- Experimental design, genetic effects, and the ratio  $\sigma_{SIGV}^2/\sigma_{DBV}^2$  influence accuracy.
- Inter\_only provides the most accurate estimates.

# Accuracy of parameter estimation



- Experimental design, genetic effects, and the ratio  $\sigma_{SIGV}^2/\sigma_{DBV}^2$  influence accuracy.
- Inter\_only provides the most accurate estimates.
- Sole\_inter\_50 helps decoupling SIGV and DBV, improving their estimation.

# Variance estimates for grain yield

$\sigma^2_{DBV}$	$\sigma^2_{SBV}$	$\sigma^2_{SIGV}$	$\sigma^2_{DBV \times SBV}$	$\sigma^2_{e-pur(w)}$	$\sum^2_{e-mix(w)}$	$\sum^2_{e-mix(p)}$
<b>10.1</b> [8.01, 11.39]	<b>1.25</b> [0.17, 247]	<b>2.49</b> [0, 5.23]	<b>2.19</b> [0.14, 5.76]	<b>16.6</b> [12.00, 20.00]	<b>12.78</b> [10.61, 13.98]	<b>18.53</b> [15.56, 21.30]

Values are shown as the estimate (first line), followed by the 95% confidence interval in brackets (second line), calculated across 500 replicates using bootstrapping.

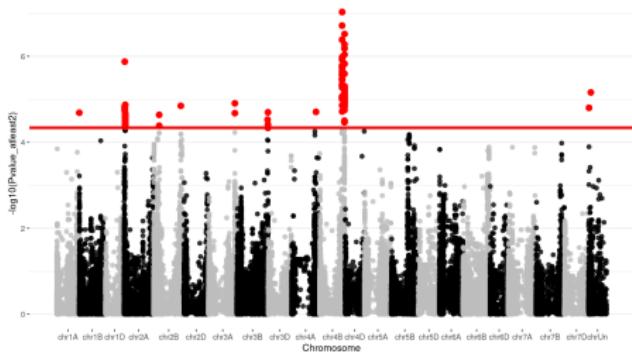
- Social genetic variances < variance of direct breeding values

# Correlation estimates for grain yield

$\rho_{DBV-SBV}$	$\rho_{\epsilon\text{-mix}}$
0.24 [0.01, 1]	-0.19 [-0.29, -0.07]

- Unexpected positive correlation observed between DBV and SBV  
⇒ favorable wheat-pea interactions

# Meta-GWAS on grain yield [DBV, SBV, SIGV]



H<sub>0</sub> rejected when a SNP is associated with at least two traits (FDR controlled at 5%)

## ► 9 pleiotropic regions detected

- Not detected in single-trait GWAS.
- Further analyses underway for validation.

# Outline

Context and motivation

Case of varietal mixtures

Case of crop mixtures

Material and methods

Results

Conclusions and perspectives

## Take-Home Messages

- Joint modeling of sole and intercrops + incomplete design + genomic relationship matrix: accurate estimations of breeding values.

## Take-Home Messages

- Joint modeling of sole and intercrops + incomplete design + genomic relationship matrix: accurate estimations of breeding values.
- Field data analyses indicated that social genetic variances were small, but still contribute significantly

## Take-Home Messages

- Joint modeling of sole and intercrops + incomplete design + genomic relationship matrix: accurate estimations of breeding values.
- Field data analyses indicated that social genetic variances were small, but still contribute significantly
- Methodology allowing breeders to fine-tune their program depending on the proportion of resources they want to allocate to sole vs intercrops.

## Take-Home Messages

- Joint modeling of sole and intercrops + incomplete design + genomic relationship matrix: accurate estimations of breeding values.
- Field data analyses indicated that social genetic variances were small, but still contribute significantly
- Methodology allowing breeders to fine-tune their program depending on the proportion of resources they want to allocate to sole vs intercrops.
- Preliminary GWAS identified several regions associated with at least two types of breeding values.

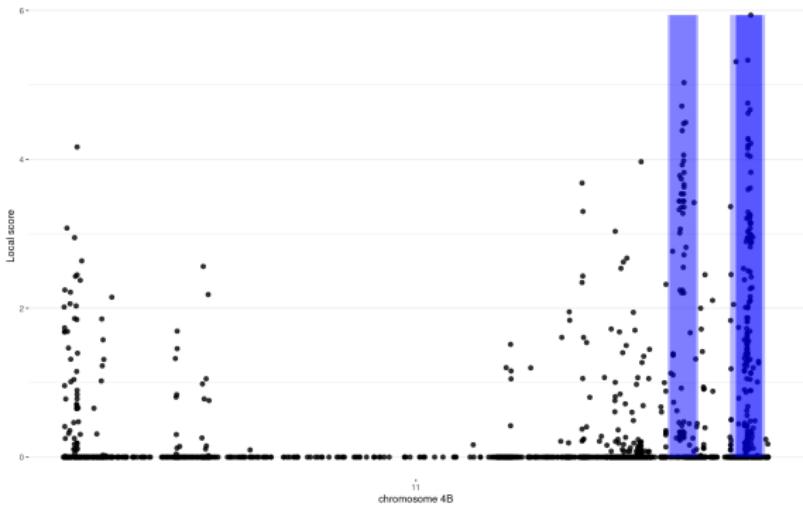
## Take-Home Messages

- Joint modeling of sole and intercrops + incomplete design + genomic relationship matrix: accurate estimations of breeding values.
- Field data analyses indicated that social genetic variances were small, but still contribute significantly
- Methodology allowing breeders to fine-tune their program depending on the proportion of resources they want to allocate to sole vs intercrops.
- Preliminary GWAS identified several regions associated with at least two types of breeding values.
- Analyze the other traits, notably those from drone imaging (PhD V. Freitas).

# Acknowledgments

- ▶ **GQE:** J. Enjalbert, T. Flutre,  
C. Bourhis-Lézier, V. Freitas
  - ▶ M. Lu, P. Briens, S. Roty,  
T. Linares, F. Legendre,  
J. Hélie, J. Le Gall, L. Salze
  - ▶ E. Akaffou, L. Wang,  
M. Mesnil, D. Wang,  
F. Petit, R. Diallo, U. Louis,  
C. Coste, F. Alléhaut
- ▶ **UEVS:** C. Bédard, F. Barriuso,  
D. Sowamber, J. Cannesson,  
O. Minguy, A. Belkian
- ▶ **ECOSYS:** J.-M. Gilliot
- ▶ **BIOGER:** T. Vidal,  
M. Delrieu
- ▶ **IGEPP:** N. Moutier,  
R. Perronne
- ▶ **AGAP:** A. Baranger

# Supp 1: meta-GWAS on grain yield [DBV, SBV, SIGV]



Local scores along chromosome 4B. The boxes represent the significant zones identified. The threshold was set to  $\xi = 2$ , and the nominal FDR level is fixed at 0.05.