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# A quantitative geneticist' journey from grapevine vineyards to wheat mixtures

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# A quantitative geneticist' journey from grapevine vineyards to wheat mixtures

Timothée Flutre

GQE-Le Moulon  
Université Paris-Saclay, INRAE, CNRS, AgroParisTech  
Gif-sur-Yvette, France



# Outline

Harnessing genome-wide association and prediction in perennials:  
two case studies on grapevine

Mobility: an opportunity to start another line of research

Genetic basis of plasticity: a case study on wheat-based mixtures

# Outline

Harnessing genome-wide association and prediction in perennials:  
two case studies on grapevine

- Domestication, current context and ideotyping

- Rationale

- Univariate study of (mainly) yield components and quality traits on a diversity panel in the vineyard

- Multivariate study on a bi-parental progeny of potted plants under water deficit

- Perspectives

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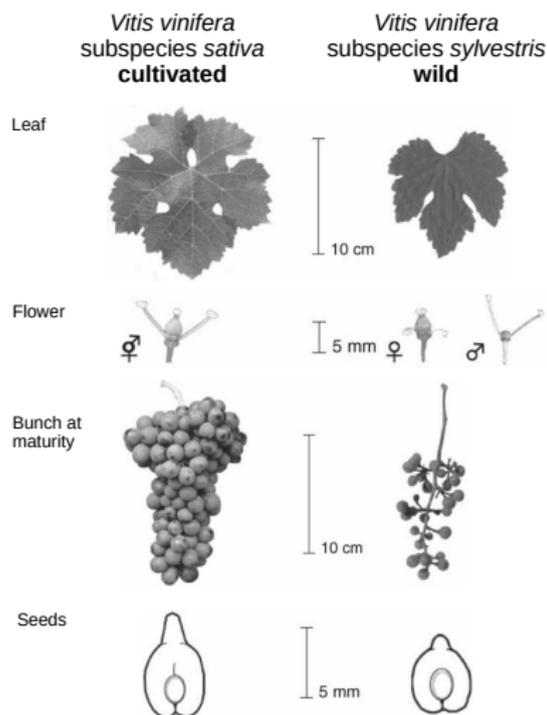
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# A few historical milestones

This *et al.* (2006), Lacombe (2012):

- ▶ **-8000/-4000**: discovery of wine and domestication of *Vitis vinifera* (modern Iran, Turkey et Georgia)
- ▶ **500**: viticulture common throughout Europe; differentiation between table and wine grapes; appearance of colors
- ▶ **Middle Ages**: first mention of names still in use (e.g., Grenache)
- ▶ **until the XIX<sup>th</sup>**: undirected allo-fecundation, massal selection and vegetative multiplication

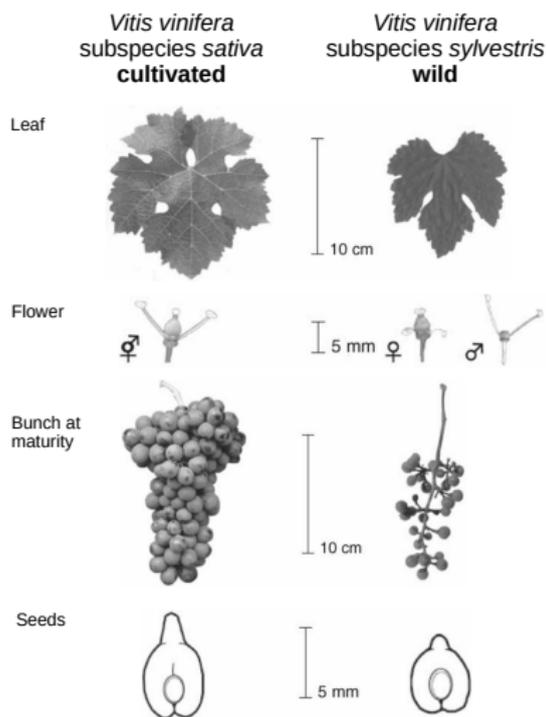


genome:  $\approx$  480 Mb

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- ▶ **Middle Ages**: first mention of names still in use (e.g., Grenache)
- ▶ **until the XIX<sup>th</sup>**: undirected allo-fecundation, massal selection and vegetative multiplication
- ▶ **1845-1885**: arrival of new pathogens from the US to Europe → chemicals, grafting, directed crosses



genome:  $\approx$  480 Mb

# Current challenges

Societal request to reduce pesticides:

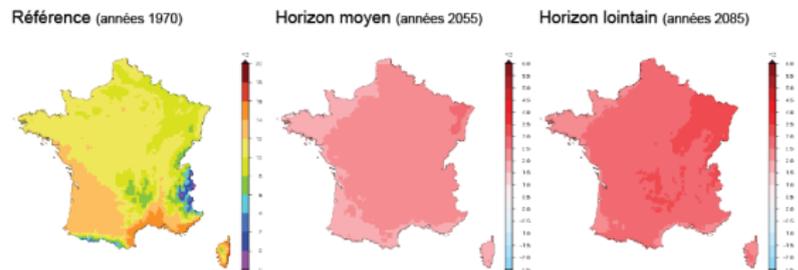


# Current challenges

Societal request to reduce pesticides:



Predicted temperatures by the ARPEGE model (CNRM):

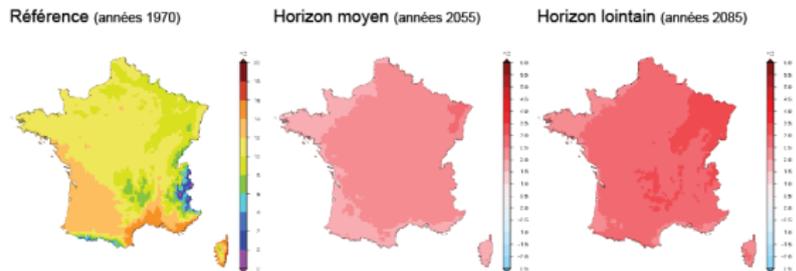


# Current challenges

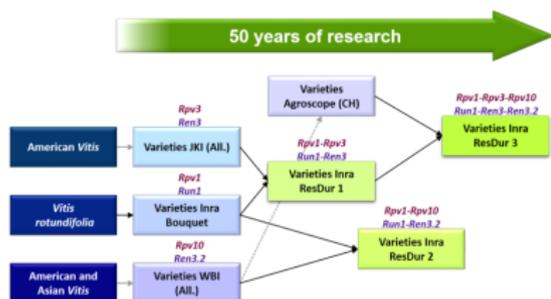
Societal request to reduce pesticides:



Predicted temperatures by the ARPEGE model (CNRM):



Resistant, hybrid cultivars registered in 2018:

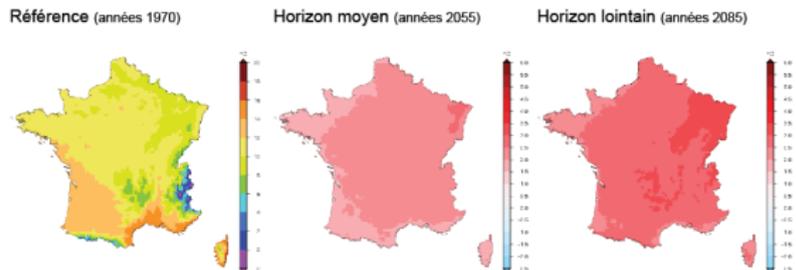


# Current challenges

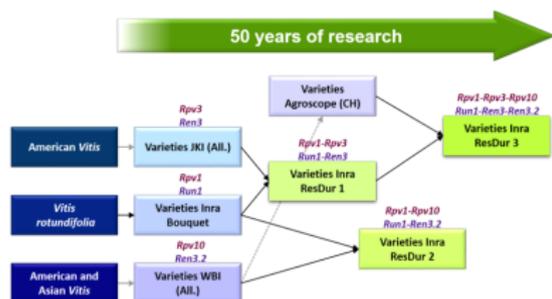
Societal request to reduce pesticides:



Predicted temperatures by the ARPEGE model (CNRM):



Resistant, hybrid cultivars registered in 2018:



Vines burned by the 2019 heat wave:



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# Possible contributions of quantitative genetics

1. study the **genetic architecture** of traits of interest to identify putatively causal genes and provide insights into their possibly-shared genetic basis
  - ▶ estimate heritability
  - ▶ determine if the architecture is polygenic or sparse
  - ▶ if sparse, identify the QTL locations and effects

# Possible contributions of quantitative genetics

1. study the **genetic architecture** of traits of interest to identify putatively causal genes and provide insights into their possibly-shared genetic basis
  - ▶ estimate heritability
  - ▶ determine if the architecture is polygenic or sparse
  - ▶ if sparse, identify the QTL locations and effects
2. introduce **genomic prediction** as a complementary approach to the current practices of grape breeders and suggest avenues of genetic gain
  - ▶ predict genotypic values
  - ▶ assess prediction accuracy

## Statistical strategy: analysis in two stages (1/2)

Stage I: model the mean and variances of phenotypic values

$$\mathbf{y} = \mathbf{X}\boldsymbol{\alpha} + \mathbf{Z}\mathbf{g} + \boldsymbol{\epsilon}^{(I)}$$

- ▶  $\mathbf{y}$ : phenotypic values
- ▶  $\boldsymbol{\alpha}$ : design effects (“fixed”)
- ▶  $\mathbf{g}$ : total genotypic values (“random”)  $\sim \mathcal{N}(\mathbf{0}, \sigma_g^2 \text{Id})$
- ▶  $\boldsymbol{\epsilon}^{(I)}$ : errors  $\sim \mathcal{N}(\mathbf{0}, \sigma_{(I)}^2 \text{Id})$
- ▶ eventually, add other “random effects” to account for genotype-year interactions and spatial heterogeneity

Broad-sense heritability ( $H^2$ ) is estimated.

## Statistical strategy: analysis in two stages (2/2)

Stage II: model the mean and variances of genotypic values

$$\text{eBLUP}(\mathbf{g}) = M\boldsymbol{\beta} + \boldsymbol{\epsilon}^{(\text{II})}$$

- ▶  $M$ : genotypes at markers ( $M_{\text{add}}$  or  $M_{\text{add+dom}}$ )
- ▶  $\boldsymbol{\beta}$ : markers' effects ( $\boldsymbol{\beta}_{\text{add}}$  or  $\boldsymbol{\beta}_{\text{add+dom}}$ )
- ▶  $\boldsymbol{\epsilon}^{(\text{II})}$ : errors  $\sim \mathcal{N}(\mathbf{0}, \sigma_{(\text{II})}^2 \text{Id})$

## Statistical strategy: analysis in two stages (2/2)

### Stage II: model the mean and variances of genotypic values

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- ▶  $\boldsymbol{\beta}$ : markers' effects ( $\boldsymbol{\beta}_{\text{add}}$  or  $\boldsymbol{\beta}_{\text{add+dom}}$ )  
→ *assumed genetic architecture*:
  - ▶ *dense* (fully polygenic):  $\boldsymbol{\beta}_{\text{add}} \sim \mathcal{N}(\mathbf{0}, \sigma_{\beta_{a,p}} \text{Id})$
  - ▶ *sparse*:  $\boldsymbol{\beta}_{\text{add}} \sim \pi_0 \boldsymbol{\delta}_0 + (1 - \pi_0) \mathcal{N}(\mathbf{0}, \sigma_{\beta_{a,s}} \text{Id})$
- ▶  $\boldsymbol{\epsilon}^{(\text{II})}$ : errors  $\sim \mathcal{N}(\mathbf{0}, \sigma_{\text{II}}^2 \text{Id})$

Narrow-sense heritability ( $h^2$ ) is estimated, QTL can be detected, and additive genotypic (“breeding”) values are predicted.

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Plant material

Phenotyping of field trials

High-throughput genotyping

GWAS results

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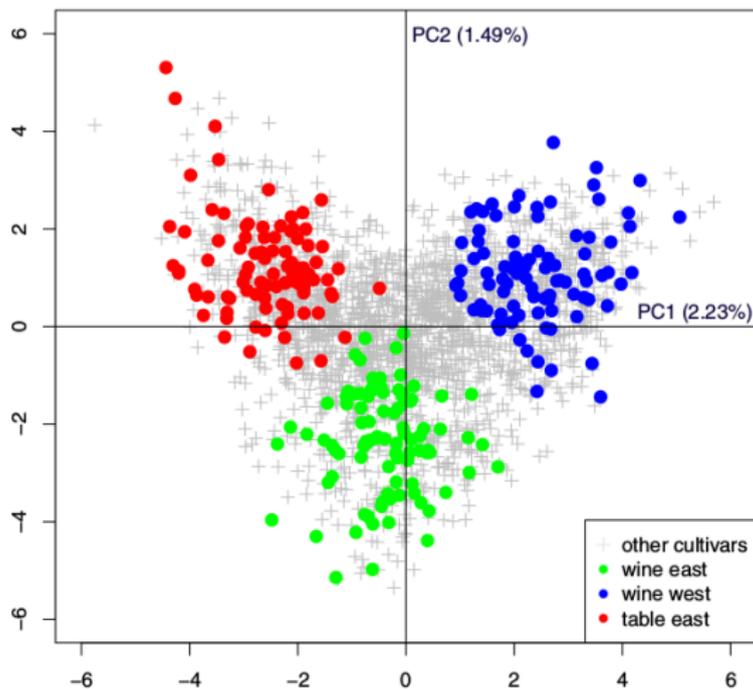
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# Association panel of 279 *V. vinifera* L. cultivars



PCA based on 20 SSRs; accessions from the Domaine de Vassal (France grapevine BRC); Nicolas *et al.* (2016)

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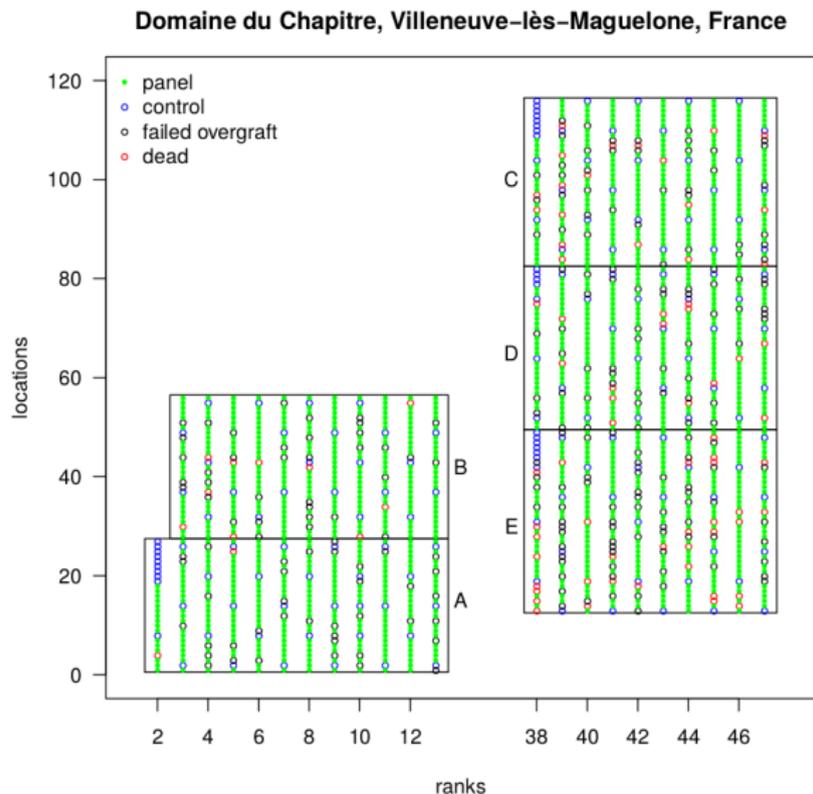
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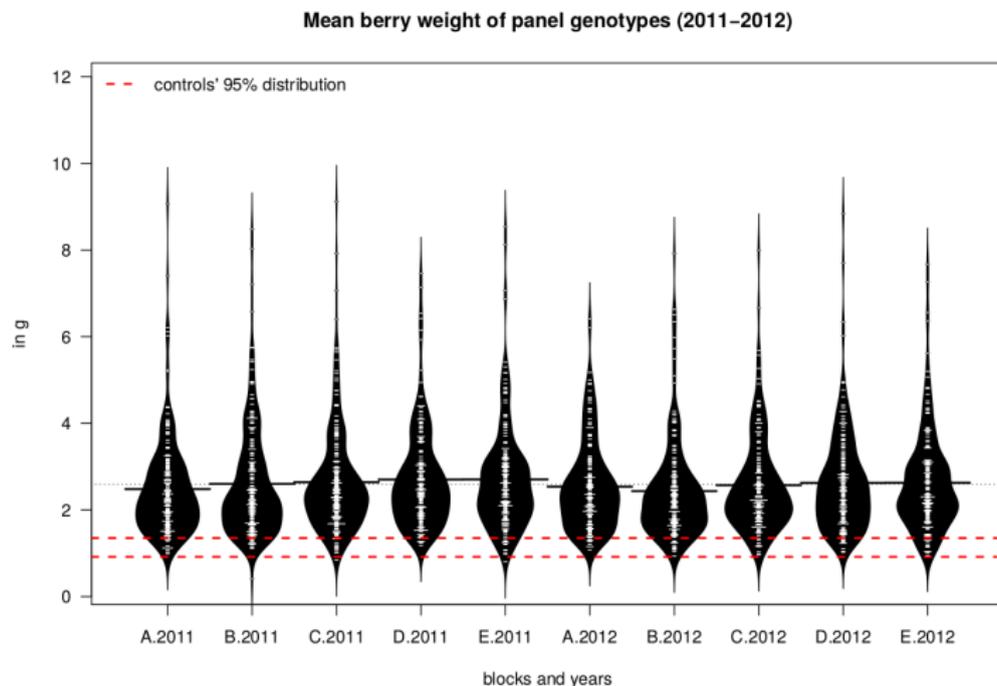
# Experiment design and field layout



Flutre *et al.*, in prep.

# Project 1: DLVitis, 2011 and 2012, with controls

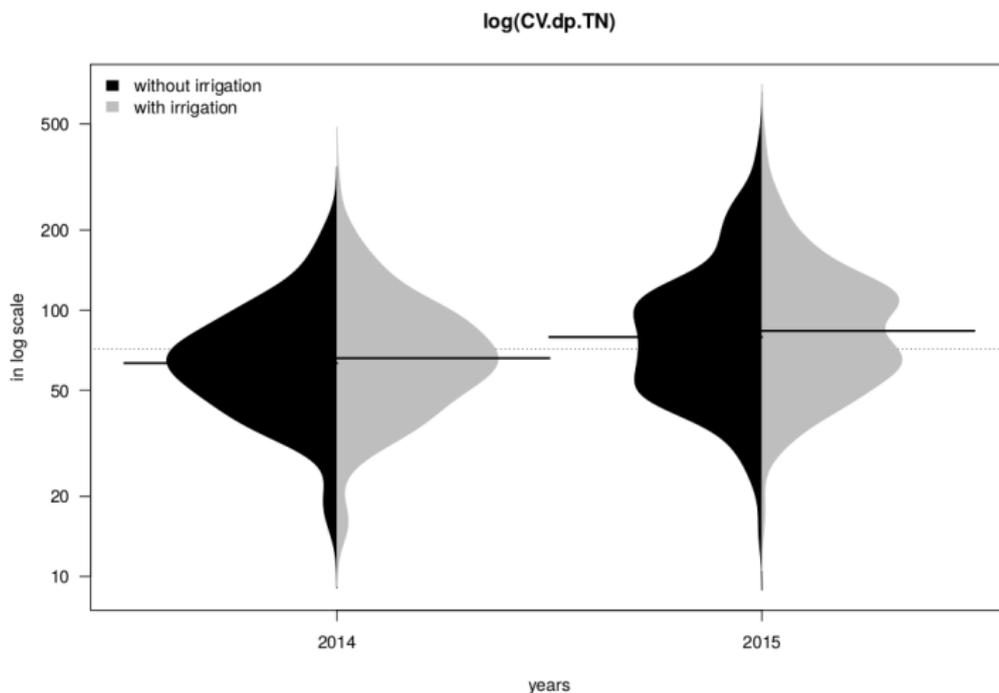
17 traits and 8 calculated variables



Flutre *et al.*, in prep.

## Project 2: Innovine, 2014 and 2015, with irrigation

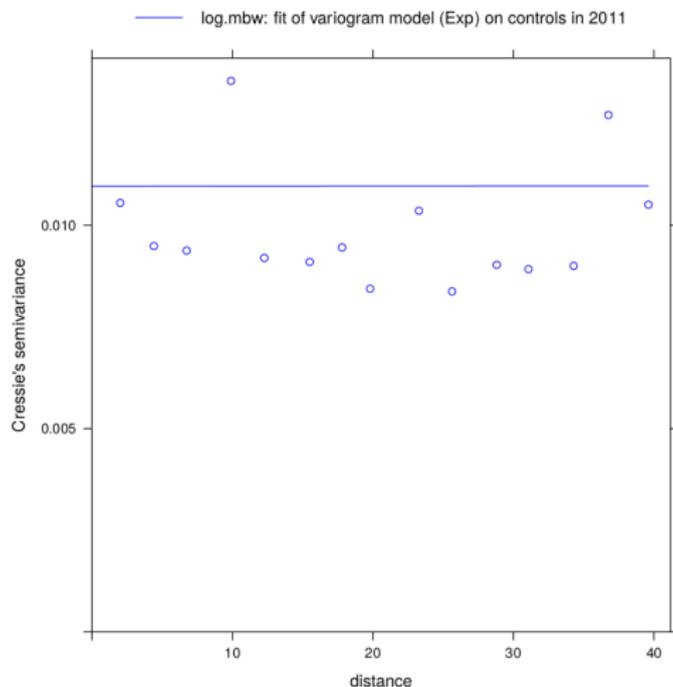
110 traits and 17 calculated variables



Flutre *et al.*, in prep.

# Stage I: no evidence of strong spatial correlation

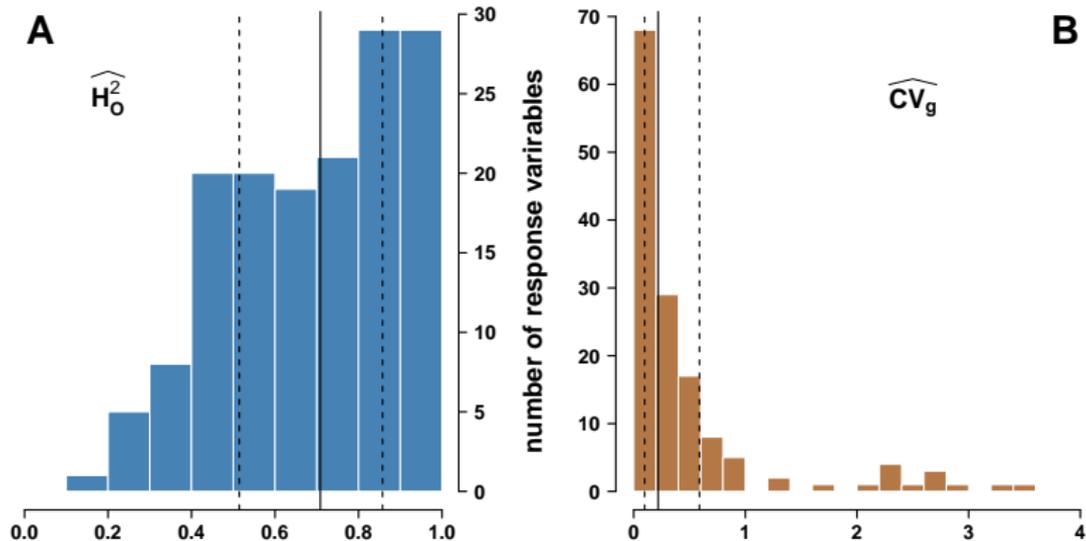
Example of mean berry weight:



Flutre *et al.*, in prep.

# Stage I: broad-sense heritabilities and genetic CV

Overall: 152 response variables



⇒ High enough to carry on with the analyzes.

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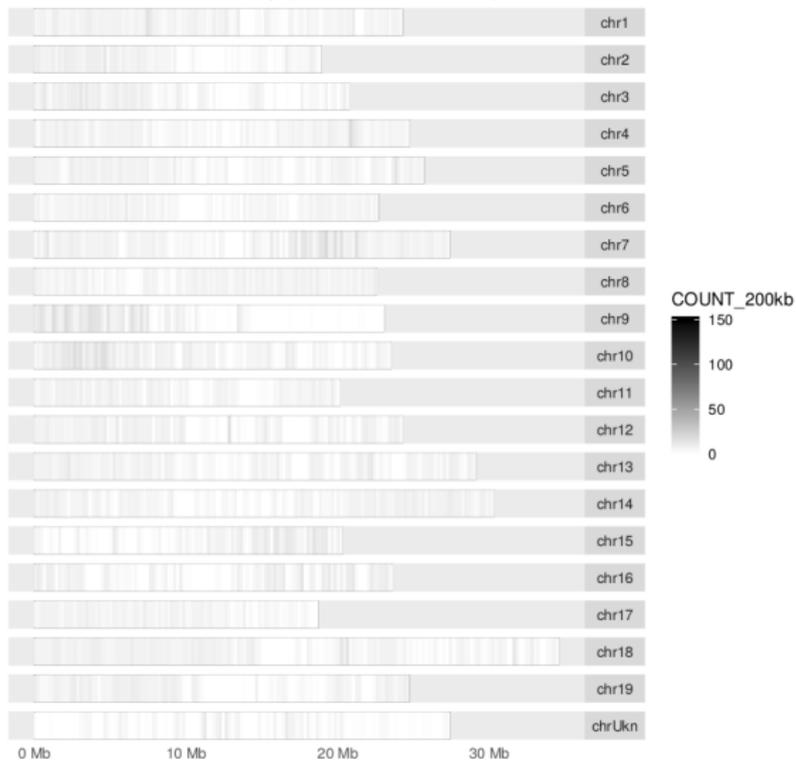
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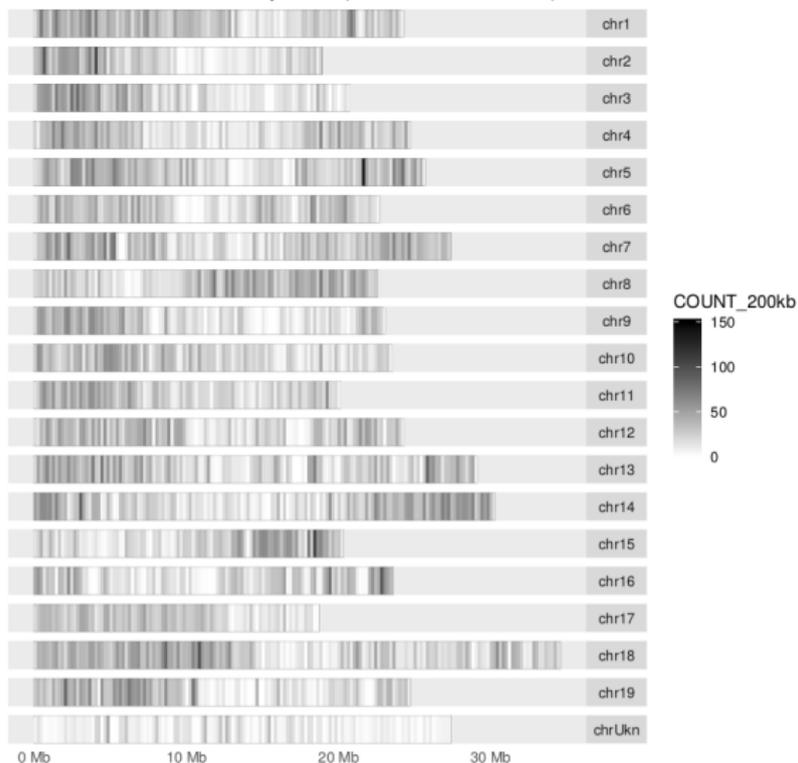
# Microarray

10503 SNPs from microarray (LD < 0.9, MAF > 0.05)

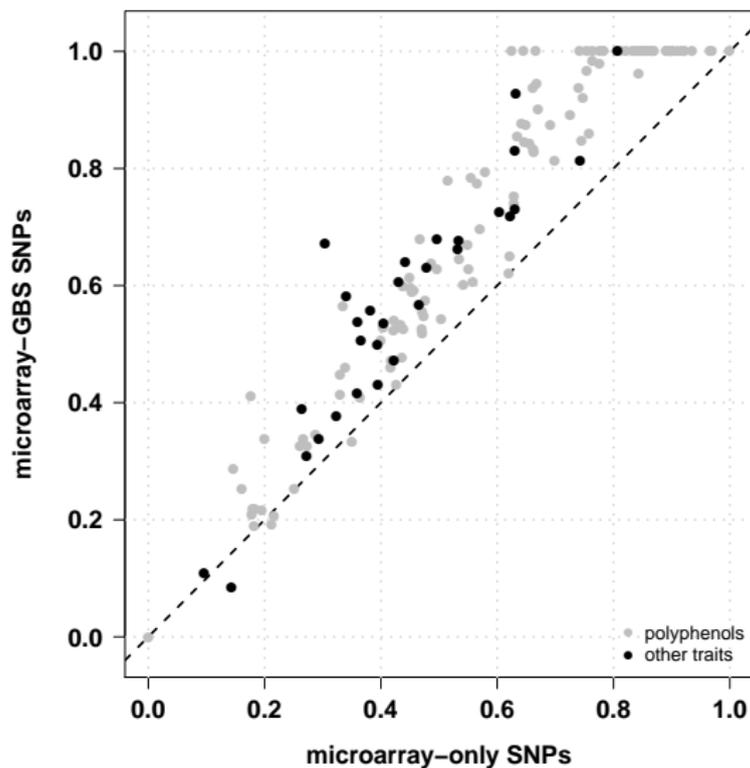


# Microarray and genotyping-by-sequencing (GBS)

63105 SNPs from microarray+GBS (LD < 0.9, MAF > 0.05)



# Increasing SNP density explains more genetic variance ( $h^2$ )



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## Stage II: comparison of univariate methods

Overall: 152 response variables (RVs)

Method		<b>microarray-only SNPs</b>		
Model	Software	#RVs	#SNPs	#QTLs
SNP-by-SNP	GEMMA	88	2295	1179

## Stage II: comparison of univariate methods

Overall: 152 response variables (RVs)

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SNP-by-SNP	GEMMA	88	2295	1179
multi-SNP	mlmm.gwas	148	1257	1243
multi-SNP	varbvs	118	266	257

## Stage II: comparison of univariate methods

Overall: 152 response variables (RVs)

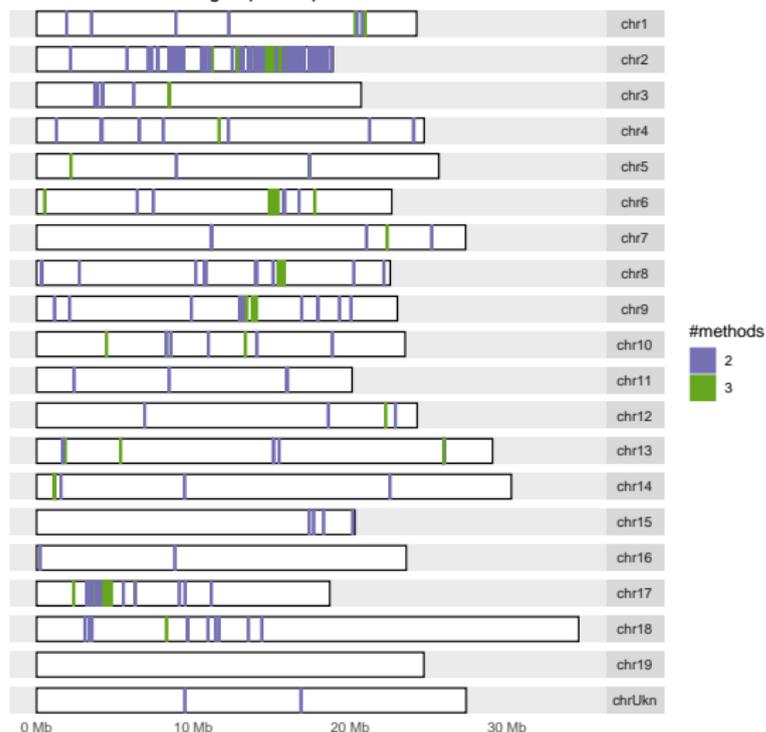
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Method		<b>microarray-GBS SNPs</b>		
Model	Software	#RVs	#SNPs	#QTLs
SNP-by-SNP	GEMMA	101	7855	1784
multi-SNP	mlmm.gwas	125	703	692
multi-SNP	varbvs	119	258	257

⇒ 150 RVs have at least one QTL

## Stage II: identification of reliable QTLs

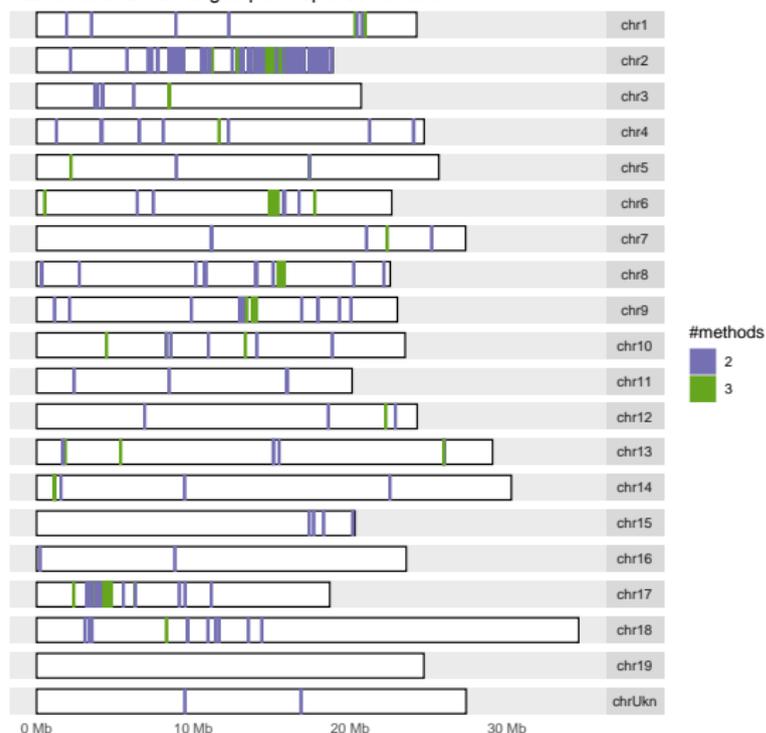
489 reliable QTLs merged per response variable



► 124 RVs with at least one “reliable” QTL

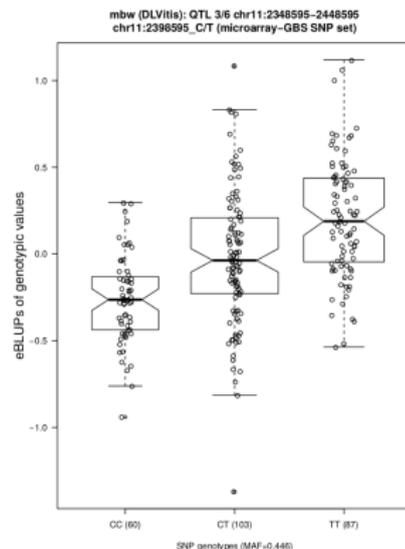
# Stage II: identification of reliable QTLs

489 reliable QTLs merged per response variable



▶ 124 RVs with at least one “reliable” QTL

▶ visual check:



# New candidate genes

not detailed here

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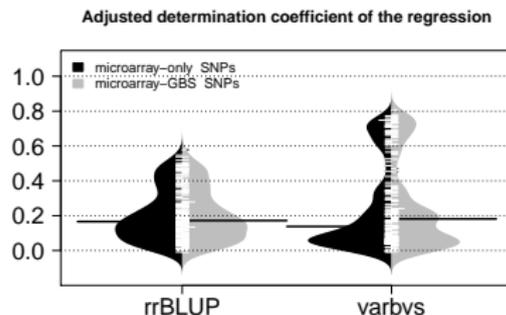
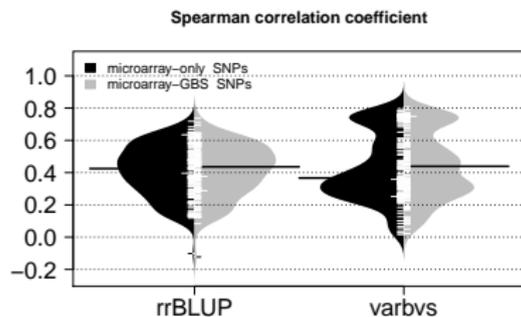
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## Stage II: assessment of prediction accuracy

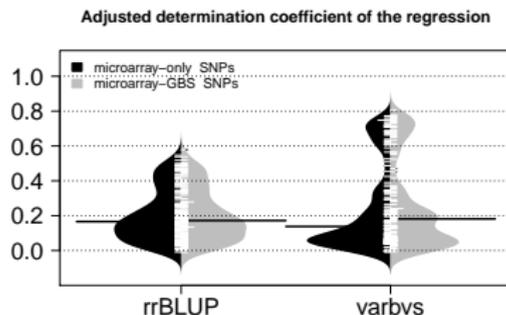
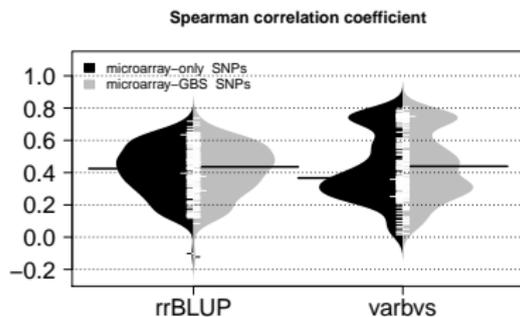
By cross-validation (out-of-sample but within-panel).



Flutre *et al.*, in prep.

## Stage II: assessment of prediction accuracy

By cross-validation (out-of-sample but within-panel).



Flutre *et al.*, in prep.

⇒ For some traits, assuming a sparse architecture (varbvs) clearly gives better predictions than with a fully-polygenic one (rrBLUP).

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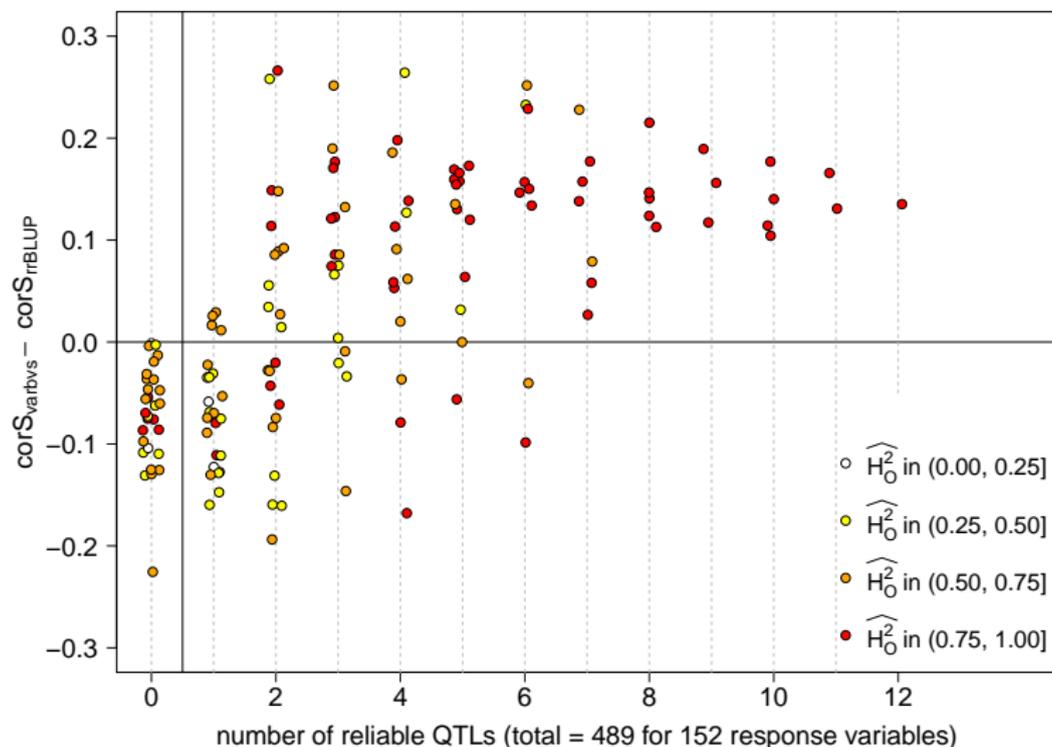
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# About the importance of $H^2$



Flutre *et al.*, in prep.

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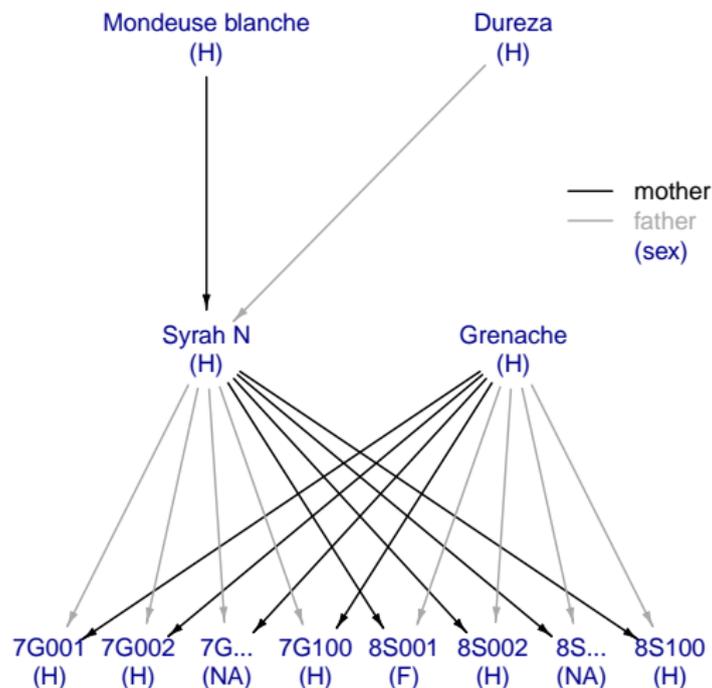
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# Reciprocal cross Syrah × Grenache: 186 pseudo-F1s



Adam-Blondon *et al.* (2005)

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# Ecophysiological framework and target traits

Proposed for cereals by Condon *et al.* (2004):

grain yield = amount of water used by the crop

× proportion actually transpired

× biomass produced per unit of transpired water

× proportion of biomass partitioned to grains

# Ecophysiological framework and target traits

Proposed for cereals by Condon *et al.* (2004):

- grain yield = amount of water used by the crop
  - × proportion actually transpired
  - × biomass produced per unit of transpired water
  - × proportion of biomass partitioned to grains

Ph.D. thesis of A. Coupel-Ledru (2015): follow this approach on grapevine by investigating the genetic basis of plant biomass, leaf water potential ( $\Psi_M$ ), transpiration rate (Tr) and several traits derived from them

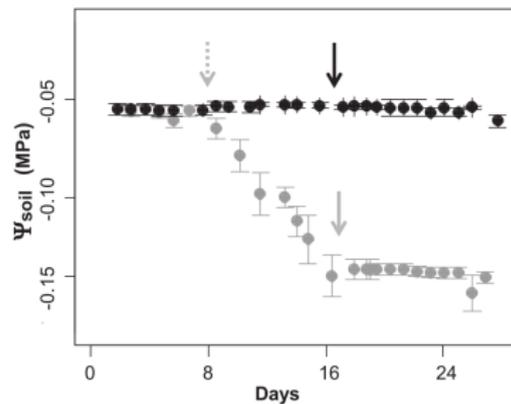
# Experiment design

PhenoArch platform:

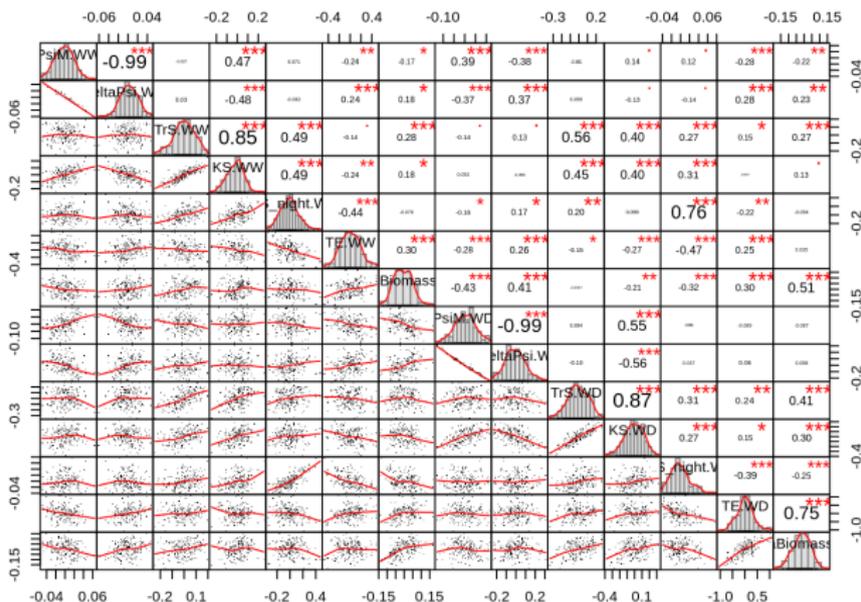


Coupel-Ledru *et al.* (2014 and 2016)

Water-deficit treatment:



# Stage I: correlations between the eBLUPs of each trait



Brault *et al.*, submitted

⇒ Various patterns of significant correlations, motivating the use of multivariate methods.

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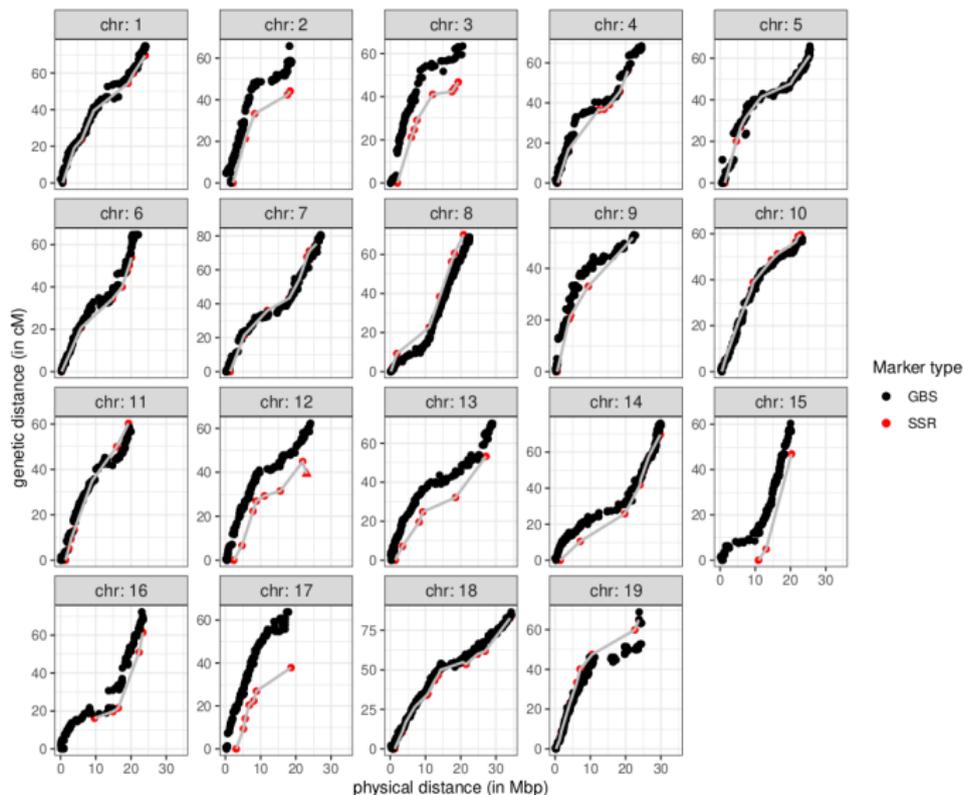
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# SSR and GBS genotyping, and genetic mapping



Brault *et al.*, submitted

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## Stage II: penalized linear regression methods

Univariate:  $\mathbf{y} = X\boldsymbol{\beta} + \boldsymbol{\epsilon}$

Ordinary least squares (OLS):  $\hat{\boldsymbol{\beta}} = \operatorname{argmin} \|\mathbf{y} - X\boldsymbol{\beta}\|_2^2$

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Ordinary least squares (OLS):  $\hat{\boldsymbol{\beta}} = \operatorname{argmin} \|\mathbf{y} - \mathbf{X}\boldsymbol{\beta}\|_2^2$

Penalized versions:  $\hat{\boldsymbol{\beta}} = \operatorname{argmin} \|\mathbf{y} - \mathbf{X}\boldsymbol{\beta}\|_2^2 + \text{penalty} \times \text{norm}(\boldsymbol{\beta})$

- ▶  $\lambda \|\boldsymbol{\beta}\|_1$ : least absolute shrinkage and selection operator (LASSO); assume a sparse architecture
- ▶  $\lambda \|\boldsymbol{\beta}\|_2^2$ : ridge regression (RR); assume full polygenicity
- ▶  $(1 - \alpha) \lambda \|\boldsymbol{\beta}\|_2^2 + \alpha \lambda \|\boldsymbol{\beta}\|_1$ : elastic net (EN); has sparse and fully-polygenic architectures as extreme cases

## Stage II: penalized linear regression methods

**Univariate:**  $\mathbf{y} = X\boldsymbol{\beta} + \epsilon$

Ordinary least squares (OLS):  $\hat{\boldsymbol{\beta}} = \operatorname{argmin} \|\mathbf{y} - X\boldsymbol{\beta}\|_2^2$

Penalized versions:  $\hat{\boldsymbol{\beta}} = \operatorname{argmin} \|\mathbf{y} - X\boldsymbol{\beta}\|_2^2 + \text{penalty} \times \text{norm}(\boldsymbol{\beta})$

- ▶  $\lambda \|\boldsymbol{\beta}\|_1$ : least absolute shrinkage and selection operator (LASSO); assume a sparse architecture
- ▶  $\lambda \|\boldsymbol{\beta}\|_2^2$ : ridge regression (RR); assume full polygenicity
- ▶  $(1 - \alpha) \lambda \|\boldsymbol{\beta}\|_2^2 + \alpha \lambda \|\boldsymbol{\beta}\|_1$ : elastic net (EN); has sparse and fully-polygenic architectures as extreme cases

**Multivariate:**  $Y = XB + E$

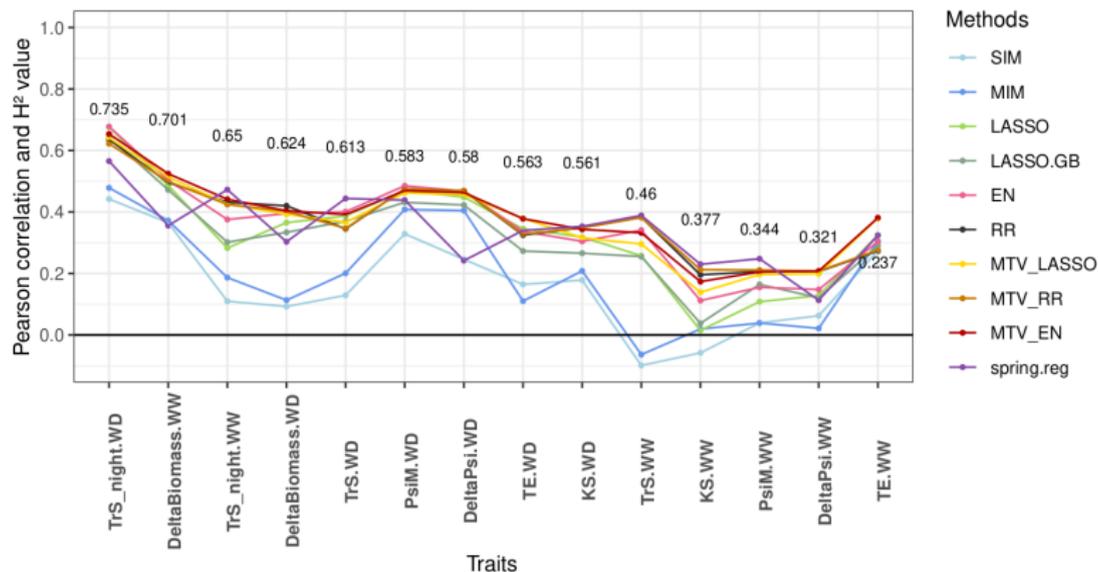
- ▶ MTV\_EN (along with MTV\_LASSO); a selected predictor has a non-zero effect on all dependent variables
- ▶ SPRING:  $B = -\Omega_{Xy} \Omega_{yy}^{-1}$ ; a selected predictor can have a non-zero effect only on some dependent variables

## Stage II: comparison on simulations

not detailed here

# Prediction accuracy on real data

Sorted by  $\hat{H}^2$ :

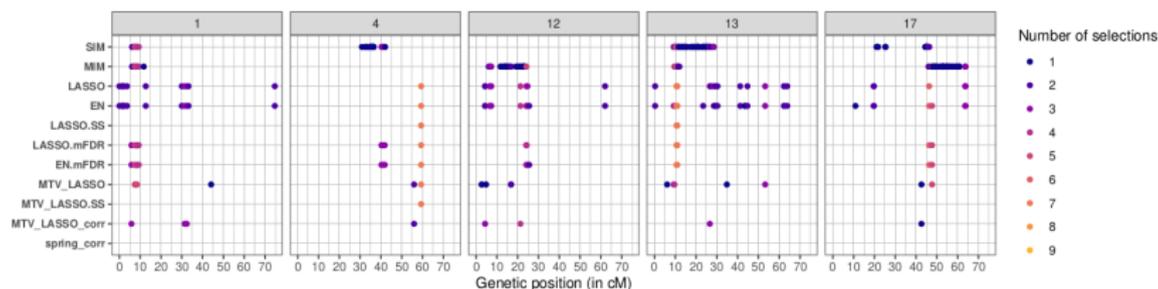


Brault *et al.*, submitted

⇒ No “best” method, but MTV\_EN is a good default.

## Stage II: identification of QTLs, ex. for TrS night

A point corresponds to a marker selected by a given method, its color indicates the number of methods that have selected it.



Brault *et al.*, submitted

⇒ Penalized regression methods found new QTLs compare to interval-mapping ones (e.g., here on chr4).

# New candidate genes

not detailed here

# Outline

## Harnessing genome-wide association and prediction in perennials: two case studies on grapevine

Domestication, current context and ideotyping

Rationale

Univariate study of (mainly) yield components and quality traits on a diversity panel in the vineyard

Multivariate study on a bi-parental progeny of potted plants under water deficit

**Perspectives**

Mobility: an opportunity to start another line of research

Genetic basis of plasticity: a case study on wheat-based mixtures

# G2WAS project (2020-2024)

Aim: study the physiological responses of the diversity panel to water deficit at intra- and inter-annual scales by:

- ▶ Coord.: L. Torregrosa (Institut Agro, AGAP; Montpellier)

More info [online](#).

→ Gathering ecophysiologicals, geneticists and statisticians to study the genetic basis of multiple traits chosen for their relevance with respect to the underlying physiological processes

- ▶ approach:  $\mathbf{y} = X\boldsymbol{\alpha} + Z\mathbf{g} + \boldsymbol{\epsilon}^{(I)}$ , then  $\hat{\mathbf{g}} = M\boldsymbol{\beta} + \boldsymbol{\epsilon}^{(II)}$

# A bit of epistemology about modelling

Gunawardena (2014):

- ▶ “[models] are designed to be accurate descriptions of our pathetic thinking about nature”

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- ▶ “*reverse modelling*: starts from experimental data and seeks potential causalities suggested by the correlations in the data, captured in the structure of a mathematical model”
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## A bit of epistemology about modelling

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Incidentally, a step of statistical modelling is used in both modelling approaches!

## Some thoughts on analyzing multiple traits

Reverse modelling  $\rightarrow P = G + E + G \times E + \epsilon$

Multiple traits in  $P \rightarrow$  extra vcov matrices for  $G$  and  $\epsilon$ , but:

- ▶ two traits  $\Leftrightarrow$  one trait in two envts (phenotypic plasticity)
- ▶ ignoring the underlying processes (time and scale dependent)

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**Forward modelling**  $\rightarrow$  integrate genetic determinism into process-based models, e.g., crop models and functional-structural plant models (FSPMs), but:

- ▶ hard to “pick out the right level of organization where genetic variability in the mechanism can explain the observed variations of the trait” (adapted from Baldazzi *et al.*, 2016)
- ▶ need for (many) more, harder-to-collect phenotyping data
- ▶ (much) more difficult to perform statistical inference

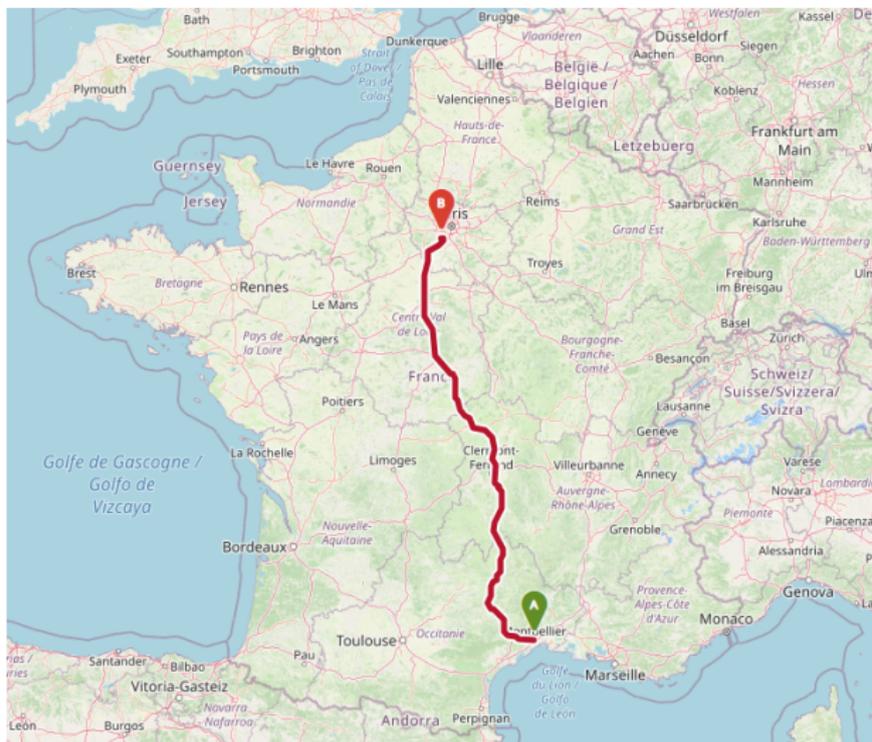
# Outline

Harnessing genome-wide association and prediction in perennials:  
two case studies on grapevine

**Mobility: an opportunity to start another line of research**

Genetic basis of plasticity: a case study on wheat-based mixtures

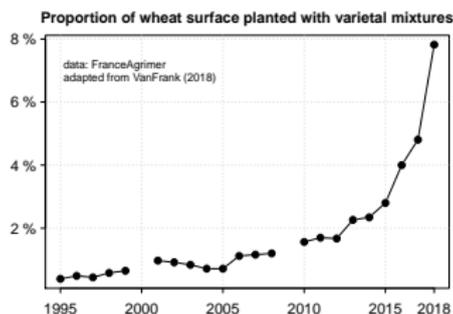
# From Montpellier to Paris-Saclay



- ▶ team DAAV in unit AGAP in Montpellier
- ▶ team DEAP in unit GQE-Le Moulon in Paris-Saclay

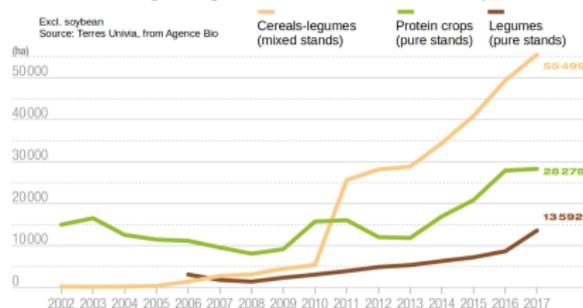
# Agroecology: French farmers' bet on intra-plot diversity

## Intra-specific mixtures:



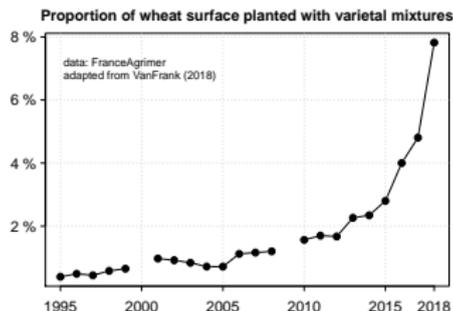
## Inter-specific mixtures:

Surfaces with organic legumes in France: mixed stands vs. pure stands

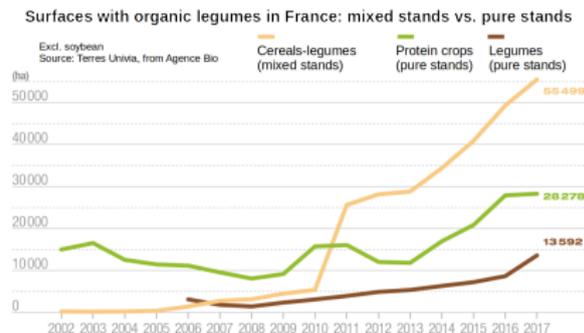


# Agroecology: French farmers' bet on intra-plot diversity

## Intra-specific mixtures:



## Inter-specific mixtures:



## Overyielding:

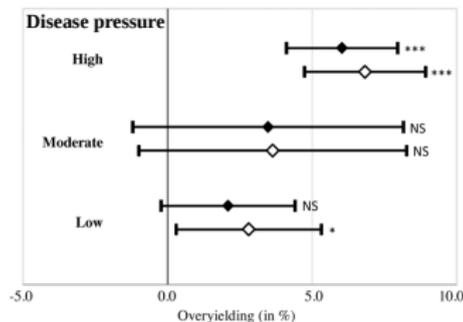
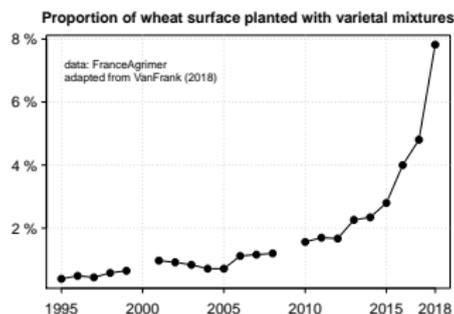
$$OY_{\text{mix}} = \frac{\text{yield of the mixed stand}}{\text{mean yield of the pure stands}}$$

## Land-equivalent ratio:

$$LER_{\text{species}} = \frac{\text{yield in the mixed stand}}{\text{yield in the pure stand}}$$

# Agroecology: French farmers' bet on intra-plot diversity

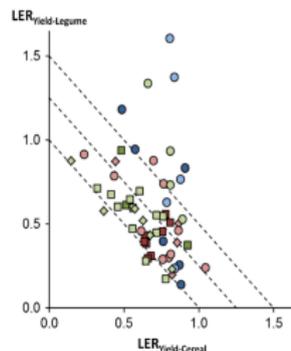
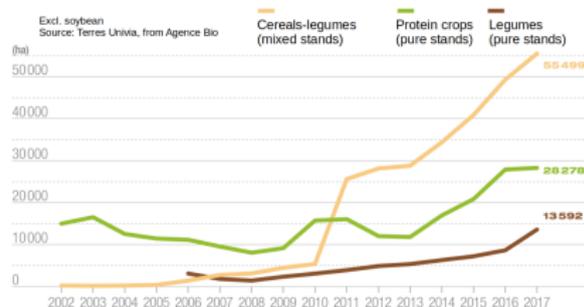
## Intra-specific mixtures:



$\log(OY)$ ; Borg *et al.* (2017)

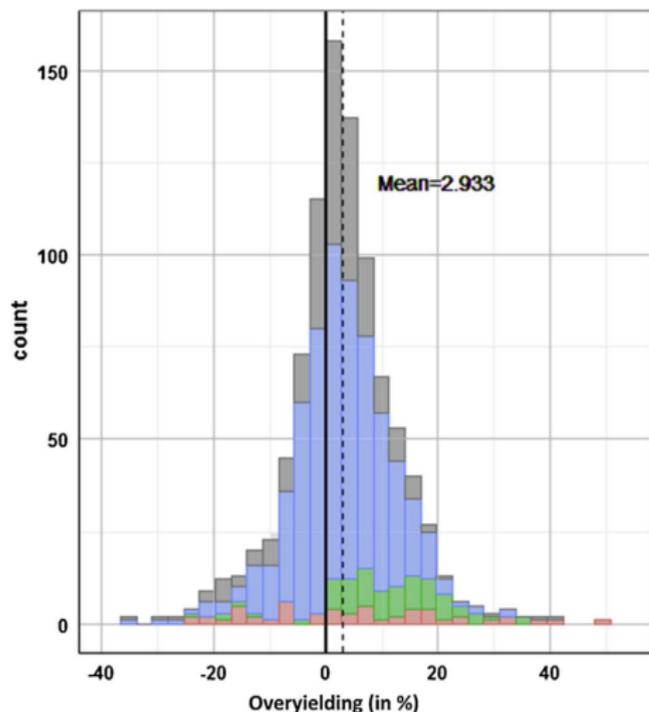
## Inter-specific mixtures:

Surfaces with organic legumes in France: mixed stands vs. pure stands



Bedoussac *et al.* (2015)

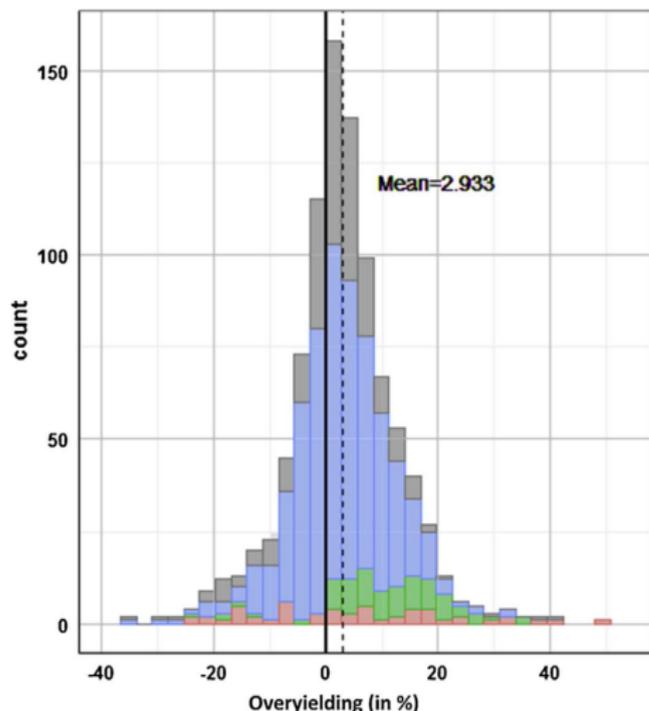
## A positive overyielding on average, and a large variance



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“Simple” question: which processes/factors explain such a distribution?

## A positive overyielding on average, and a large variance



$\log(\text{OY})$ ; Borg *et al.* (2017)

“Simple” question: which processes/factors explain such a distribution?

- ▶ Which genetic variance?
- ▶ How did/do they evolve?
- ▶ Fitness trade-offs between the plant and stand scales?
- ▶ Impact of artificial selection?

# Outline

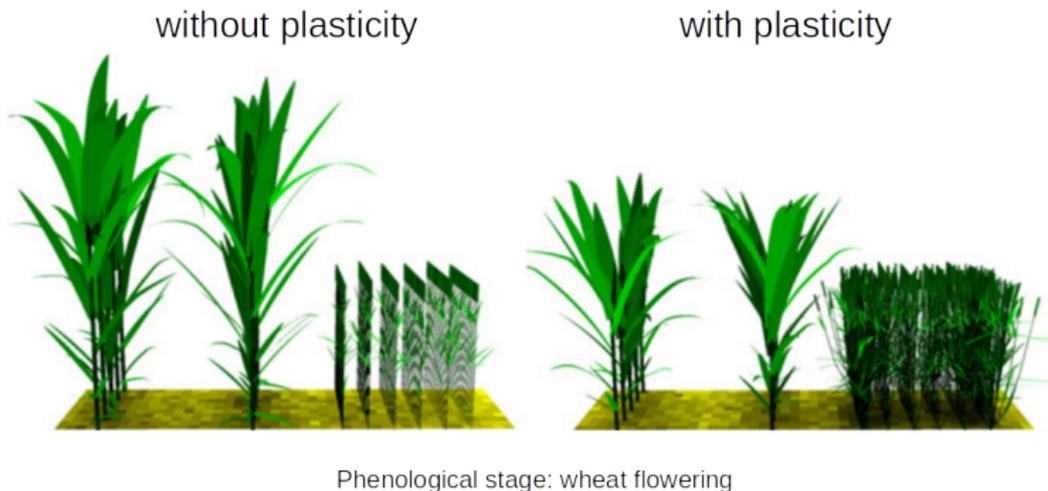
Harnessing genome-wide association and prediction in perennials:  
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Mobility: an opportunity to start another line of research

Genetic basis of plasticity: a case study on wheat-based mixtures

# Role of plant-plant interactions and phenotypic plasticity

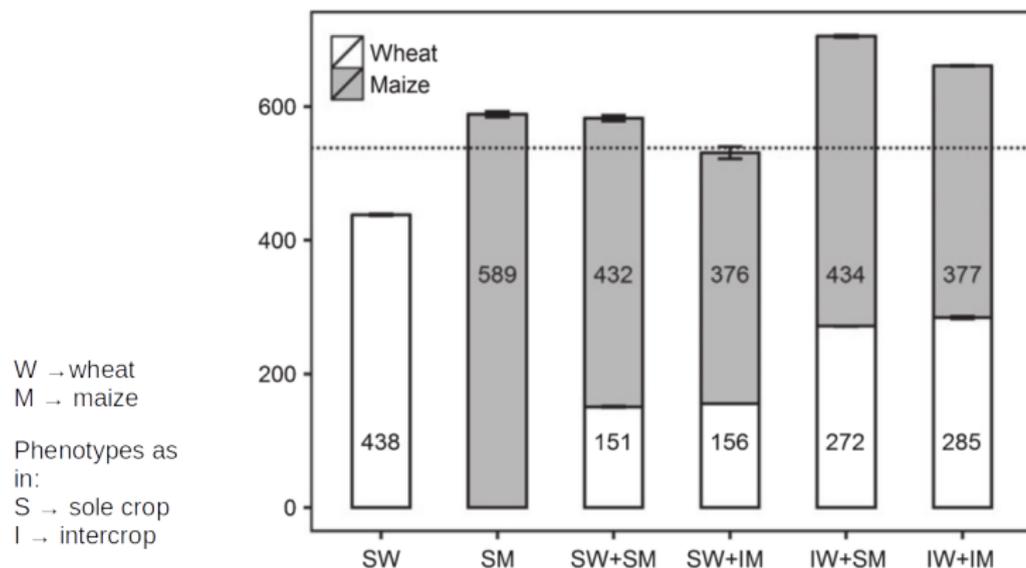
Simulation of wheat-maize intercropping:



Zhu *et al.* (2015)

# Role of plant-plant interactions and phenotypic plasticity

Simulations of PAR (in MJ.m<sup>-2</sup>) accumulated over the season

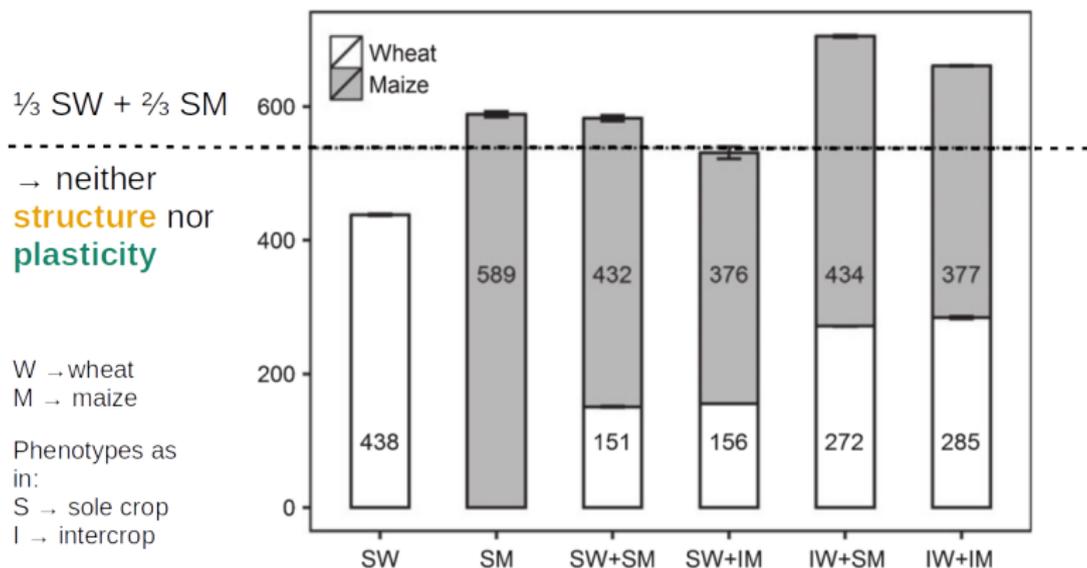


W → wheat  
M → maize  
Phenotypes as  
in:  
S → sole crop  
I → intercrop

Zhu *et al.* (2015)

# Role of plant-plant interactions and phenotypic plasticity

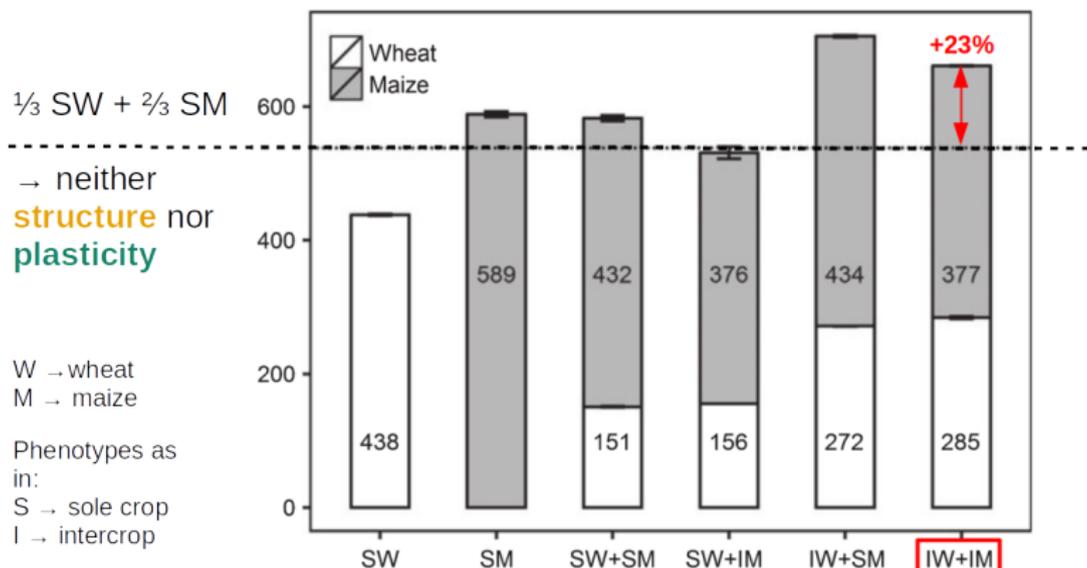
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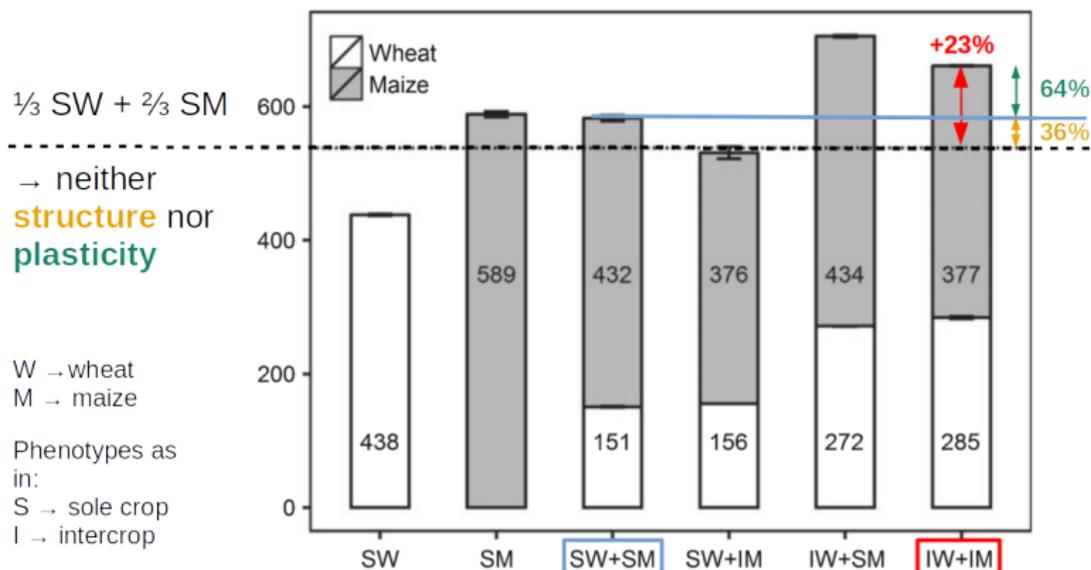
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# Role of plant-plant interactions and phenotypic plasticity

## Simulations of PAR (in MJ.m<sup>-2</sup>) accumulated over the season



Zhu *et al.* (2015)

## My intuition

Answer(s) to the “simple” question likely to be found by:

- ▶ developing a *forward*-modelling approach of a mixed canopy, combining ecophysiological processes and their genetic basis, with ecological interactions at the scale of individual plants,
- ▶ and scaling up to the level of experimental designs used in breeding programs and confronting it to a *reverse*-modelling approach.

For both, need to account for **indirect genetic effects** (“social”): “when the genotype of an individual affects the phenotype of another conspecific individual” (Bijma, 2014).

# Current attempts on wheat varietal mixtures (1/2)

Burden of proof → agricultural conditions

Nano-plots ( $\approx 1.5\text{m}^2$ ):



Ph.D. of M. Gawinowski and PerfoMix project

- ▶ modelling: forward
  - ▶ phenology, biomass production and allocation, yield components, competition for light
- ▶ data: plant-by-plant phenotyping
  - ▶ two years and densities

# Current attempts on wheat varietal mixtures (2/2)

Burden of proof → agricultural conditions

Micro-plots ( $\approx 7.5\text{m}^2$ ):



PerfoMix and MoBiDiv projects

- ▶ data: medium-throughput phenotyping
  - ▶ canopy development, yield components, grain yield per genotype
  - ▶ two years with fungicides, two years without
- ▶ modelling: reverse

# MoBiDiv project (2021-2025)

Aim: mobilize and breed intra and inter-specific crop diversity for a systemic change towards pesticide-free agriculture

- ▶ Coord.: J. Enjalbert (INRAE, GQE; Paris-Saclay) and A. Fugeray-Scarbel (INRAE, GAEL, Grenoble)

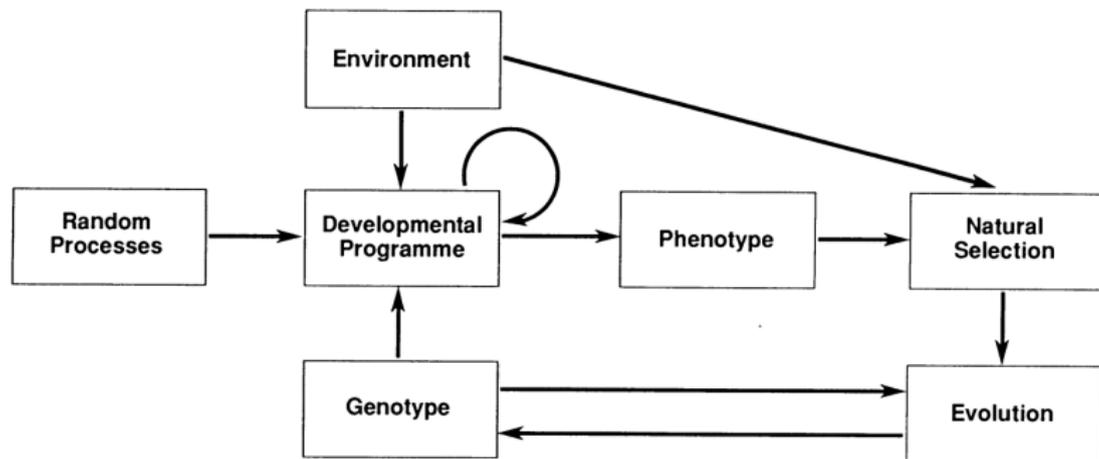
More info [online](#).

→ Stay tune for internships and PhD proposals from this network!

- ▶ ex. GWAS on wheat-pea mixtures

# Perspective: evolutionary trajectories

Conceptual framework:



Scheiner (1993)

Application: cycles of sowing and re-sowing of varietal mixtures.

# Acknowledgments

## Studies on grapevine GWAS/GenPred:

- ▶ colleagues from the AGAP, IFV, LEPSE and MIA research units, notably A. Doligez, L. Le Cunff and P. This
- ▶ INRAE and ANR for funding

## Studies on mixtures:

- ▶ colleagues from the GQE, MICS, AGAP, MIA and LEPSE research units, notably J. Enjalbert and P.-H. Cournède, and IGEPP and FiBL-Switzerland
- ▶ INRAE and ANR for funding