Plant-plant interactions in wheat: insights from social evolution

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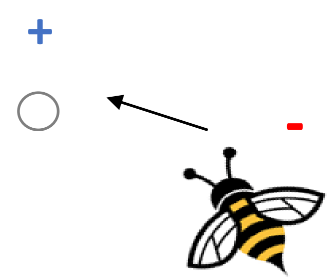
UNIL | Université de Lausanne

MARIE CURIE ACTIONS

Agroscope

Social evolution theories

- Social evolution theories helped to explain the evolution of social behaviors such as altruism and cooperation
- Social behavior or social phenotypes = phenotypes which have fitness consequences on the social partner
- Altruistic phenotype = fitness cost for the actor, fitness benefit for the recipient

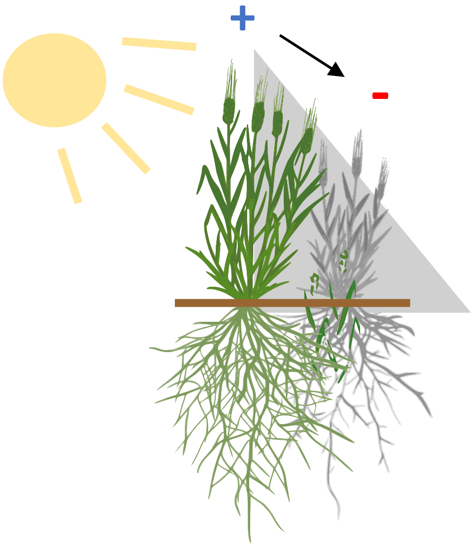


Hamilton, 1964

Why using social evolution theories in crops ?

- Crops live and evolve as groups: most cropping systems are made of densely packed plants of the same species

- Some plant traits do affect the fitness of their neighbours

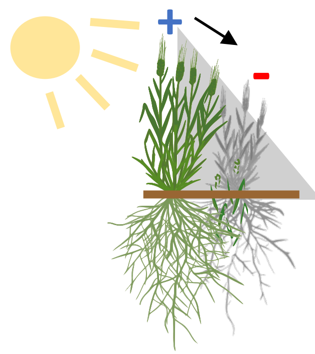


<u>Example:</u> competition for light through plant height differences

Why using social evolution theories in crops ?

- Negative plant-plant interactions can have dramatic consequences on crop productivity:

1. Loss incurred by the weak competitor can be > gain incurred by the strong competitor



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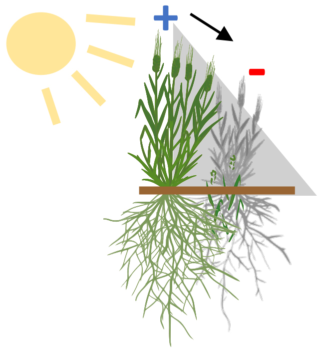
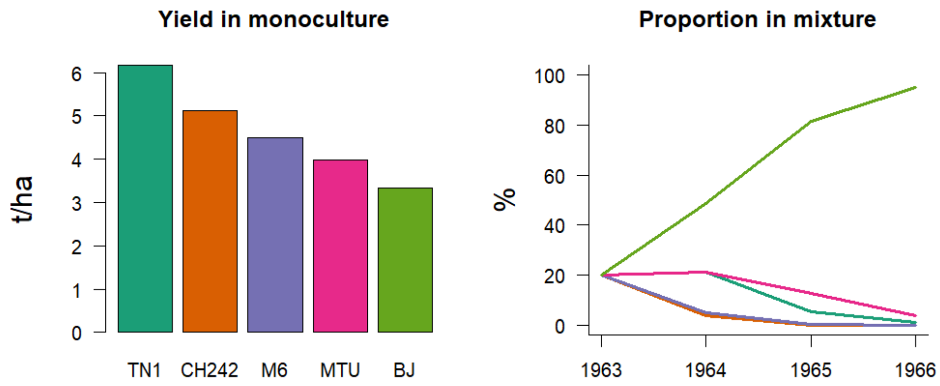


2. Strong competitors can invade the population, further reducing the overall productivity



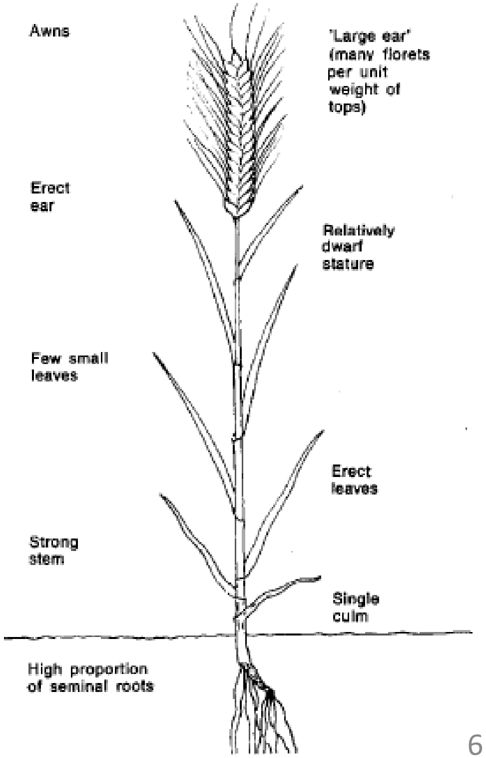
Jennings & de Jesus, 1968

Why using social evolution theories in crops ?

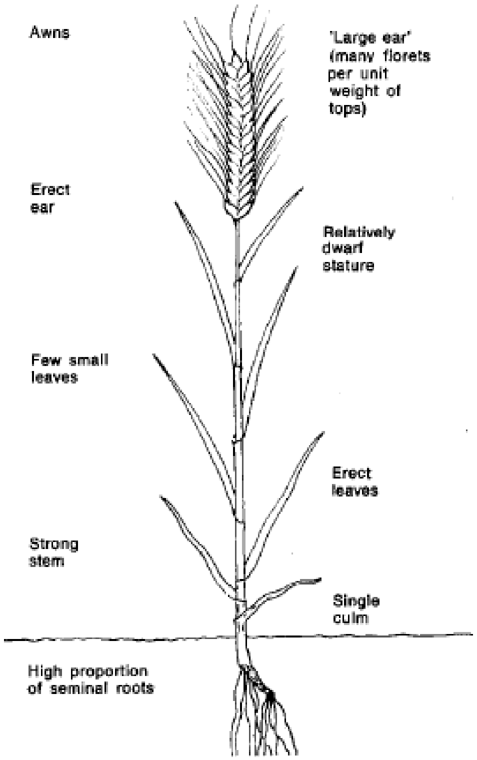
Donald, 1968

« While strong competitive ability is advantageous against other species such as weeds, it will lead in a monoculture to intensified competition and heavy mutual depression among the crowded plants »

Breeding target → "Donald's ideotype"



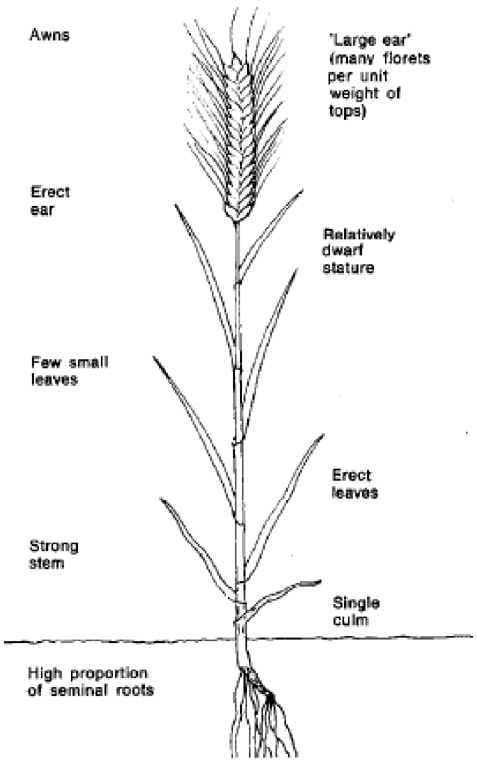
Why using social evolution theories in crops ?



- **Donald's view**

→ **"communal" phenotype**, adapted to succeed as a community

Why using social evolution theories in crops ?



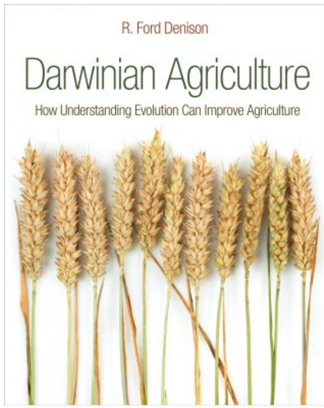
- **Donald's view**

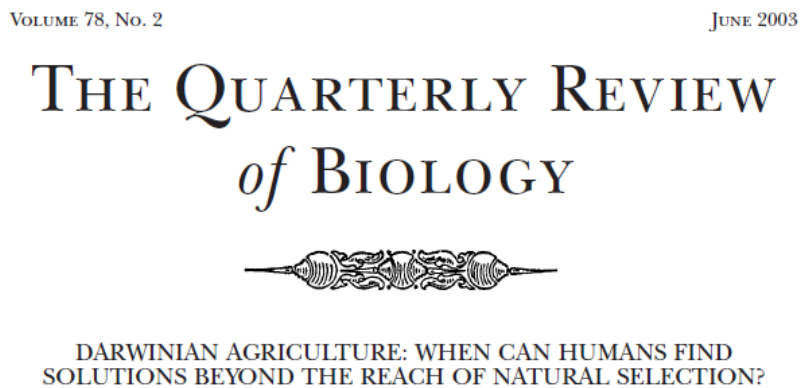
→ **"communal" phenotype**, adapted to succeed as a community

- **Hamilton's view**

→ **Altruistic phenotype**

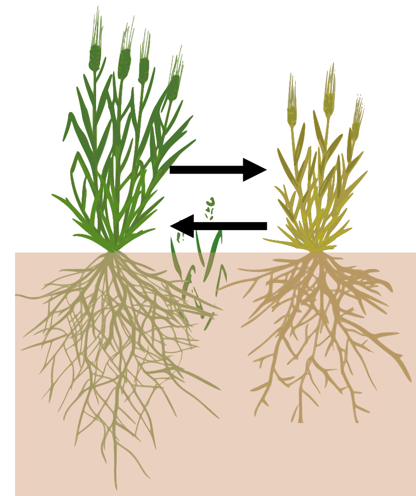
Revisiting intraspecific interactions in crops with evolutionary theories




VOLUME 78, NO. 2 JUNE 2003

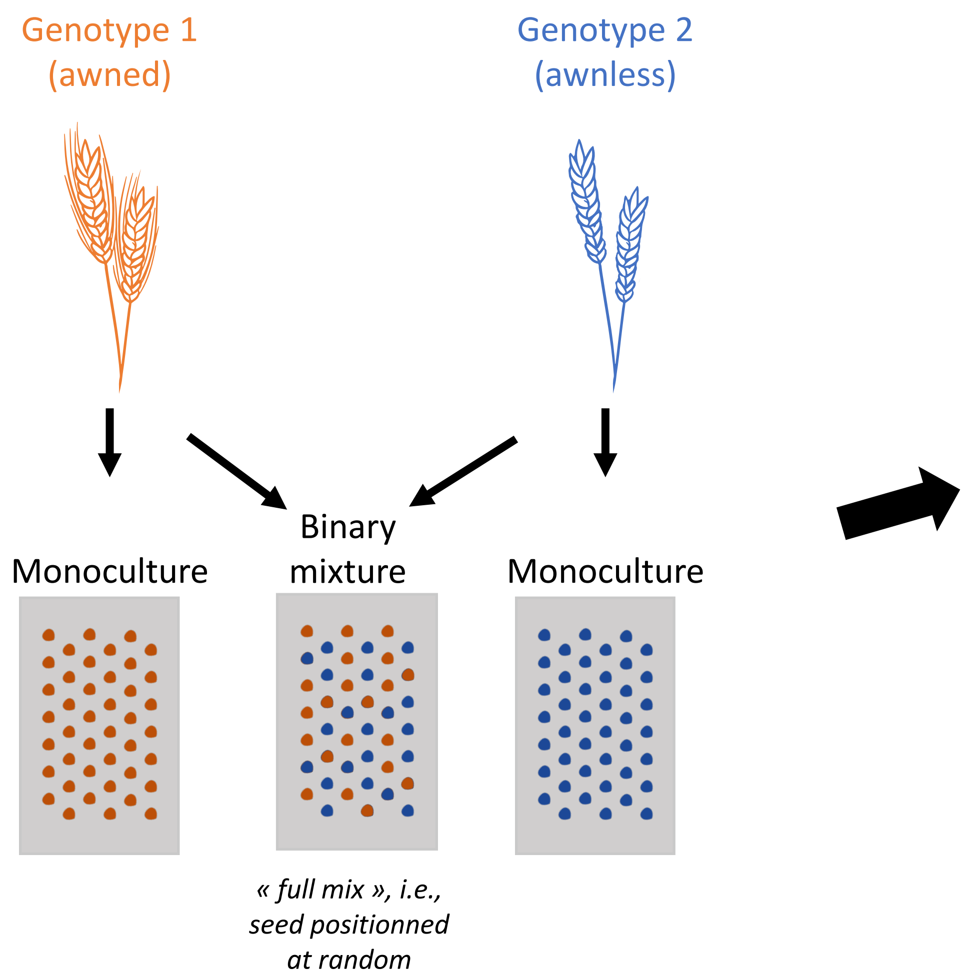
THE QUARTERLY REVIEW of BIOLOGY

DARWINIAN AGRICULTURE: WHEN CAN HUMANS FIND SOLUTIONS BEYOND THE REACH OF NATURAL SELECTION?

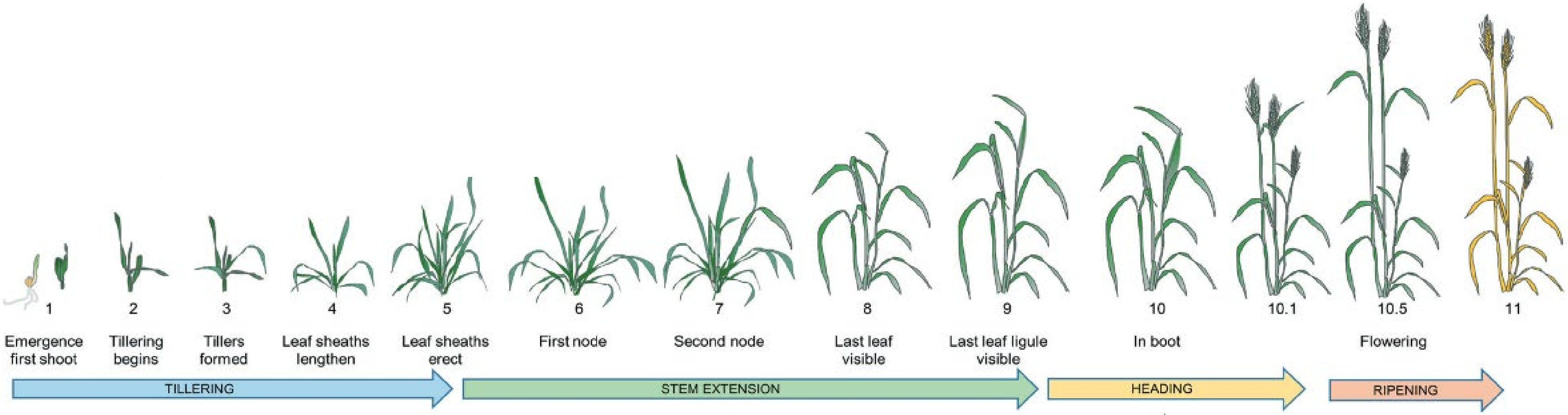


- **What is the contribution of social interactions to variation in productivity-related traits in crops?**
- **What are the traits that underlie social interactions?**
- **What are the genes that underlie social interactions?**

100 genotypes (50 awned, 50 awmless)
commercial varieties + breeding material



400 plots:
100 monocultures
300 binary mixtures
No replicates



Nb spikes/plant

Nb seeds/spike

Seed mass/plant

- **What is the contribution of social interactions to variation in productivity-related traits in crops?**

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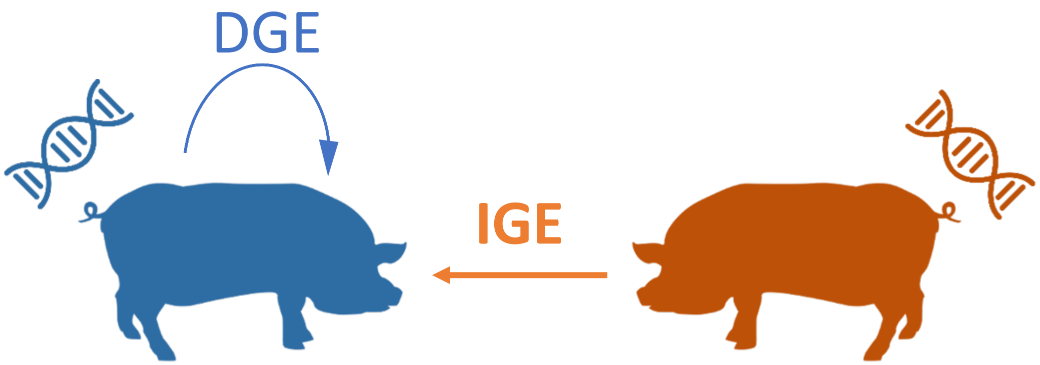
- **What are the genes that underlie social interactions**

Quantitative genetics approach:

Direct Genetic Effects (DGE): effects that genes have on their bearer

Indirect Genetic Effects (IGE): effects that genes have on individuals other than their bearers

IGE models are used to decrease aggressiveness in animal breeding



Griffing, 1967
Bijma, 2007

Mixed model formalism

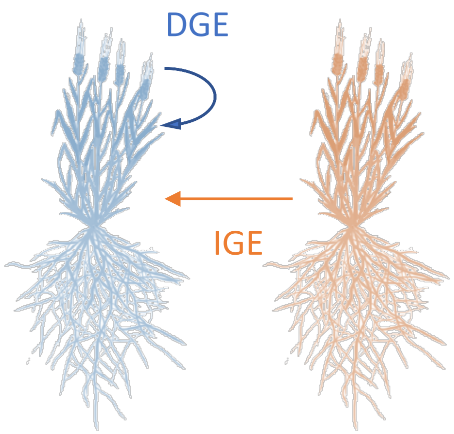
Fixed effects — Residuals

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_D a_D} + \boldsymbol{Z_S a_S} + \boldsymbol{\varepsilon}$$

Productivity trait of the focal genotype

Effect of the focal genotype (DGE)

Effect of the neighbour genotype (IGE)



Mixed model formalism

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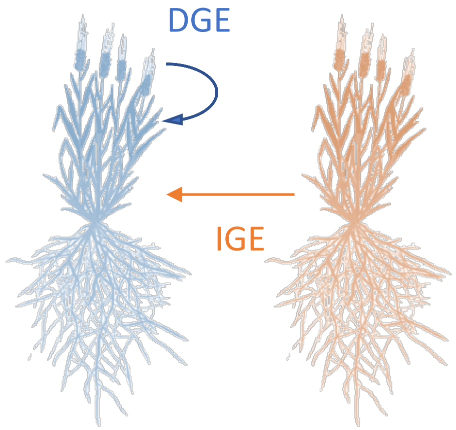
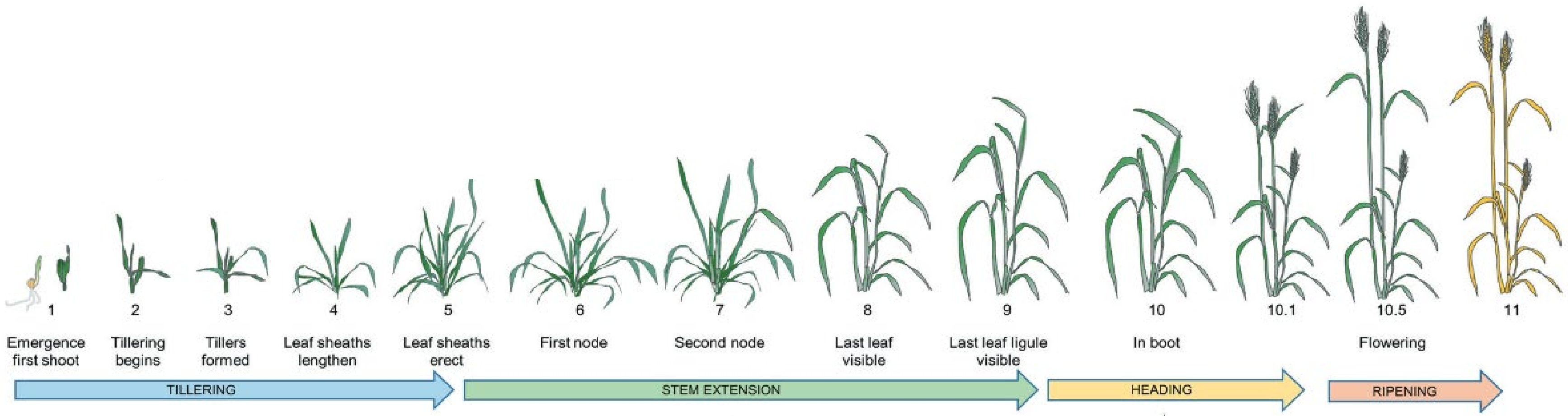


Model comparison

Model 1: only DGE vs Model 2: DGE + IGE

Results

Best models:



Nb spikes/plant

Model 2

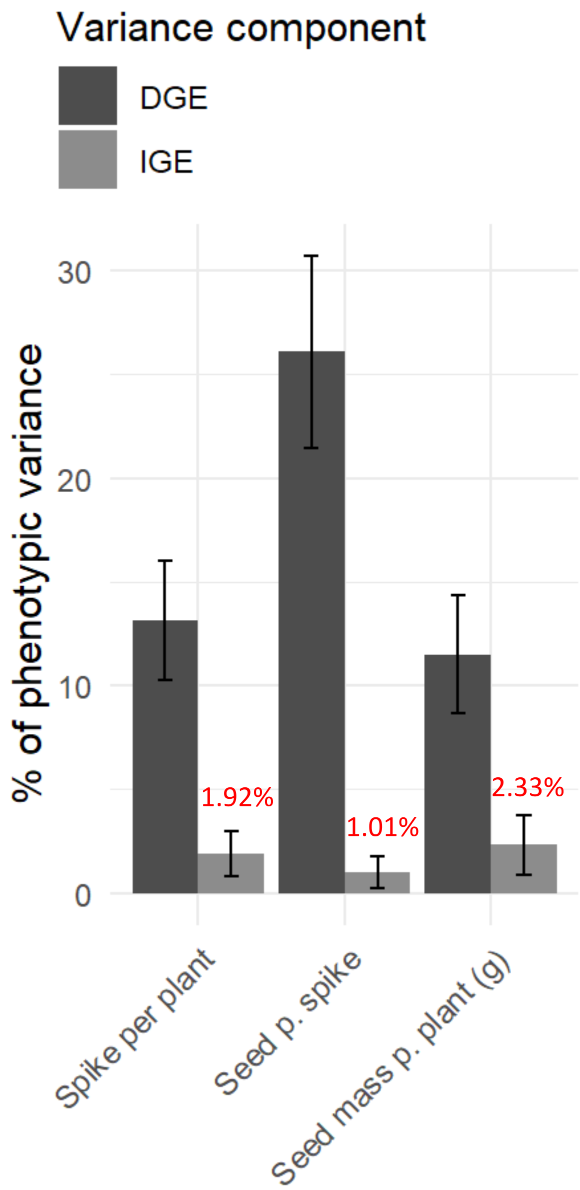
Nb seeds/spike

Model 2

Seed mass/plant

Model 2

Results



Variance component
DGE
IGE
% of phenotypic variance
30
20
10
0
1.92%
1.01%
2.33%
Spike per plant
Seed p. spike
Seed mass p. plant (g)

What is the contribution of social interactions to variation in productivity-related traits?

→ Social interactions affects both early and late established productivity(fitness) traits

→ They contribute ~ 2.3% of the variation of the final yield

→ ~ Similar contributions in animals (Bergsma et al., 2008; Ellen et al., 2008; Alemu et al., 2014)

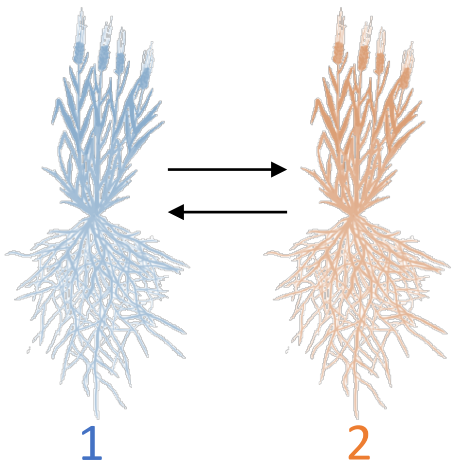
- **What is the contribution of social interactions to variation in productivity-related traits in crops?**

- **What are the traits that underlie social interactions?**

- **What are the genes that underlie social interactions**

How to identify social traits ?

The regression formalization of Hamilton's theory



$$W_1 = \alpha + \beta_d P_1 + \beta_i P_2 + \varepsilon$$

$W_.$: fitness
$P_.$: Phenotype
β_d: direct effect of the phenotype
β_i: indirect effect of the phénotype

$\beta_d \Leftrightarrow -c$ Hamilton's « cost »
$\beta_i \Leftrightarrow b$ Hamilton's « benefit »

Queller, 1992
Gardner et al., 2011
Rousset, 2015

Candidate traits

Phenology	Heading date (°C.day)
Morphology	Height (cm) Nb of leaves (#) Nb of tillers (#) Flag leaf area (cm^2) Stem diameter (mm)
Metabolism	Specific Leaf Area ($m^2.kg^{-1}$) Photosynthetic activity (µmol $CO_2.m^{-2}.s^{-1}$) Transpiration rate (µmol H_2O $.m^{-2}.s^{-1}$)
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)

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Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)

eLIFE
elifesciences.org

Blumenols as shoot markers of root symbiosis with arbuscular mycorrhizal fungi

Ming Wang[1†], Martin Schäfer[1†‡], Dapeng Li[1], Rayko Halitschke[1], Chuanfu Dong[2§], Erica McGale[1], Christian Paetz[3], Yuanyuan Song[1#], Suhua Li[1], Junfu Dong[1,4], Sven Heiling[1¶**], Karin Groten[1], Philipp Franken[5,6], Michael Bitterlich[5], Maria J Harrison[7], Uta Paszkowski[8], Ian T Baldwin[1*]

Number of spikes per plant

		$\widehat{\beta_d}$	$\widehat{\beta_i}$
Phenology	Heading date	-0.08	0.01
Morphology	Height	0.00	0.00
	# leaves	-0.05	-0.05
	# tillers	**0.27*** **	**-0.16*** **
	Flag leaf area	-0.10*	-0.04
	Stem diameter	-0.10*	0.00
Metabolism	Specific leaf area	0.06	-0.01
	Photosynthetic activity	-0.13*	-0.11
	Transpiration rate	-0.07	-0.10
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	0.02	-0.03

Number of seeds per spike

		$\widehat{\beta_d}$	$\widehat{\beta_i}$
Phenology	Heading date	**0.40****	**0.35****
Morphology	Height	**-0.31****	-0.28*
	# leaves	**0.48*****	0.00
	# tillers	**-0.53*****	-0.01
	Flag leaf area	0.16	-0.10
	Stem diameter	**0.32***	-0.15
Metabolism	Specific leaf area	-0.01	0.05
	Photosynthetic activity	-0.37	0.23
	Transpiration rate	-0.08	0.10
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	**-0.36***	0.21

Seed mass per plant

		$\widehat{\beta_d}$	$\widehat{\beta_i}$
Phenology	Heading date	0.01	0.15
Morphology	Height	0.08	-0.22*
	# leaves	0.09	-0.07
	# tillers	0.16	**-0.28****
	Flag leaf area	0.03	-0.11
	Stem diameter	0.00	-0.06
Metabolism	Specific leaf area	0.08	-0.03
	Photosynthetic activity	-0.30*	-0.25
	Transpiration rate	-0.04	-0.22
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	-0.04	-0.02

What are the traits that underlie social interactions?

→ High tillering reduce spike number in the neighbour

→ Early heading and tall stem reduce seeds/spike in the neighbour

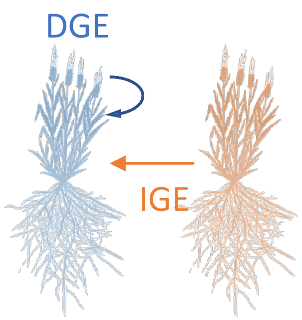
→ Overall, yield is significantly reduce by higher tillering and tall stature in the neighbour

- What is the contribution of social interactions to variation in productivity-related traits in crops?

- What are the traits that underlie social interactions?

- **What are the genes that underlie social interactions ?**

Approach 1: correlation



Fixed effects

Residuals

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_D a_D} + \boldsymbol{Z_S a_S} + \boldsymbol{\varepsilon}$$

Productivity trait

DGE

IGE

Indirect breeding values

Average trait values (monoculture + mixtures)

$$\boldsymbol{a_S} = \begin{pmatrix} a_{S_1} \\ a_{S_2} \\ a_{S_3} \\ \vdots \\ \vdots \\ \vdots \\ a_{S_{100}} \end{pmatrix} \qquad \boldsymbol{t} = \begin{pmatrix} t_1 \\ t_2 \\ t_3 \\ \vdots \\ \vdots \\ \vdots \\ t_{100} \end{pmatrix}$$

Correlation (*r*)

Approach 2: Genome-wide associations

Indirect breeding values

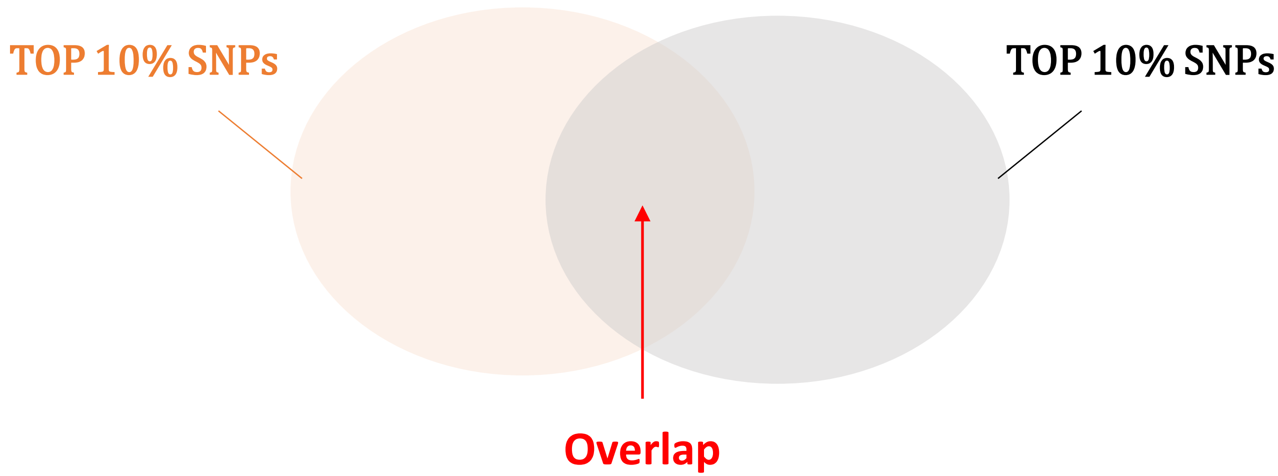
$$a_S = \begin{pmatrix} a_{S_1} \\ a_{S_2} \\ a_{S_3} \\ \vdots \\ \vdots \\ \vdots \\ a_{S_{100}} \end{pmatrix}$$

GWAS (25K SNPs)

Average trait values (monoculture + mixtures)

$$\boldsymbol{t} = \begin{pmatrix} t_1 \\ t_2 \\ t_3 \\ \vdots \\ \vdots \\ \vdots \\ t_{100} \end{pmatrix}$$

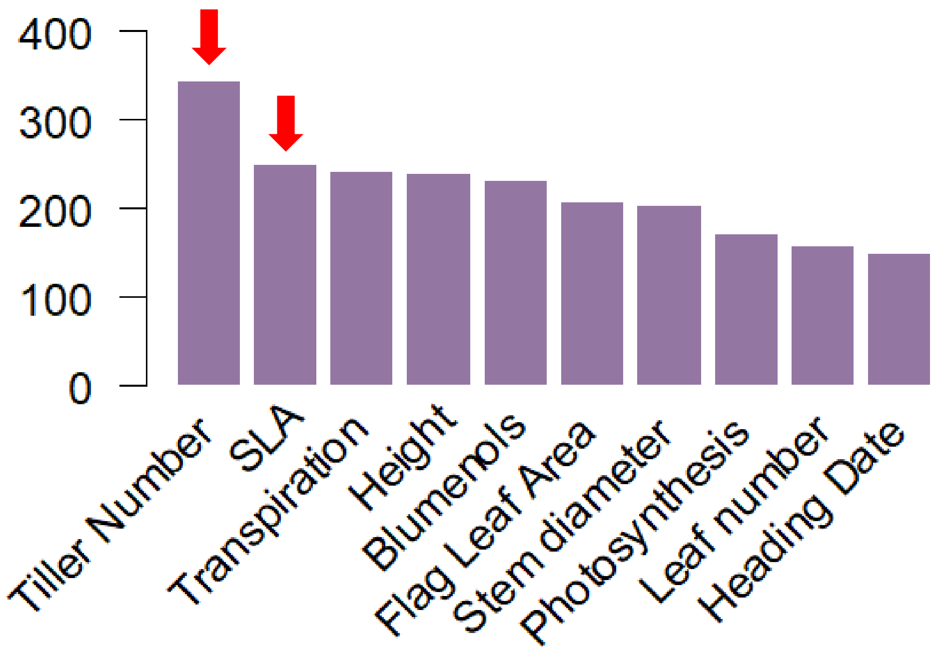
GWAS (25K SNPs)



Phenotypic correlation with IGE on spike/plant

		r
Phenology	Heading date	0.05
Morphology	Height	-0.14
	# leaves	0.08
	# tillers	-0.35***
	Flag leaf area	0.11
	Stem diameter	0.18
Metabolism	Specific leaf area	-0.23*
	Photosynthetic activity	-0.05
	Transpiration rate	0.05
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	-0.13

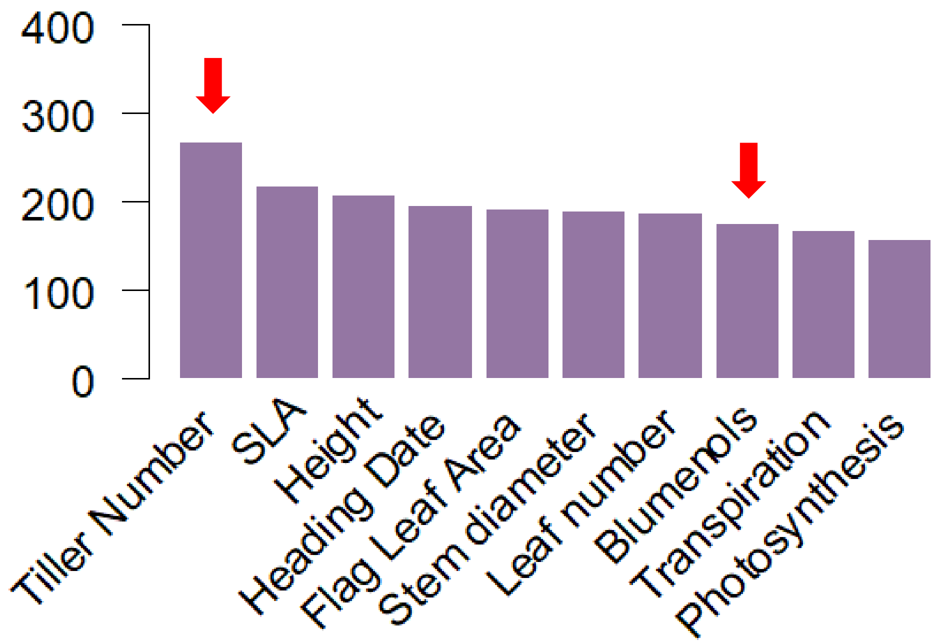
Size of SNPs overlap between IGE on spike/plant and plant traits



Phenotypic correlation with IGE on seeds/spike

		r
Phenology	Heading date	0.08
Morphology	Height	-0.05
	# leaves	-0.07
	# tillers	0.23*
	Flag leaf area	0.02
	Stem diameter	-0.08
Metabolism	Specific leaf area	0.01
	Photosynthetic activity	0.07
	Transpiration rate	-0.11
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	0.23*

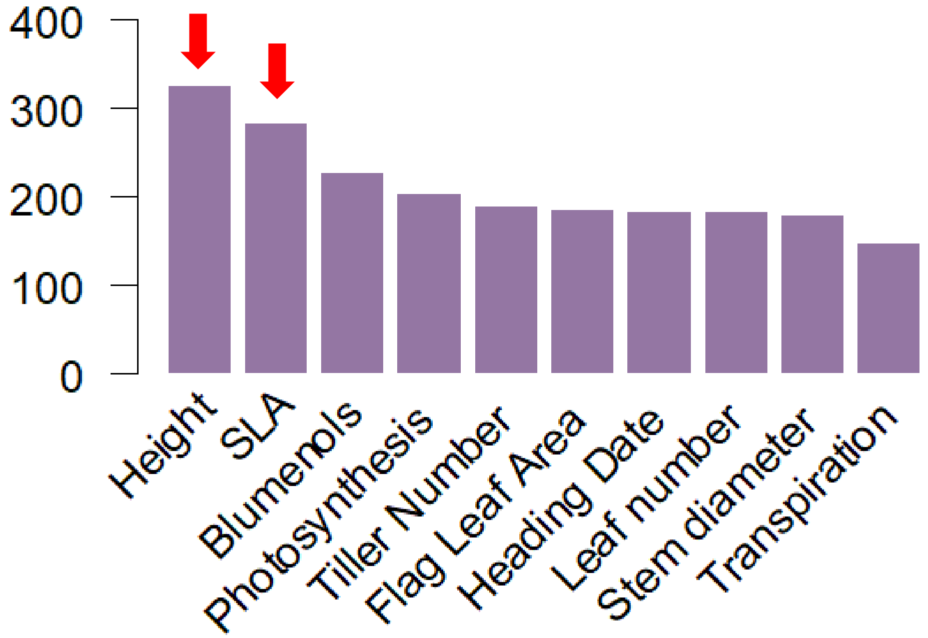
Size of SNPs overlap between IGE on seeds/spike and plant traits



Phenotypic correlation with IGE on seed mass/plant

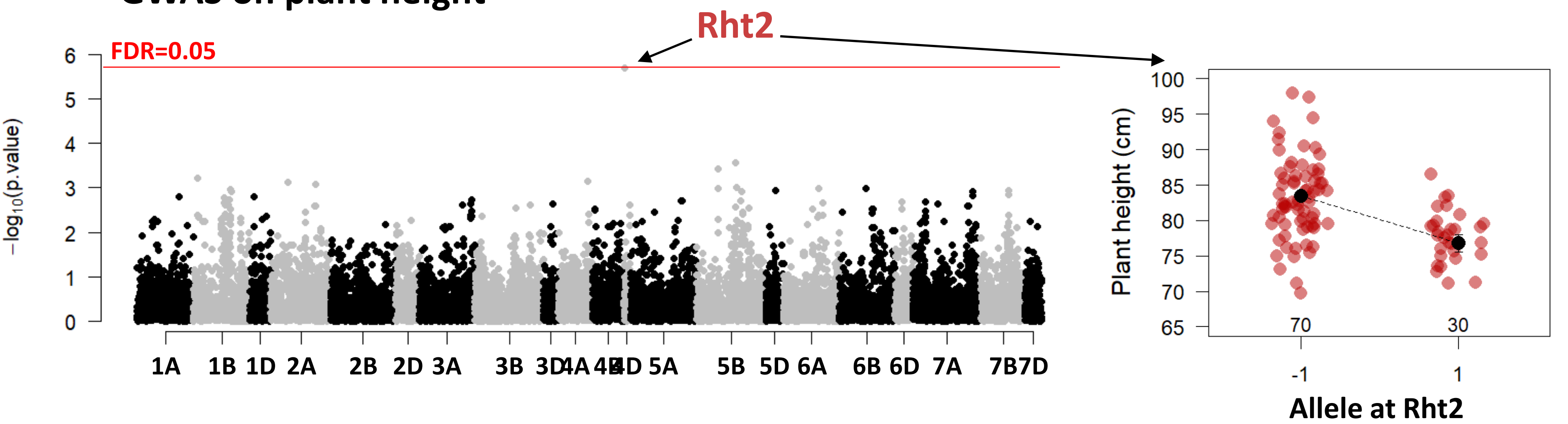
		r
Phenology	Heading date	0.11
Morphology	Height	-0.33***
	# leaves	0.03
	# tillers	-0.03
	Flag leaf area	-0.04
	Stem diameter	0.11
Metabolism	Specific leaf area	-0.22*
	Photosynthetic activity	-0.08
	Transpiration rate	-0.08
Soil symbiosis	Intensity of intracellular mycorrhizal colonization (intra-root)	-0.06

Size of SNPs overlap between IGE on seed mass/plant and plant traits



Results

GWAS on plant height



Results

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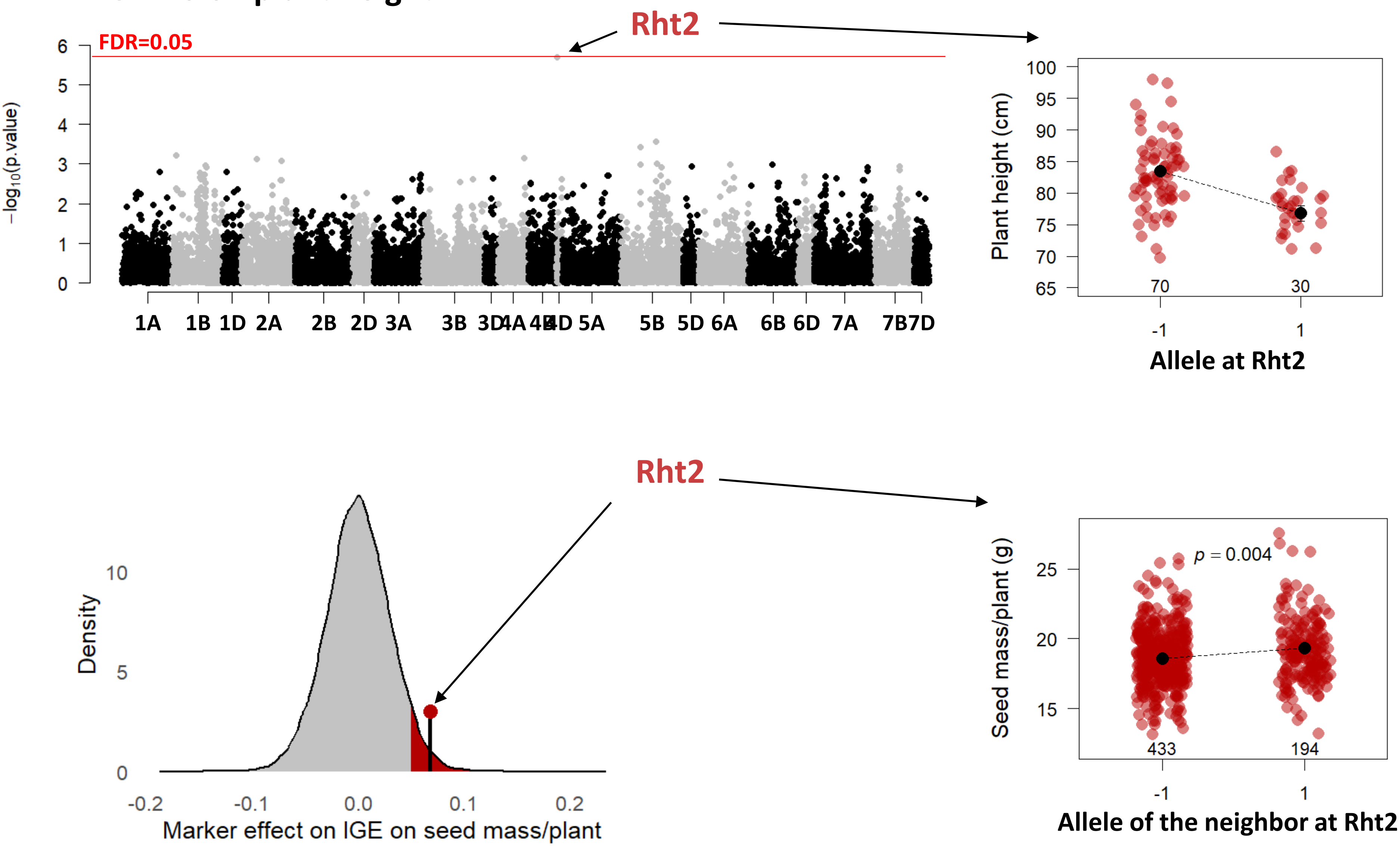
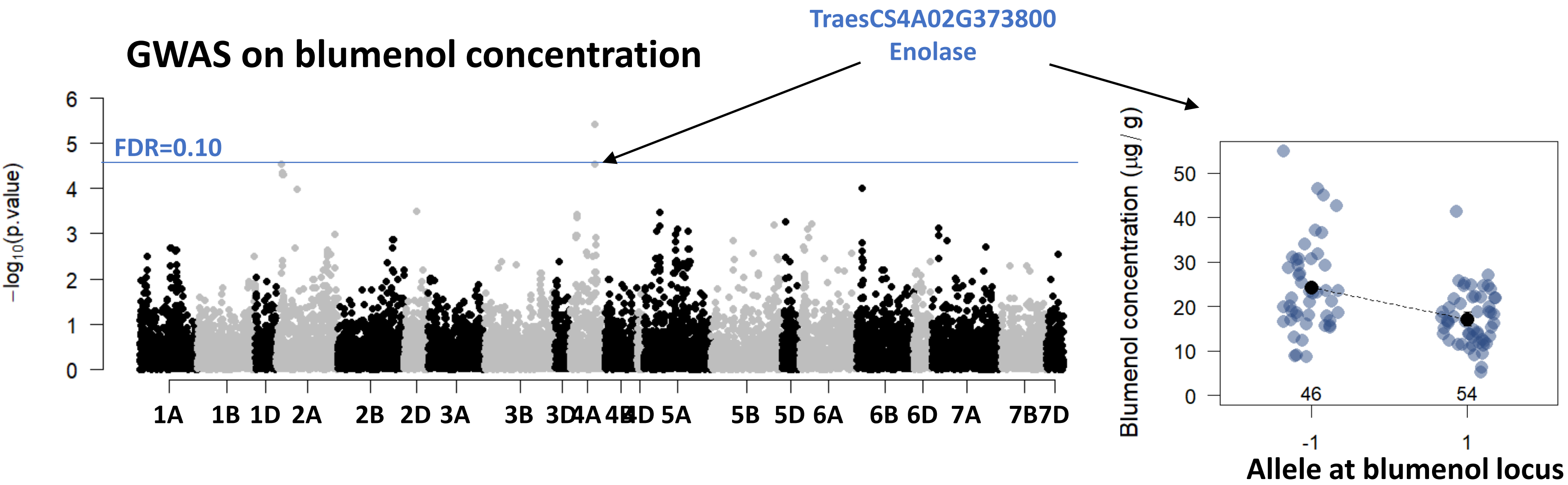
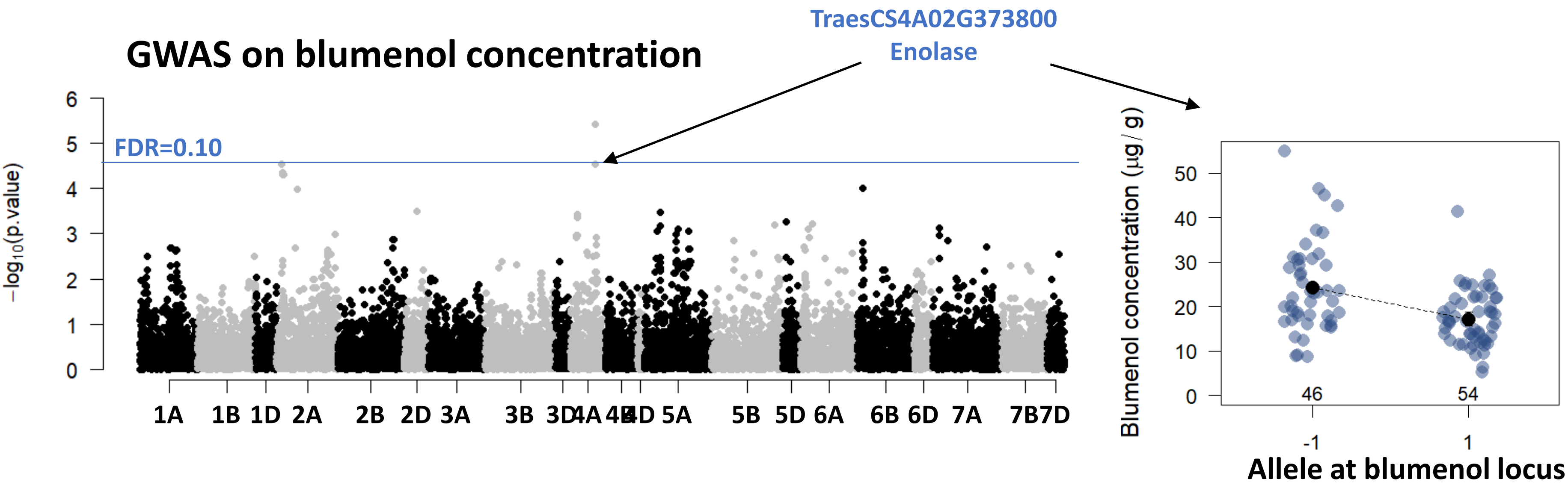
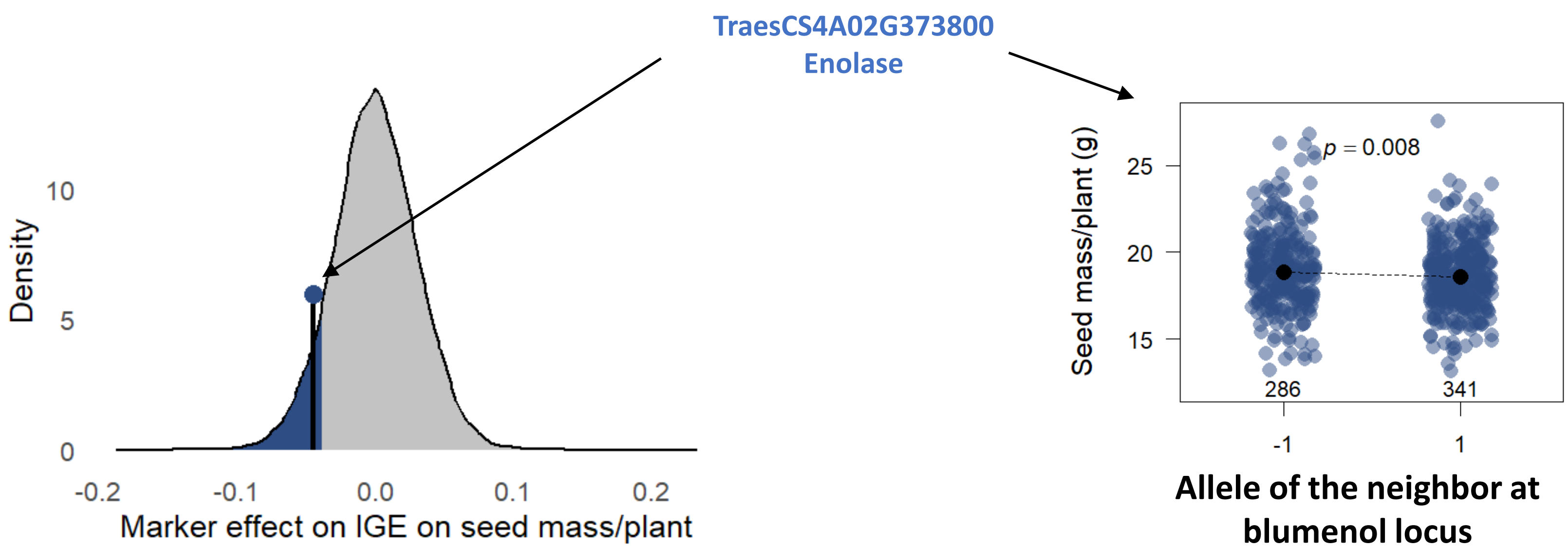


Results


GWAS on blumenol concentration
TraesCS4A02G373800
Enolase
FDR=0.10
−log10(p.value)
0
1
2
3
4
5
6
1A
1B
1D
2A
2B
2D
3A
3B
3D
4A
4B
4D
5A
5B
5D
6A
6B
6D
7A
7B
7D
Blumenol concentration (µg / g)
0
10
20
30
40
50
46
54
-1
1
Allele at blumenol locus

Results


GWAS on blumenol concentration
TraesCS4A02G373800
Enolase
FDR=0.10
−log10(p.value)
0 1 2 3 4 5 6
1A 1B 1D 2A 2B 2D 3A 3B 3D 4A 4B 4D 5A 5B 5D 6A 6B 6D 7A 7B 7D
Blumenol concentration (µg/ g)
0 10 20 30 40 50
46
54
-1
1
Allele at blumenol locus


TraesCS4A02G373800
Enolase
Density
0 5 10
-0.2 -0.1 0.0 0.1 0.2
Marker effect on IGE on seed mass/plant
Seed mass/plant (g)
15 20 25
p = 0.008
286
341
-1
1
Allele of the neighbor at blumenol locus

What are the genes that underlie social interactions?

→ Alleles associated with more tillers and a taller stature are associated with negative effects on neighbor productivity (consistent w/ phenotypic results)

→ Alleles associated with heading date do not associate with IGE

→ SLA and mycorrhizal colonization, which were not identified with the phenotypic approach, associate with IGE at the genetic level

General conclusions – Perspectives

→ Wheat productivity is affected by plant-plant interactions

→ Part of these interactions are heritable (~2.3 % at very low density)

→ Most of these interactions are related to competition for light

→ There is exploitable sources of genetic variation on several traits such as tillering, plant height, and SLA

→ Other sources of variation might be available on mycorrhizal symbiosis (follow-up experiments to come)

Laurent Keller

Samuel Wuest

Erica McGale

Ian Sanders

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MARIE CURIE ACTIONS

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Agroscope

Christine La Mendola (UNIL)
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Gaétan Glauser (UNINE)
Juan Herrera (Agroscope)
Nicolas Vuille (Agroscope)
Zoé Domenjoz (UNIL)
Arno Gatoliat (UNIL)
…
Many field assistants

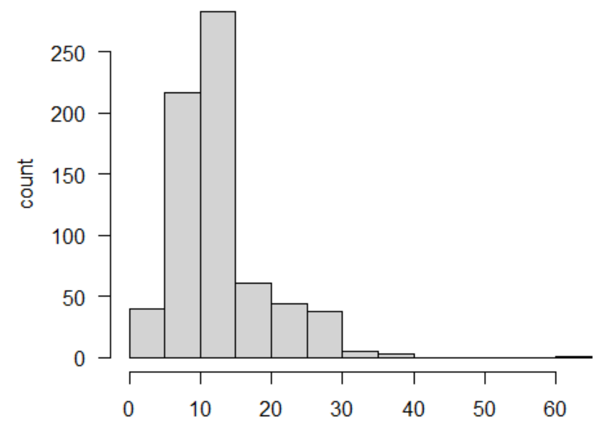
THANK YOU!

(Sowing problem)

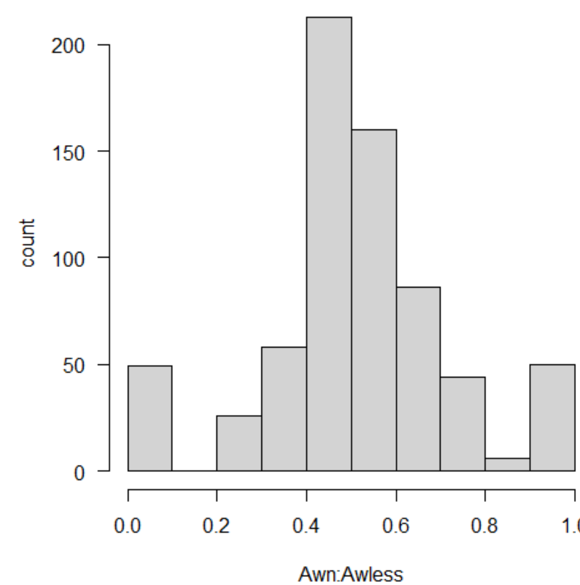
Different plot sizes (variation in # of plants/plot)

Awned:Awnless ratios different from 1:1 in many plots

Low plant densities (~ 50 plant/m^2)



All productivity-related variables are normalized by the number of plants in the plot



Genotype choice

The D-Method: Three stage stratified random sampling (Franco et al., 2005 & 2006)

50 inbred lines, ~ 20 000 SNPs

↓

Pairwise genetic distances (Roger's genetic distances)

↓

Clustering genotypes into groups (Ward method)

↓

Computing the average genetic distance within each group

↓

500 random samplings of 50 genotypes such that the number of genotypes selected from each group is proportional to the mean genetic distance within the group

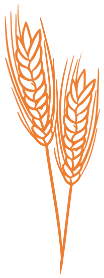
↓

Retain the sampling with the maximal average genetic distance between the 50 selected genotypes

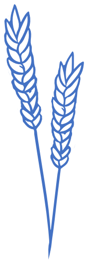
Same procedure for awned and awnless genotypes

Genotype assembly

50 awned genotypes



50 awnless genotypes

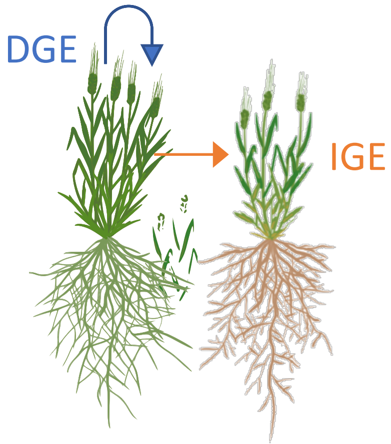


↓

1000 set of 300 binary pairs drawn at random

↓

Retain the set of binary pairs with the greatest variance in genetic distances between the two components of the pair



Fixed effects

Residuals

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_D a_D} + \boldsymbol{Z_S a_S} + \boldsymbol{\varepsilon}$$

Productivity trait of the focal genotype

Effect of the focal genotype (DGE)

Effect of the neighbour genotype (IGE)

$$\begin{bmatrix} \boldsymbol{a_D} \\ \boldsymbol{a_S} \end{bmatrix} \sim MVN\,(\boldsymbol{0}, \boldsymbol{C} \otimes \boldsymbol{A})$$

Where A $=$ Additive genomic relationship matrix

And $\boldsymbol{C} = \begin{bmatrix} \sigma^2{}_{A_D} & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma^2{}_{A_S} \end{bmatrix}$

Direct genetic variance

DGE – IGE covariance

Indirect genetic variance

Trait heritabilities

trait	v_g	v_r	h_a
heading_date_GDD	6.917354e+02	3.865486e+02	0.64151502
height_cm	1.962788e+01	1.990198e+01	0.49653297
blumenol_concentration_ng_g	3.475221e+07	6.902485e+07	0.33487370
leaf_number	5.147210e-02	1.703109e-01	0.23208319
stem_diameter_mm	4.274672e-02	1.454636e-01	0.22712207
leaf_area_cm2	6.633523e+00	3.060729e+01	0.17812509
E_mol_m2_s.1	9.047250e-08	4.876183e-07	0.15650223
sla_m2_kg	6.794942e-01	5.989332e+00	0.10189113
A_umol_m2_s.1	8.129114e-01	1.185078e+01	0.06419230
tiller_number	3.526537e-01	6.336617e+00	0.05271931