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Genetic mapping of resistance factors to *Melampsora* sp in *Populus* sp: a review

Véronique Jorge, Alois Bresson, Arnaud Dowkiw, Patricia Faivre-Rampant,
Brigitte Viguiet, Marc Villar, Vedrana Vlainic, Elise Albert, Christopher
Mangel, Redouane El Malki, et al.

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BioForA



Genetic mapping of resistance factors to *Melampsora* sp in *Populus* sp

A review



Véronique Jorge

CONTRIBUTORS to the present work :

V. Jorge, A. Bresson, A. Dowkiw, P. Faivre-Rampant, B. Viguier, M. Villar, V. Vlainic, E. Albert, C. Mangel, R. El-Malki, M. Pegard, V. Segura, V. Guérin, C. Ridet, C. Bastien

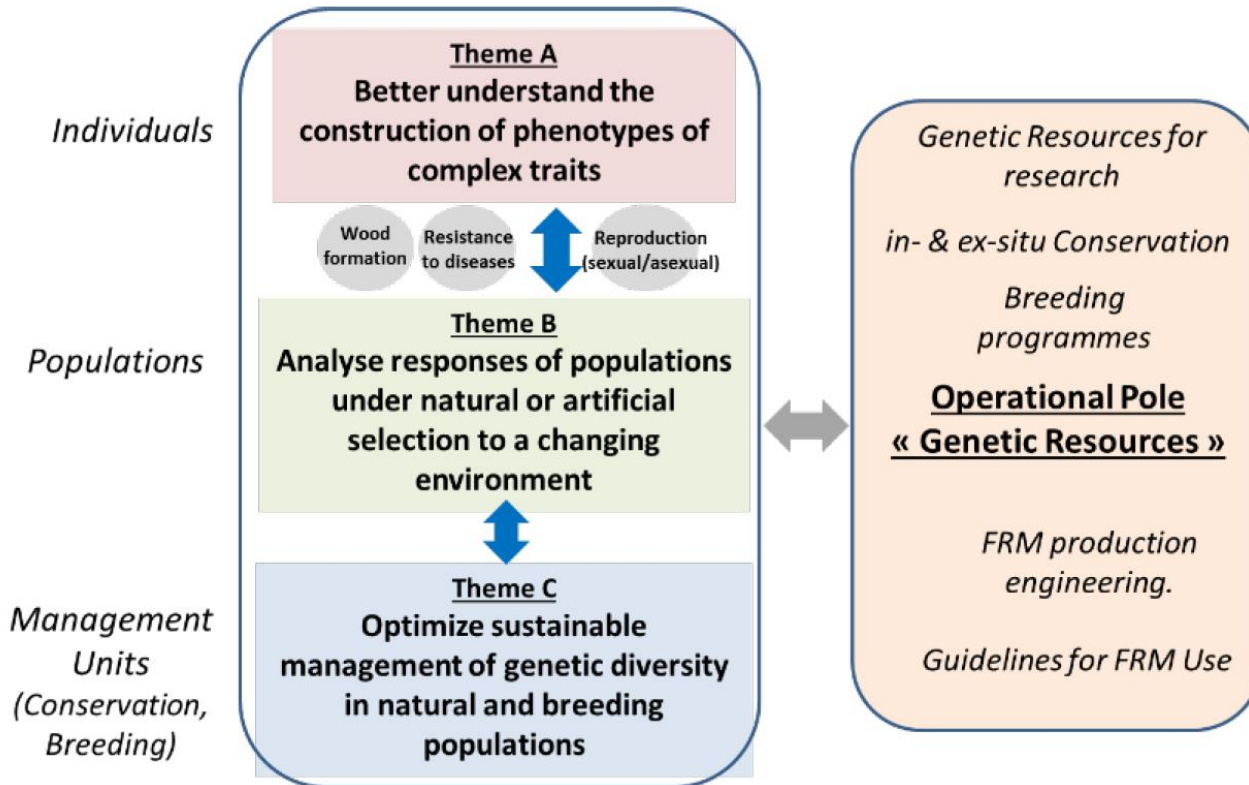
INRA Experimental unit GBFOR



18/ 04/ 2018

Our research objective

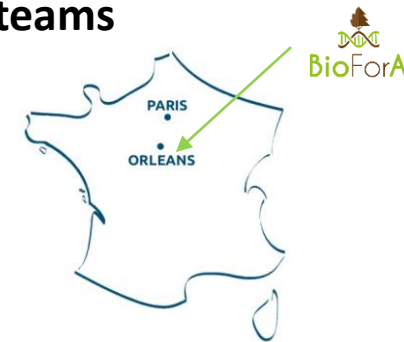
Management of forest genetic resources for sustainable timber production in a changing climate context



- **Joint unit between INRA and ONF** (French National Forest Service)



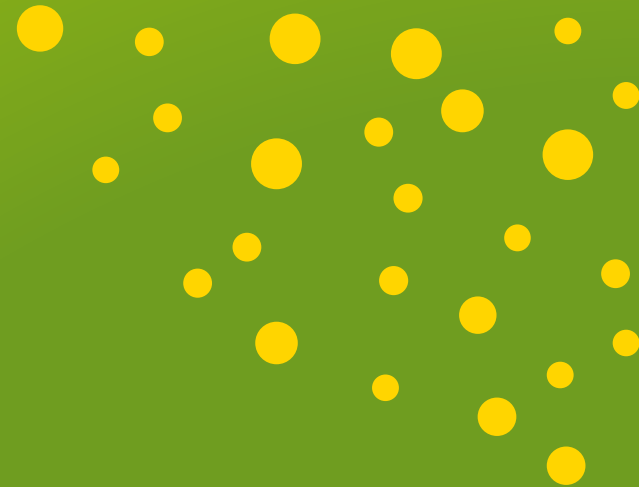
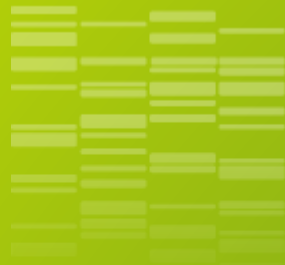
- **~50 persons (40 perm.)**
- **4 teams**



Species studied : Poplars, Douglas Fir, Scot Pine, wild cherry, larches, ash

SUMMARY

1. Poplar rust pathosystems
2. Questions and strategies to identify R factors
3. How to measure resistance components ?
4. Variability for resistance components
5. Genetic mapping: from QTL to QTN
6. Comparative genomics
7. Conclusion: potential uses for breeding

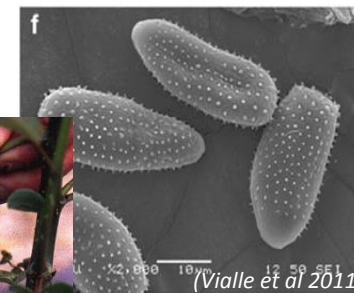


1

Poplars / rusts pathosystems

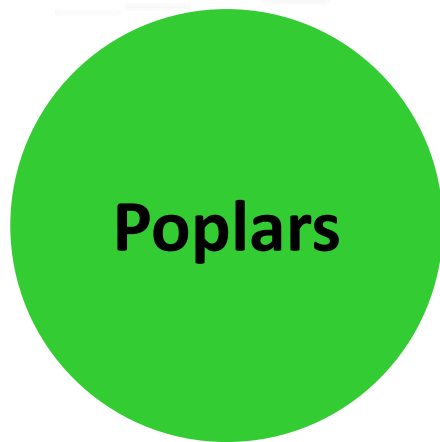
Poplar rusts

- Causes by *Melampsora* spp
- Biotrophic, heterotic cycle.
- Losses in biomass :
 - 32% per year (Dowkiw, 2003)
 - 57% (Steenackers et al. 1996)
- Resistance/tolerance is as major breeding issue
- **Qualitative resistances** deployed in hybrid cultivars overcame

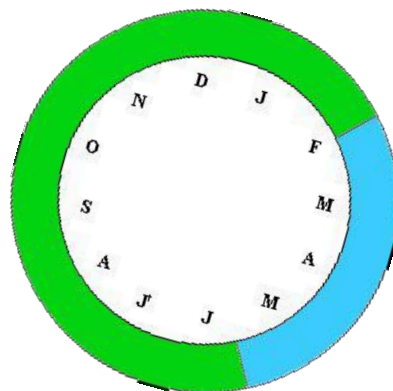


A complex biological cycle ...

... favouring rapid pathogen evolution



Asexual reproduction
Epidemics

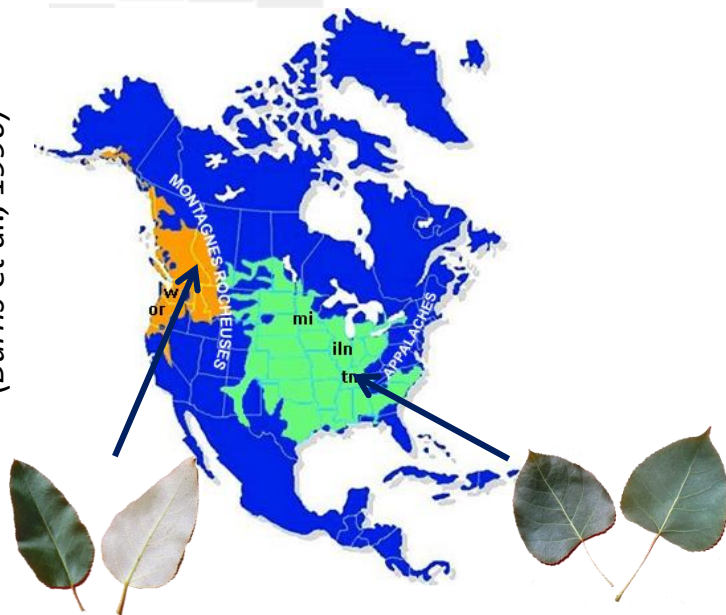


Sexual reproduction



Natural poplars-foliar rusts pathosystems

(Burns et al., 1990)

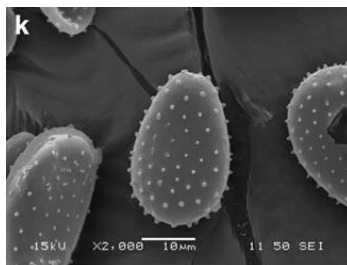


Populus trichocarpa
Melampsora occidentalis

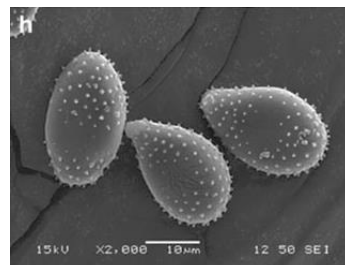
Populus deltoides
Melampsora medusae
f.sp. deltoideae



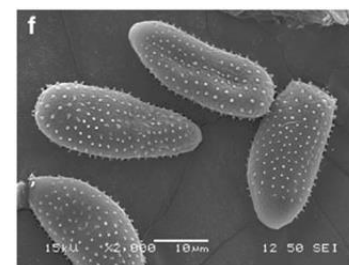
Populus nigra
Melampsora larici-populina



(Vialle et al 2011)



(Vialle et al 2011)



(Vialle et al 2011)

Poplar/rust « exapted » pathosystems

- Use of *Populus* exotic species => showdown of host and pathogen that did not **co-evolved**.
- The interaction is **compatible**



Exapted pathosystem

(Gould et Vrba, 1982; Newcombe 1998)

	<i>Melampsora occidentalis</i>	<i>Melampsora medusae</i> <i>f.sp. deltoideae</i>	<i>Melampsora larici-populina</i>
<i>Populus trichocarpa</i>	natural	exapted	exapted
<i>Populus deltoides</i>	?	natural	exapted
<i>Populus nigra</i>	?	exapted^a	natural

	<i>Pt</i>	<i>Pd</i>	<i>Pn</i>
<i>Pt</i>	○	○	○
<i>Pd</i>	○	○	○
<i>Pn</i>	○	✗	○

Possible interspecific hybridation both in host and pathogen

Mo x *Mmd*



Melampsora x columbiana

^a Pinon et Frey, 2005, ? : no published data



2

Questions and strategies to identify R factors



➤ Questions

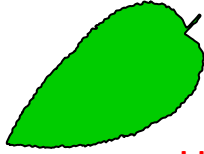
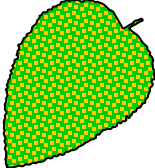
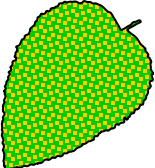
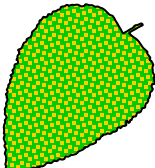
- What is the variability for resistance in the different type of pathosystems (natural/exapted)?
- What is the genetic determinism (loci and genes)?

➤ Strategies/approaches

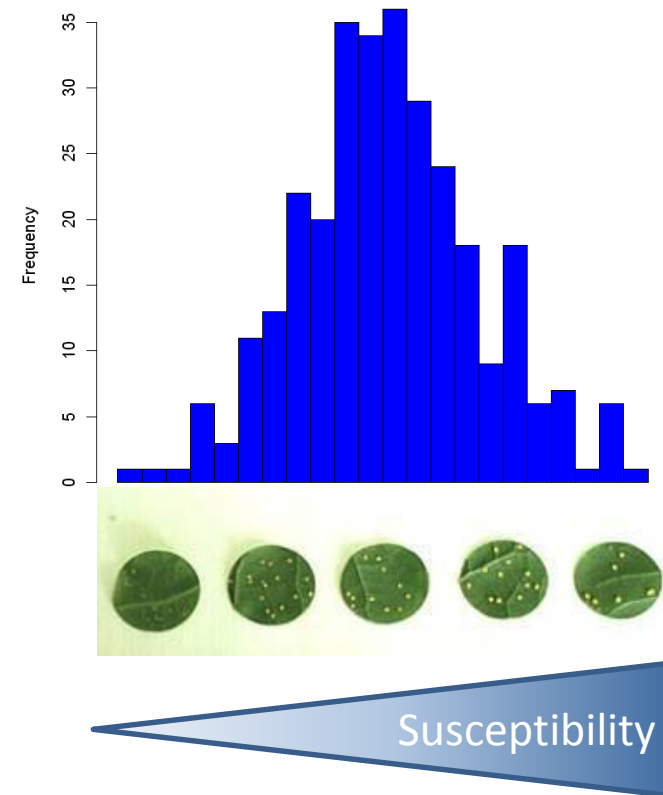
- Identify resistance components
- Evaluate variability for these components
- Map genetic factors : from QTLs to QTNs.
- Comparative genomics

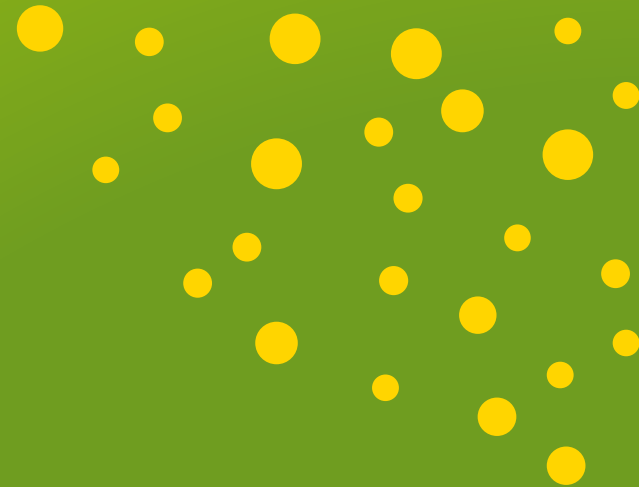
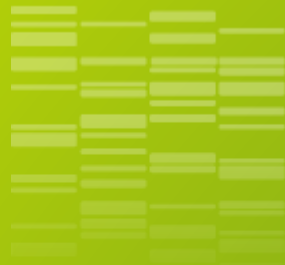
A simple classification of resistance types

Qualitative resistance
Gene for gene hypothesis
 (Flor, 1942)

		Pathogen	
		Avr/Avr Avr/vir	Vir/vir
Plant			
R/R or R/r	 +HR		
r/r			

Quantitative resistance









3

How to measure resistance components ?

3. How to measure resistance components ?

Qualitative resistance

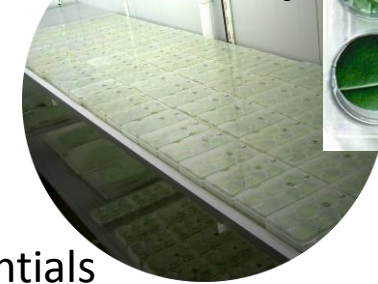
Plant	Pathogen	
	Avr/Avr Avr/vir	Vir/vir
R/R or R/r	 +HR	
r/r		

Specific

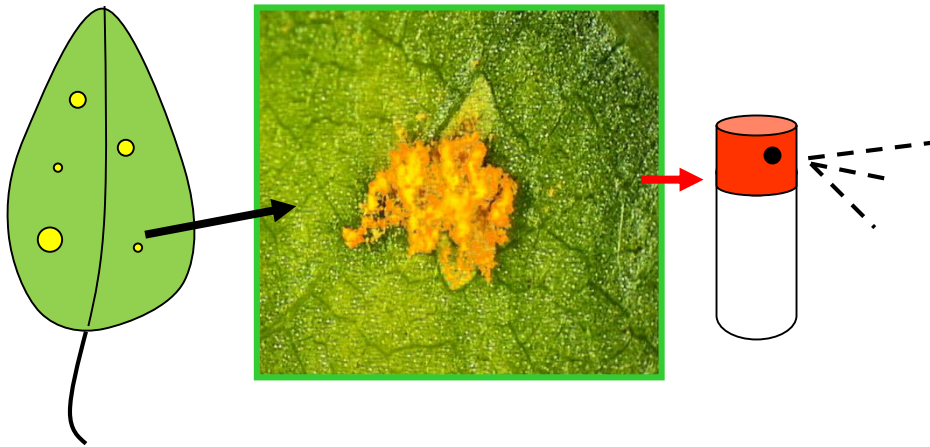


Control and characterise
Pathogen variability









In laboratory



1 uredia = 1 clone of uredospores



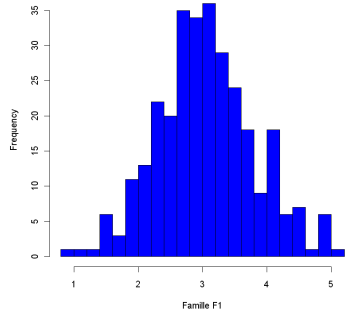
Host differentials

cv. 'Ogy'	R1	
cv. 'Candicans'	R2	
cv. 'Brabantica'	R3	
cv. 'Unal'	R4	
cv. 'Rap'	R5	
87B12	R6	
cv. 'Beaupré'	R7	
cv. 'Hoogvorst'	R8	

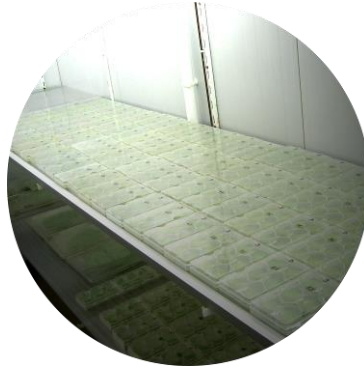
Qualitative resistances / virulences well documented in exapted pathosystem :
Also for TxD hybrids/Mxc (Newcombe et al. 2001) *P. deltoides*/Mlp

3. How to measure resistance components ?

Epidemiological components of quantitative resistance



In laboratory

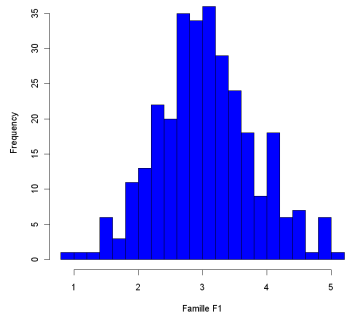


Field

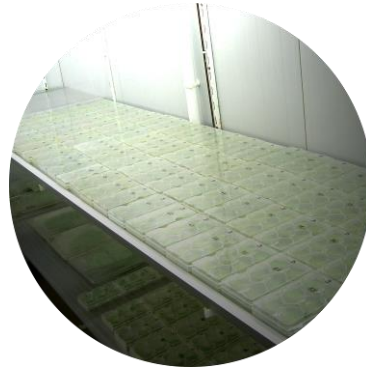


3. How to measure resistance components ?

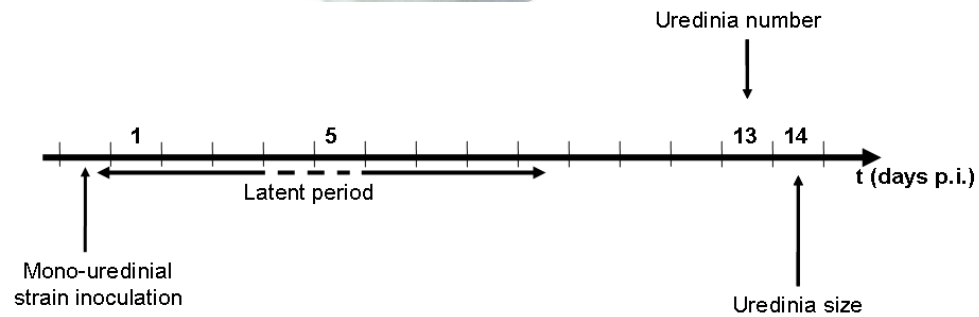
Epidemiological components of quantitative resistance



In laboratory

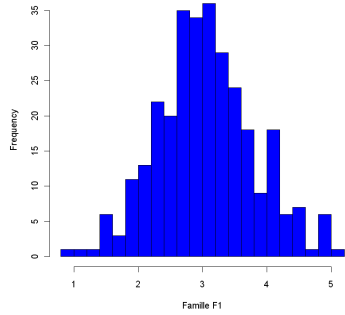


Field

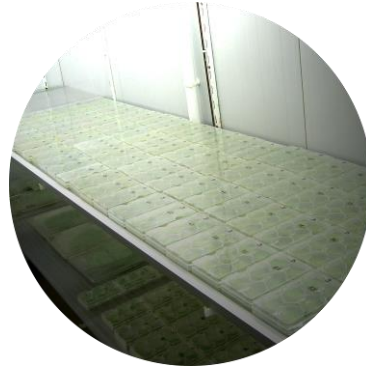


3. How to measure resistance components ?

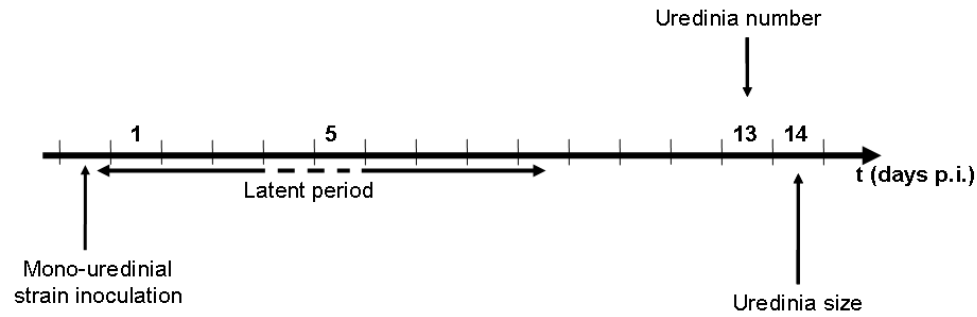
Epidemiological components of quantitative resistance



In laboratory



Field

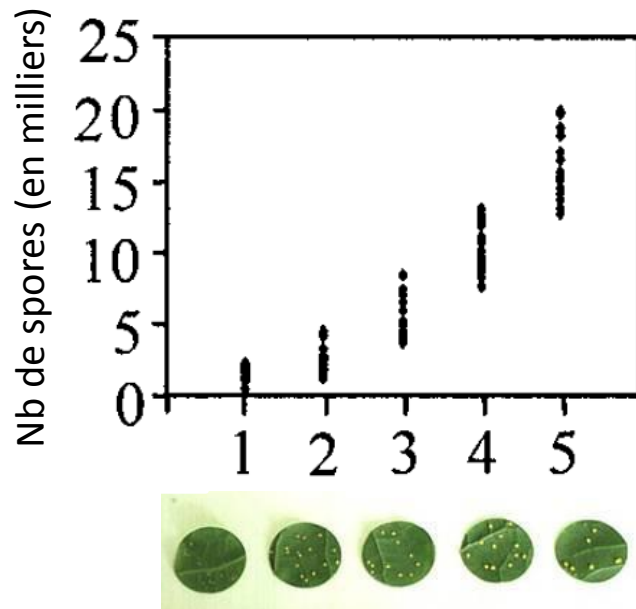


Rust score on the most infected leaf

Epidemiological components of quantitative resistance

In laboratory

1 infection cycle

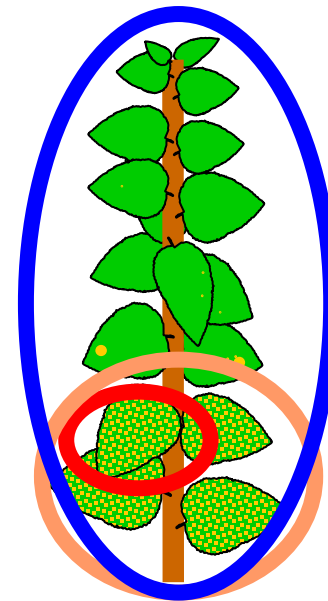


(Dowkiw et al 2003)

Measure of interaction on
the pathogen

Field

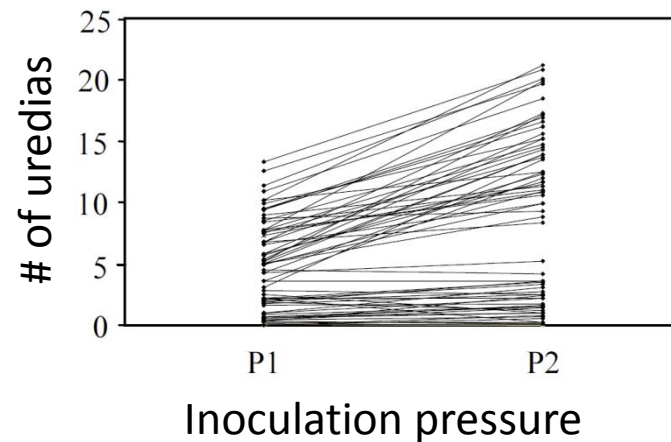
several infection cycles



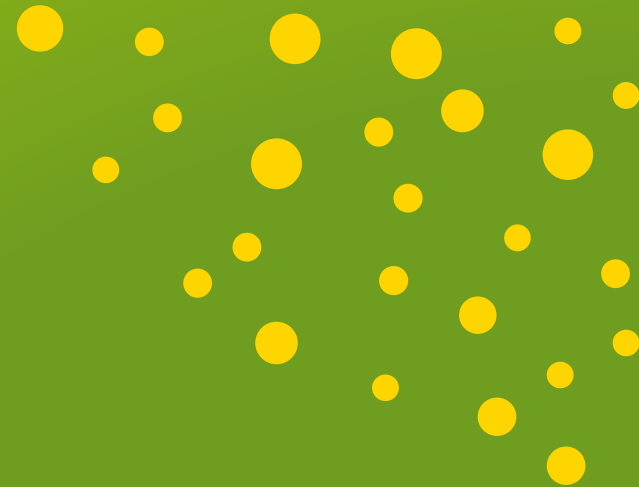
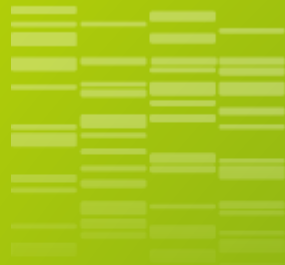
Measure of interaction on
the host plant
(symptoms, leaf losses)

Epidemiological components of quantitative resistance

- Conditions of inoculation, scales to be tuned depending on the host and on level of infection:
 - hybrids/pure species
 - Qualitative R / quantitative R
 - period of evaluation (field)
 - age of plants
- We are sure about susceptibility not resistance



(Dowkiw et al 2003)



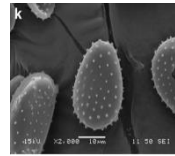
4

Variability for resistance components

4. Variability for resistance components

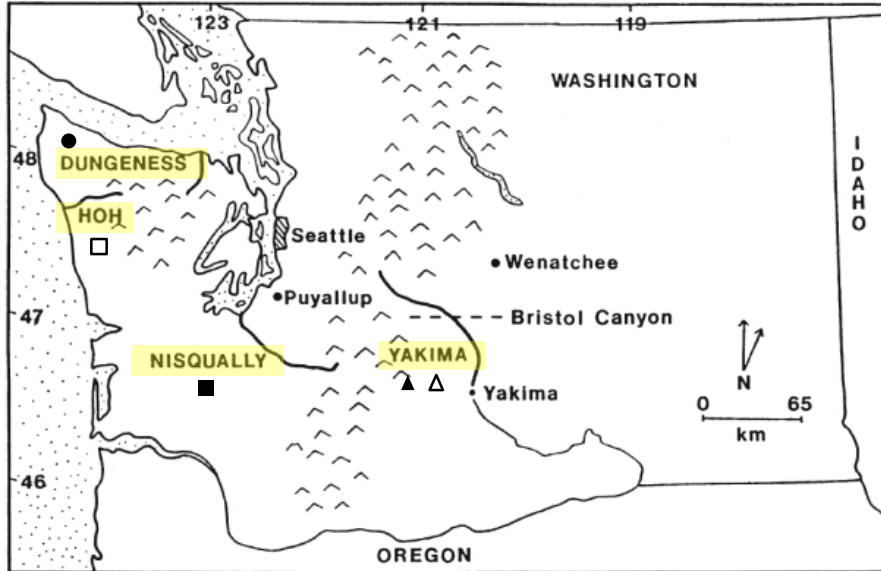
Populus trichocarpa

Natural pathosystems

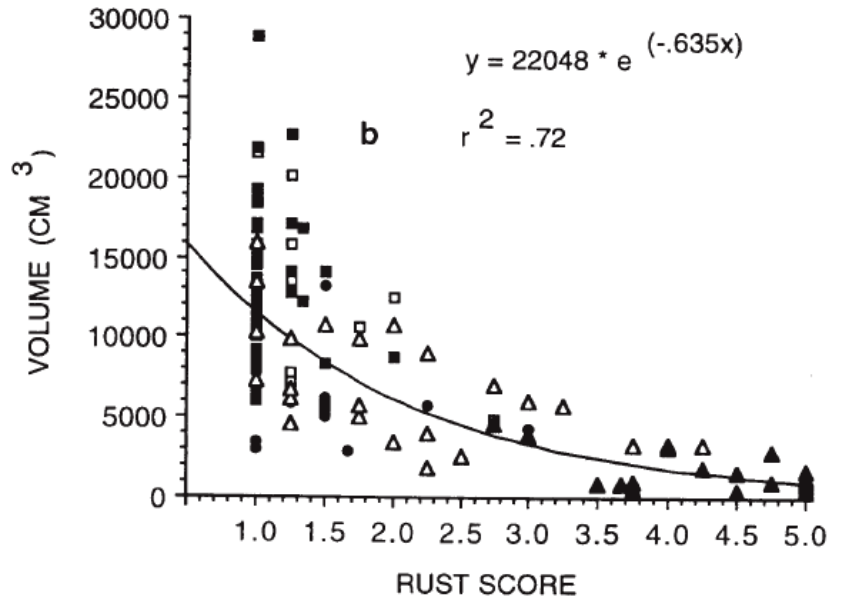


(Vialle et al 2011)

Melampsora occidentalis



5 provenances, 126 clones
Washington state



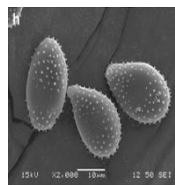
- Field evaluation
- Highly resistant genotypes
- Variability geographically structured

4. Variability for resistance components



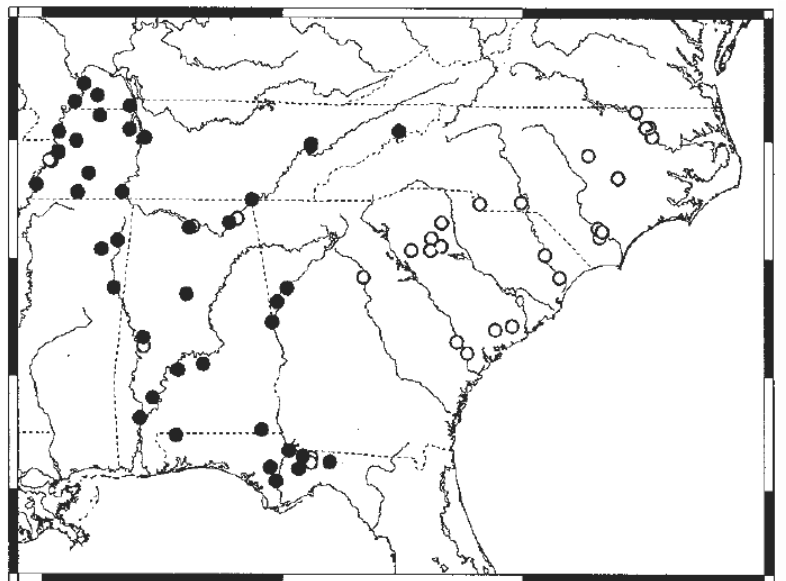
Populus deltoides

Natural pathosystems

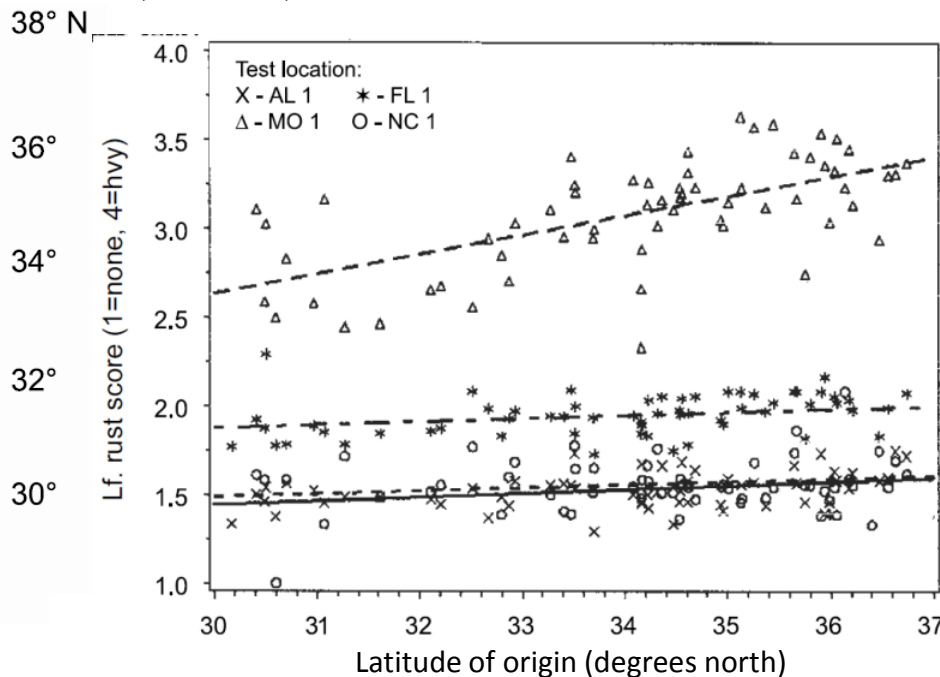


(Vialle et al 2011)

Melampsora medusae
f.sp. deltoideae



90° W 85° 80° 75°

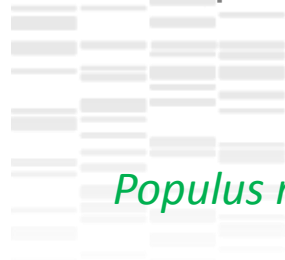


62 provenances
Eastern USA
4 clonal trials

➤ Variability geographically structured

(Land and Jeffreys, 2006)
(Nelson and Tauer, 1986)
(Hamelin et al 1993, 1992)

4. Variability for resistance components

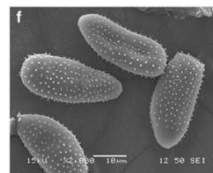


Populus nigra



(Vialle et al 2011)

Natural pathosystems

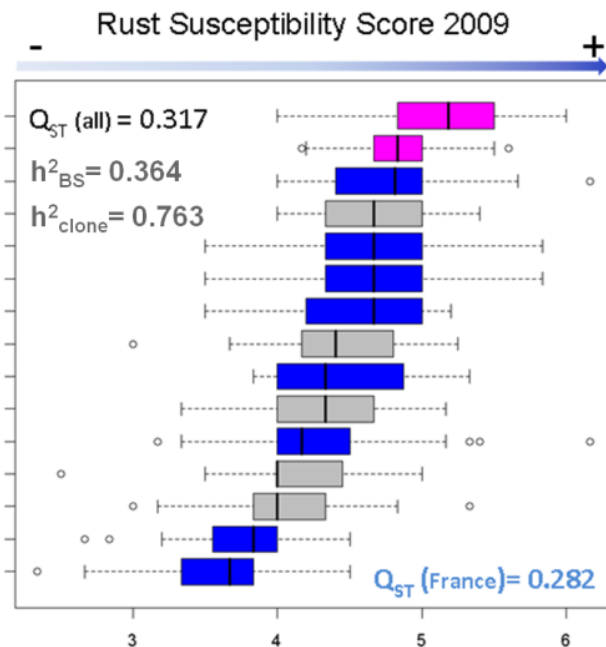


(Vialle et al 2011)

Melampsora larici-populina



14 metapopulations, 1141 clones
Western Europe



- No immune genotypes but some very resistant.
- Variability geographically structured

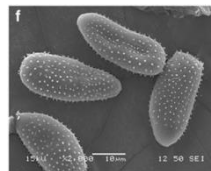
4. Variability for resistance components



Populus deltoides

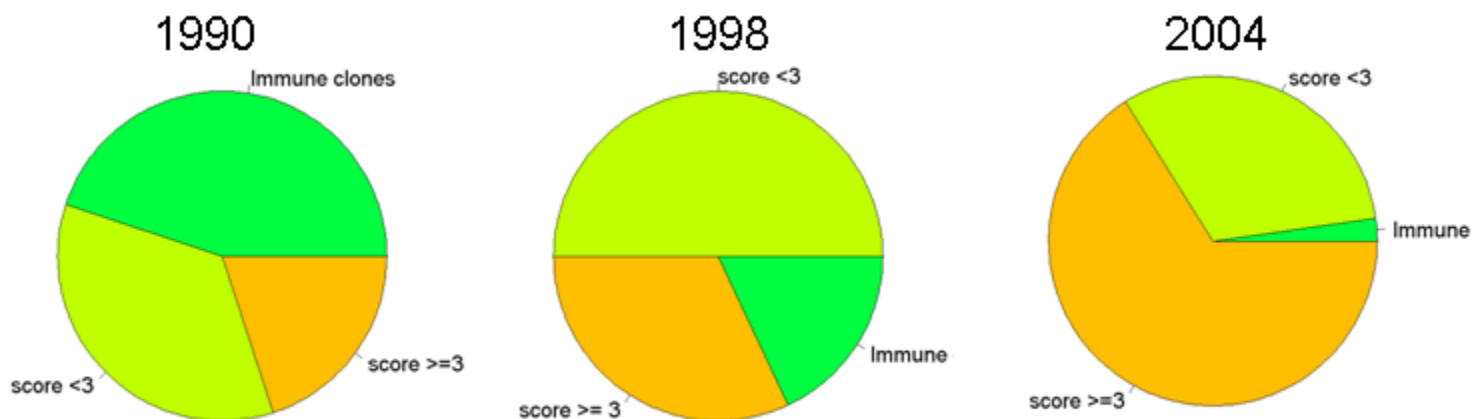


Exapted pathosystems



(Vialle et al 2011)

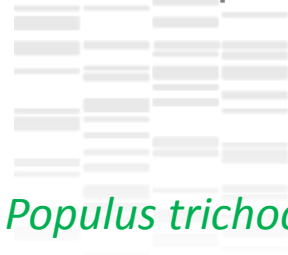
Melampsora larici-populina



545 *P. deltoides* genotypes – Field rust susceptibility (Orléans)

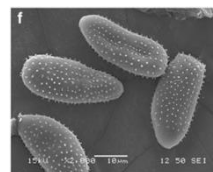
- Qualitative resistances
- Erosion of resistance over time

4. Variability for resistance components



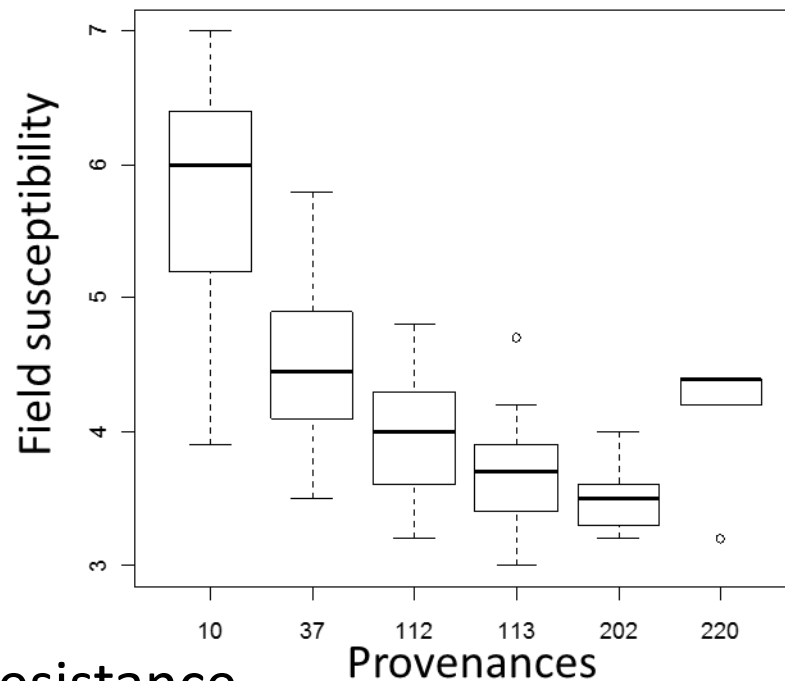
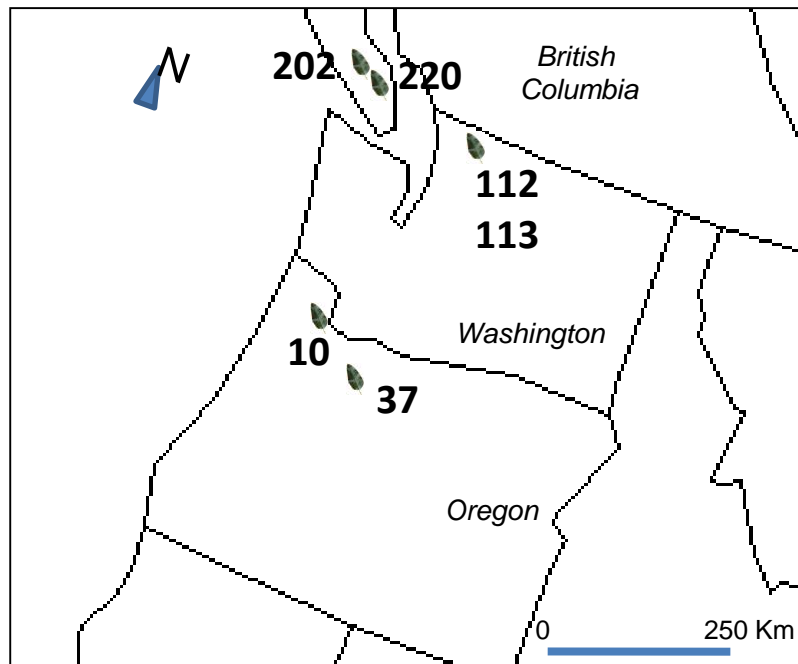
Populus trichocarpa

Exapted pathosystems



Melampsora larici-populina

(Vialle et al 2011)



6 provenances, 102 clones
Clonal trial, Orléans (F)

- Quantitative resistance
- Strong geographic structuration
- Idem *P. trichocarpa* / Mxc (La Mantia et al 2013)

(Bastien et al, unpublished)

.024

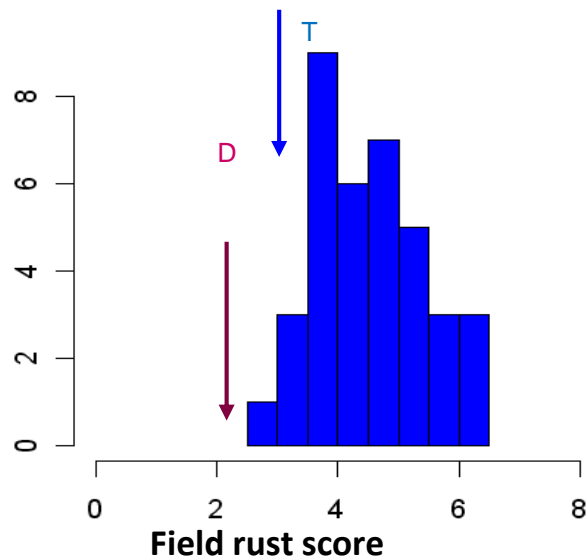
4. Variability for resistance components



Exapted pathosystems

Case of interspecific hybridization

Hybrides **DxT** / **DxN** vs *Mlp*



Negative heterosis

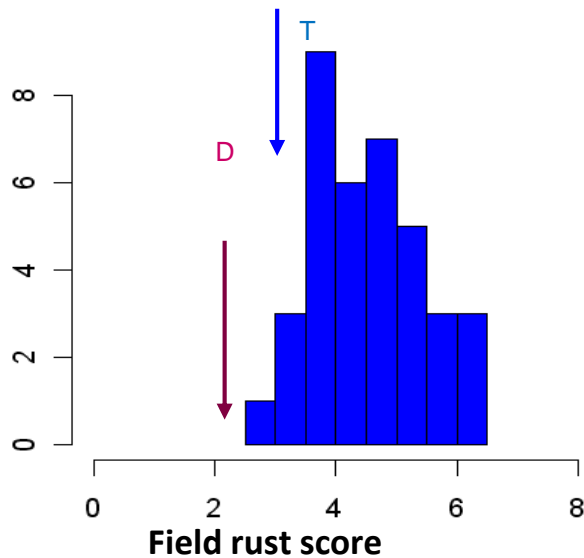
4. Variability for resistance components



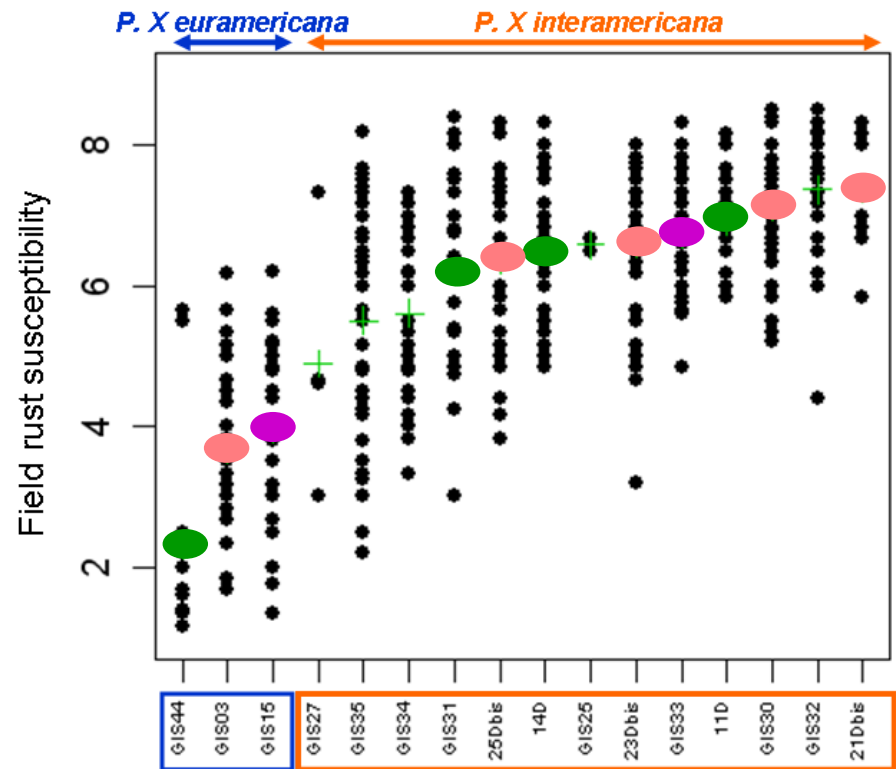
Exapted pathosystems

Case of interspecific hybridization

Hybrides **DxT** / **DxN** vs **Mlp**



Negative heterosis

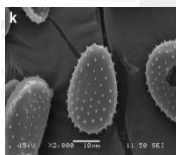


16 F₁ families involving common *P. deltoides* female parents

4. Variability for resistance components

To sum up about variability !

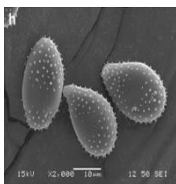
Natural pathosystems



(Vialle et al 2011)

P. trichocarpa (Dunlap and Stettler, 1998)

Mo

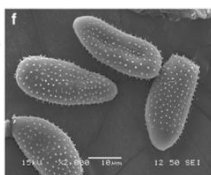


(Vialle et al 2011)

P. deltooides (Land and Jeffreys, 2006)

Mmd

(Nelson and Tauer, 1986)
(Hamelin et al 1993, 1992)



(Vialle et al 2011)

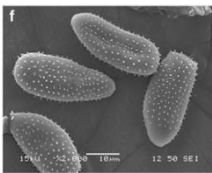
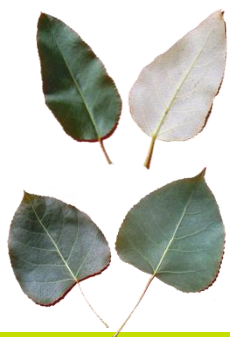
P. nigra (Bastien et al, in prep.)

Mlp

(Légionnet et al, 1999)

- Some genotypes strongly resistant, no qualitative resistance
- Quantitative resistance strongly geographically structured

Exapted pathosystems



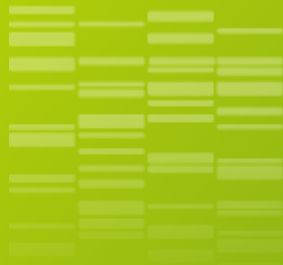
(Vialle et al 2011)

P. deltooides (Bastien et al, unpublished)

P. trichocarpa (La Mantia et al 2013)

Mlp, Mxc

- Qualitative resistances in *P. deltooides* almost all overcome after 15 years
- Quantitative resistance in both sp., structured in *P. trichocarpa*

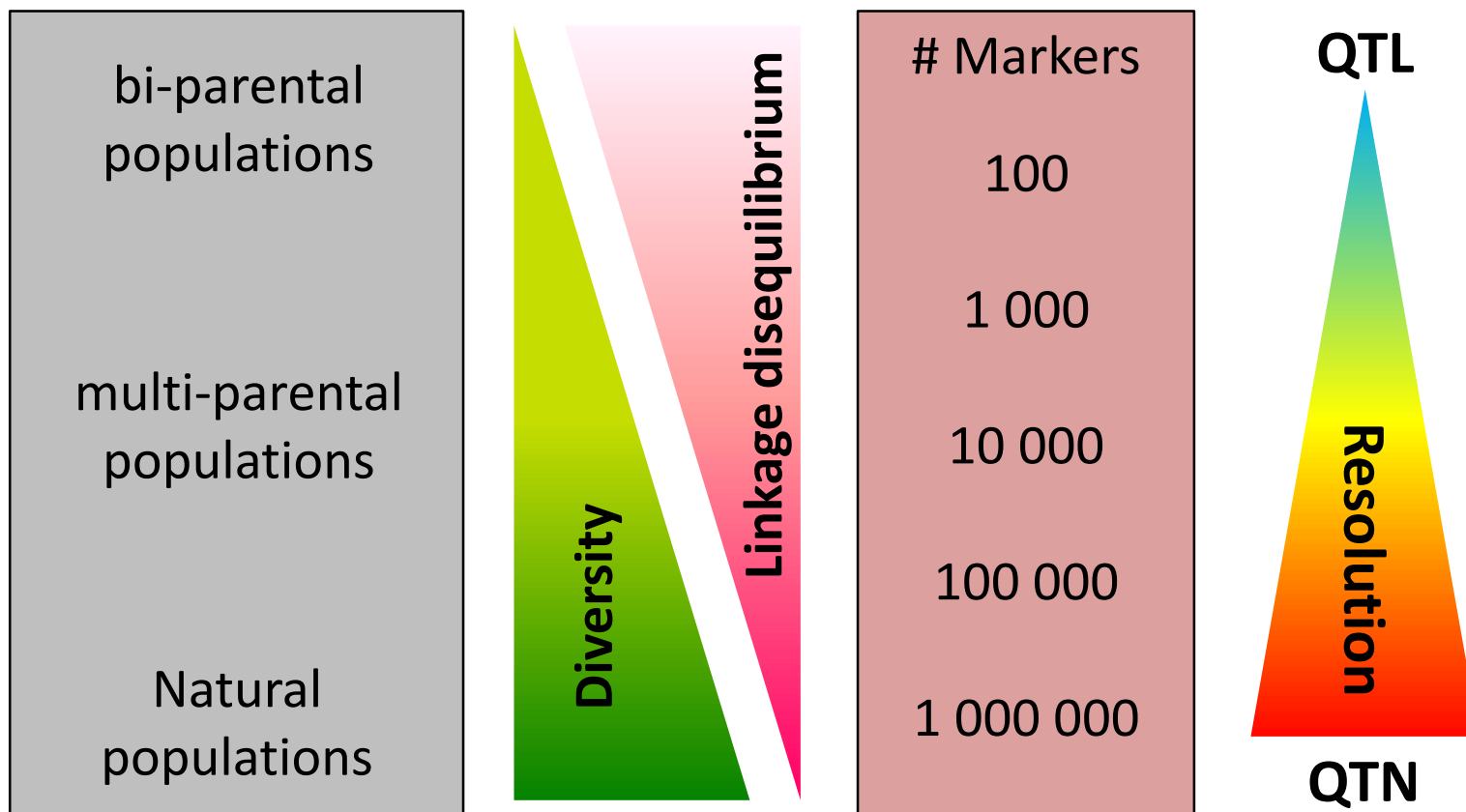


5

Genetic mapping: from QTL to QTN

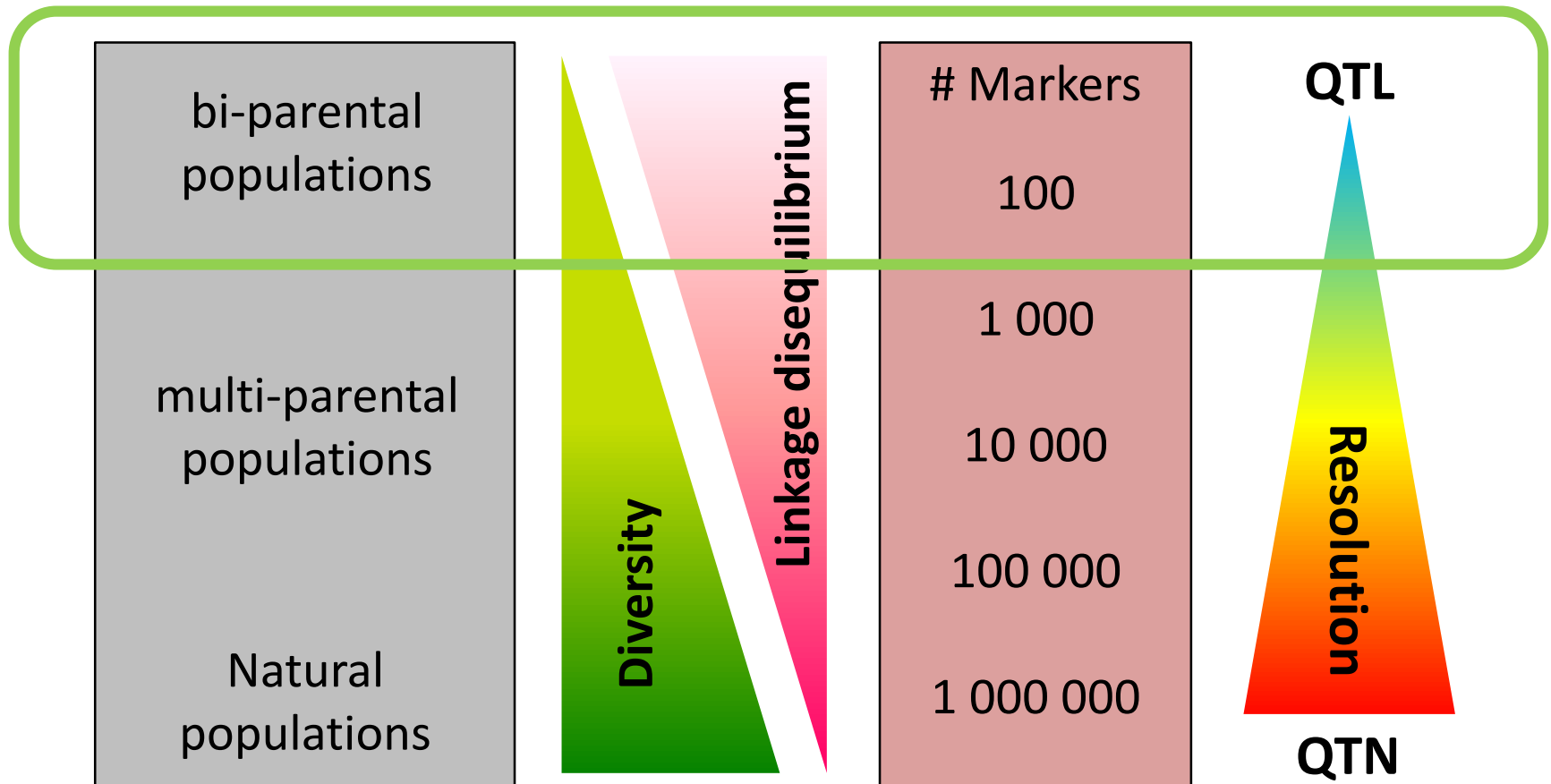
Strategies to study genetic architecture of resistance

From QTLs to QTNs



Strategies to study genetic architecture of resistance

From QTLs to QTNs



Natural pathosystem

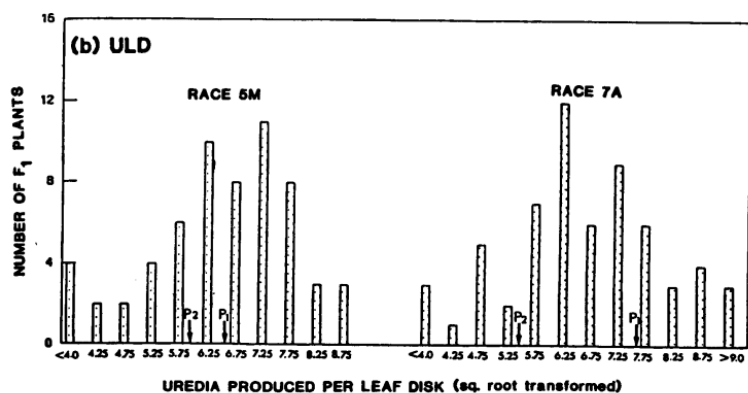
bi-parental populations

P. deltooides x *P. deltooides* F1

2 strains *Mmd*

P. nigra x *P. nigra* F1

5 strains *Mlp*



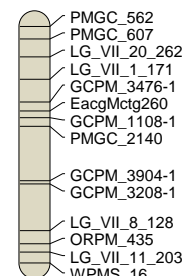
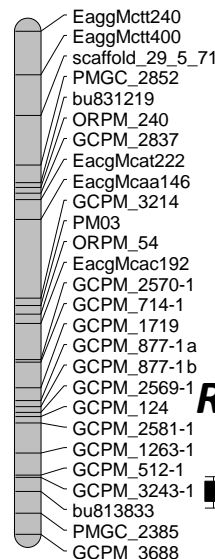
(Prakash & Heather, 1989)

- Qualitative resistance (locus *Lrd1* ; Tabor et al, 2000)
- Genetic variability for quantitative resistance (Prakash & Haether 1989a)
- Interaction genotype/strain (Prakash & Heather 1989b, Tabor et al 2000)

No map localisation

Chro 1

Chro 7

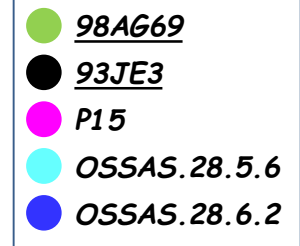


RMlp2

86%

RMlp1

61% 12%

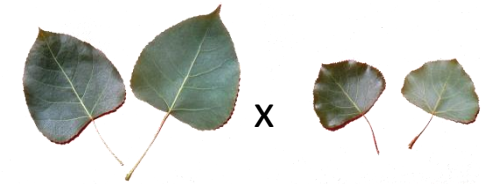
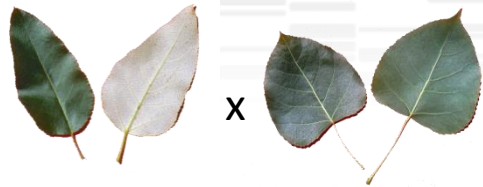


- 20 QTLs (2% - 86.2% variance explained)
- 2 major QTLs (chro 1 & 7, *RMlp1*, *RMlp2*)
- QTLs and their effect are strain specific (no QTL for OSSAS.28.5.6).
- Colocalisation with R-genes clusters
- « HR » mainly controlled by 1 locus

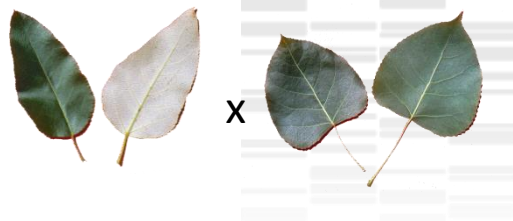
Exapted pathosystem

bi-parental populations

Mainly hybrid families used



Family	Type	Taxon	Challenged against
Family 331	F2	<i>P. trichocarpa</i> x <i>P. deltoides</i>	<i>Mmd</i> <i>Mlp</i>
Family 545	F1	<i>P. trichocarpa</i> x <i>P. deltoides</i>	<i>Mcx</i>
Family 54	F1	<i>P. deltoides</i> x <i>P. trichocarpa</i>	<i>Mlp</i>
Family 87001	F1	<i>P. deltoides</i> x <i>P. trichocarpa</i>	<i>Mlp</i>
Family 87002	F1	<i>P. deltoides</i> x <i>P. nigra</i>	



Exapted pathosystem

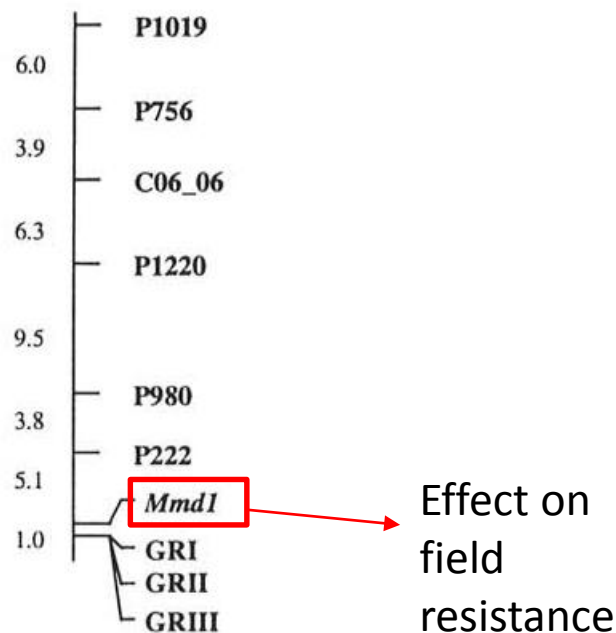
bi-parental populations

Family 331, *P. trichocarpa* x *P. deltoides*

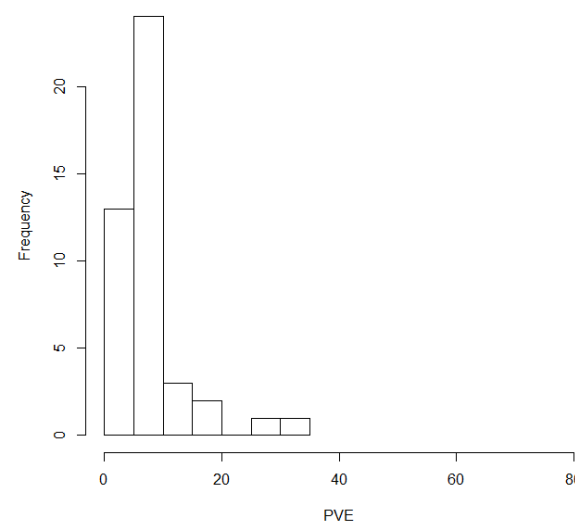
1 *Mmd* strain & field assessment

5 *Mlp* strains

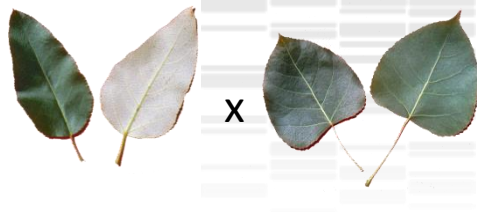
Chromosome 4



- 17 regions (44 QTLs)
- The largest on chro 15
- Strain specific QTLs



The qualitative R against *Mmd* is not working against *Mlp* !



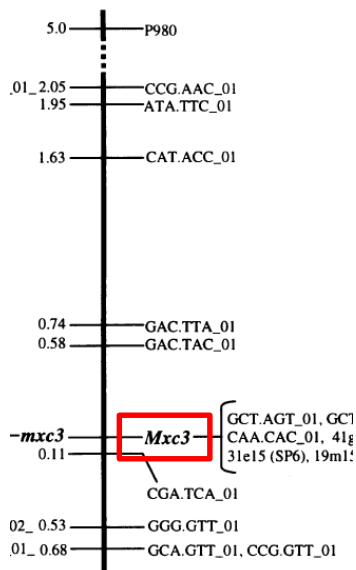
Exapted pathosystem

bi-parental populations

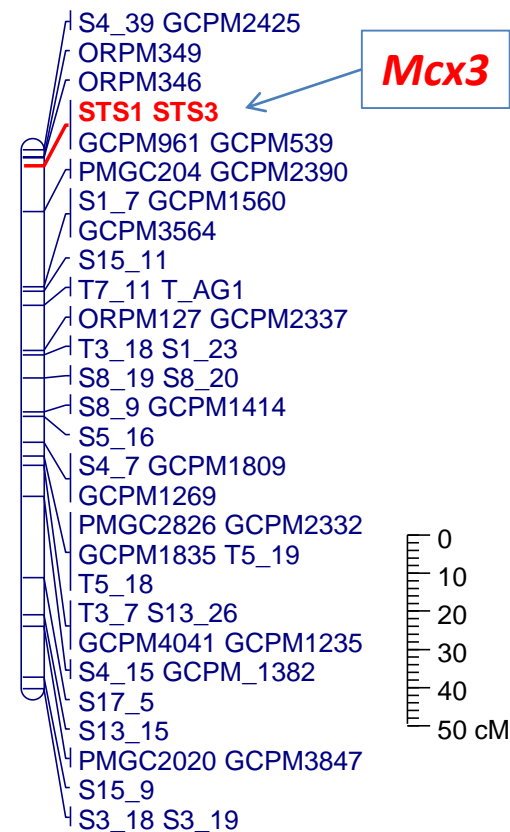
Family 545, *P. trichocarpa* x *P. deltoides*

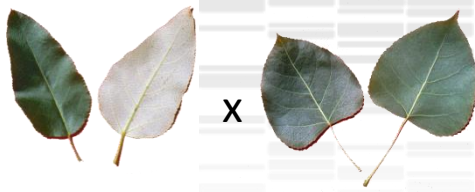
1 *Mxc* strain

Fam 13



Confirmed location on
 Chromosome 4



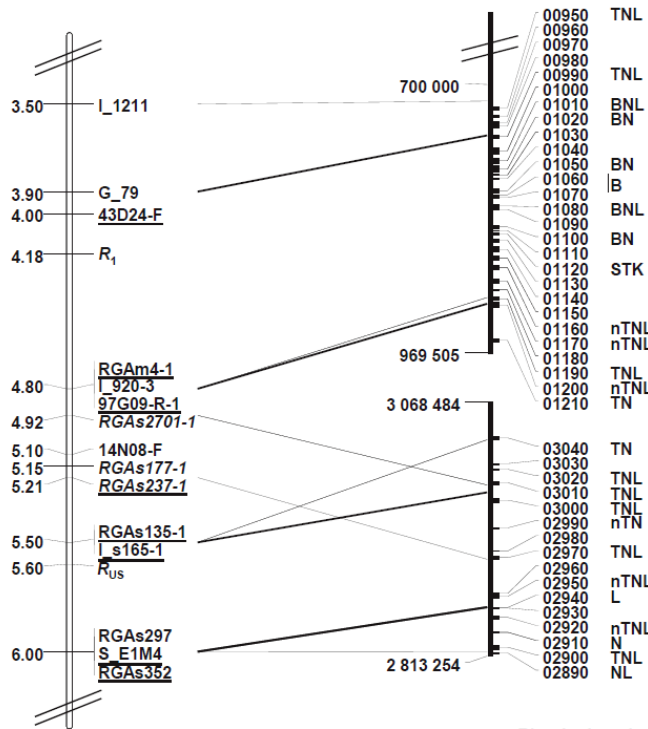
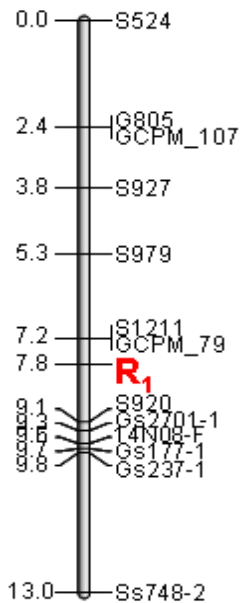


Exapted pathosystem

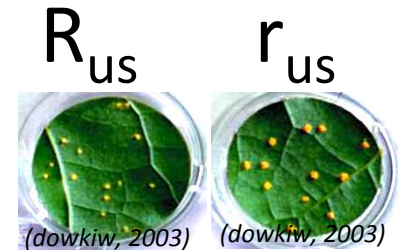
bi-parental populations

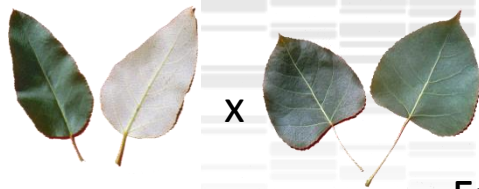
Family 54 *P. deltooides* x *P. trichocarpa*

5 *Mlp* & field assessment



- 2 major factors on Chromosome 19
 - R_1 inherited from *P. deltooides*
 - R_{US} from *P. trichocarpa*
- Several minor QTLs
- Specificity
- Fine and physical mapping, cloning R_{US}
- In major R-gene cluster





Exapted pathosystem

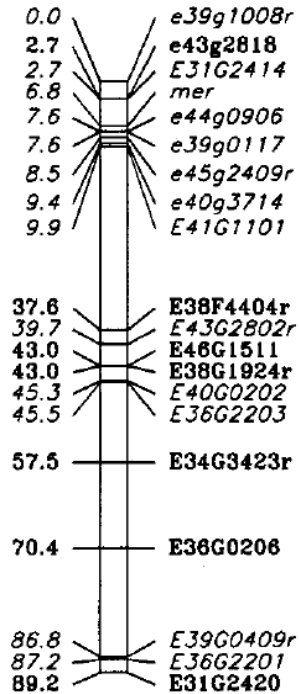
bi-parental populations

Family 87001 *P. deltoides* x *P. trichocarpa*

Family 87002 *P. deltoides* x *P. nigra*

3 *Mlp* strains

Chromosome 19

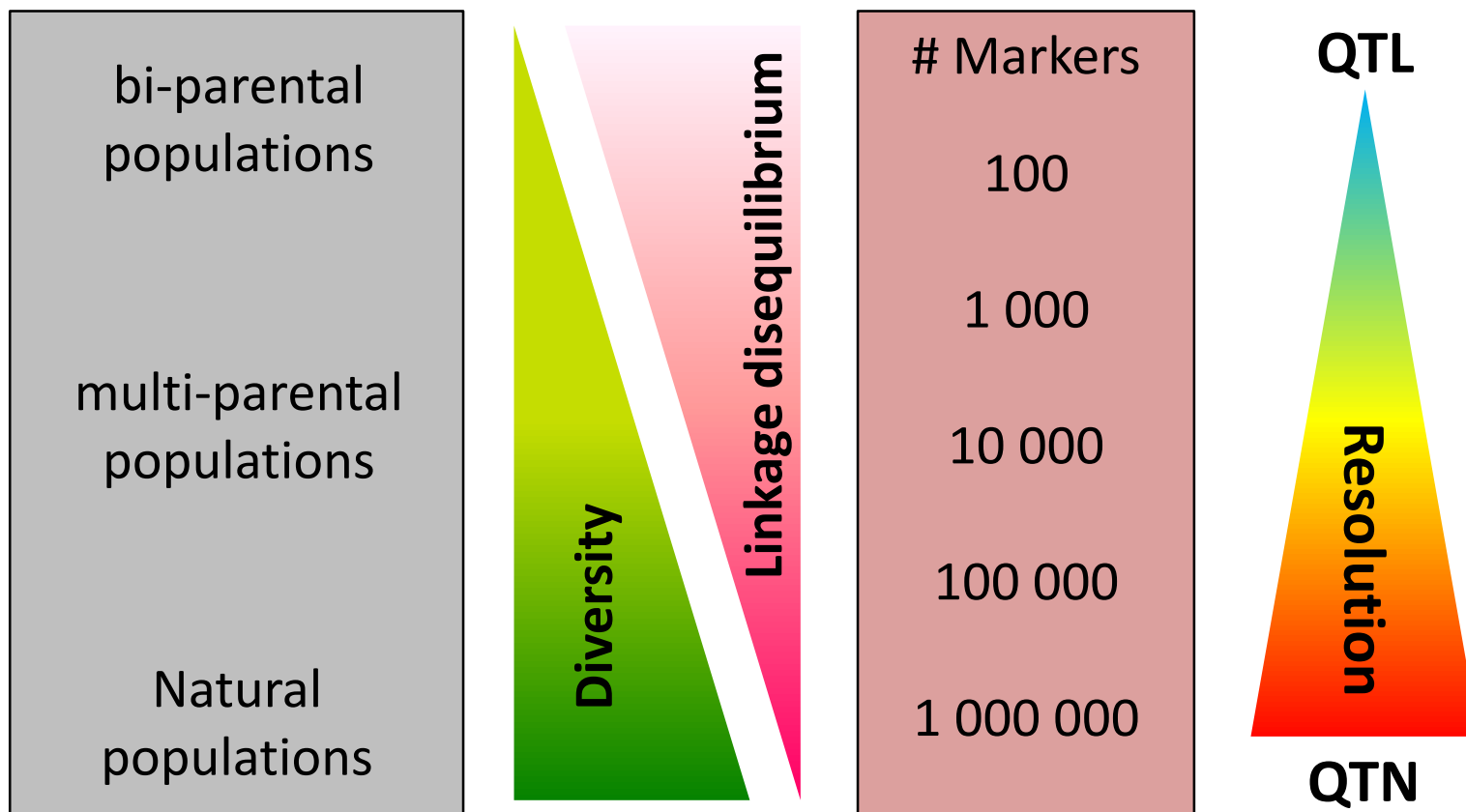


Mer locus inherited from *P. deltoides*

Fine and physical mapping, cloning failed

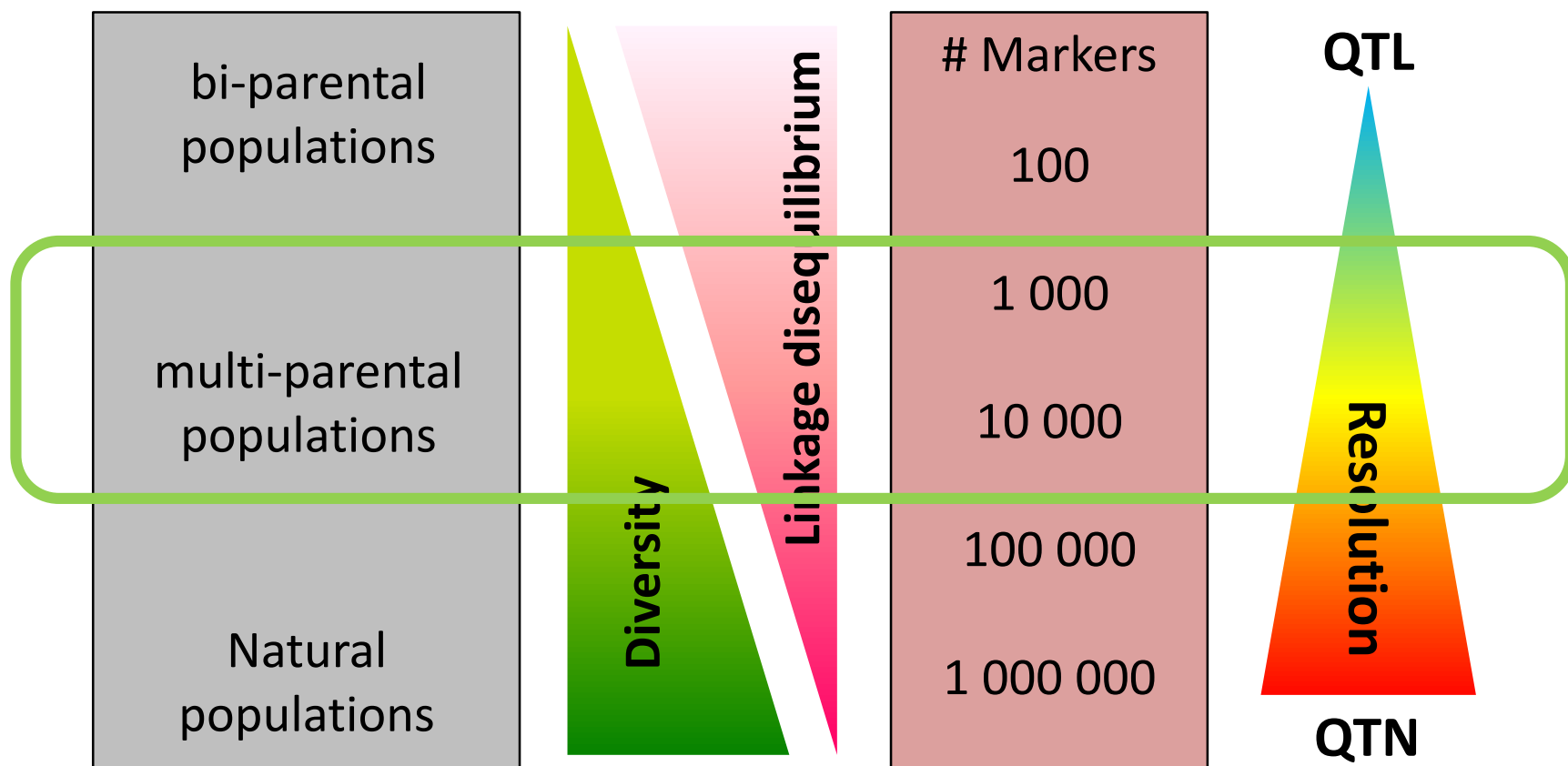
Strategies to study genetic architecture of resistance

From QTLs to QTNs



Strategies to study genetic architecture of resistance

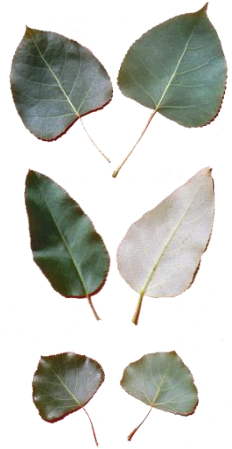
From QTLs to QTNs





Natural and exapted pathosystem

multiparental populations



INRA, C. Vialle, 2011

14 x 14 factorial mating design

	D ₅	T ₄	N ₅
D ₅	Dark Green	Light Blue	Light Purple
T ₄	Light Blue	Dark Green	White
N ₅	Grey X	White	Bright Green

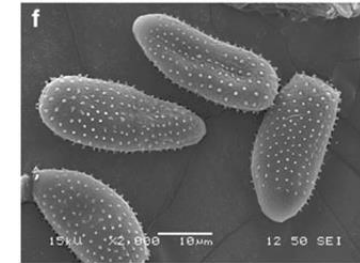
118 FS families

3480 clones

INRA
1988-2000

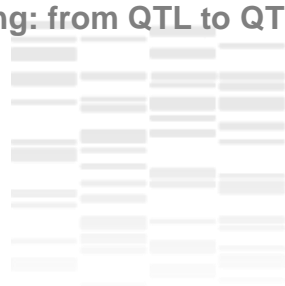
VS.

Melampsora larici-populina



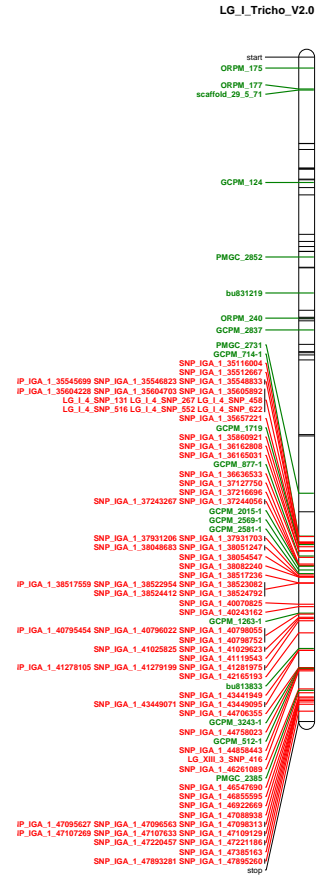
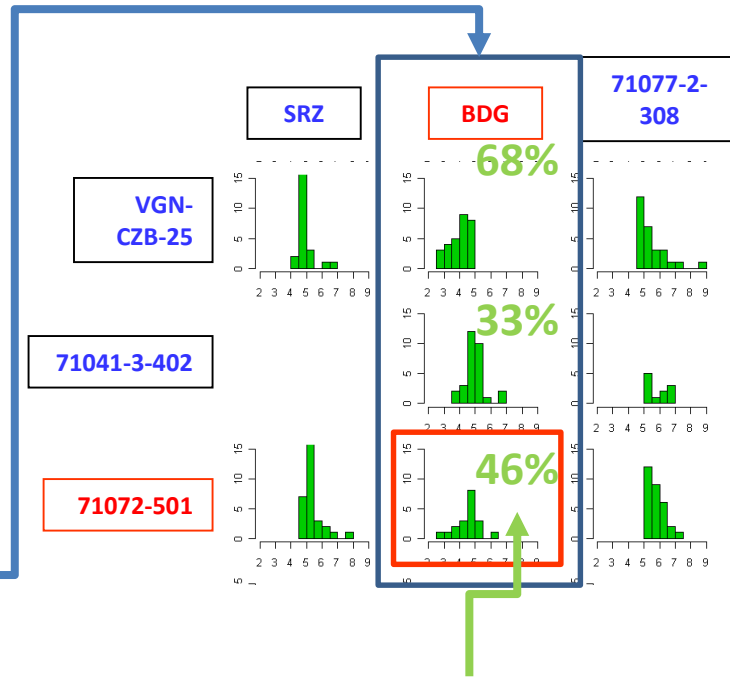
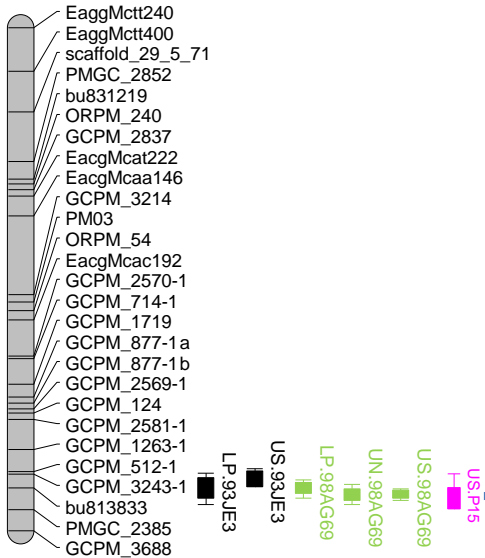
(Vialle et al 2011)

- Several characterized strains
- Field trials



Natural pathosystem multiparental populations

Chromosome 1



- In each family, markers explaining the variation for US
- The region of the QTL has been densely in markers (72 SNP on 11 Mb)
- Validation for strain 98AG69

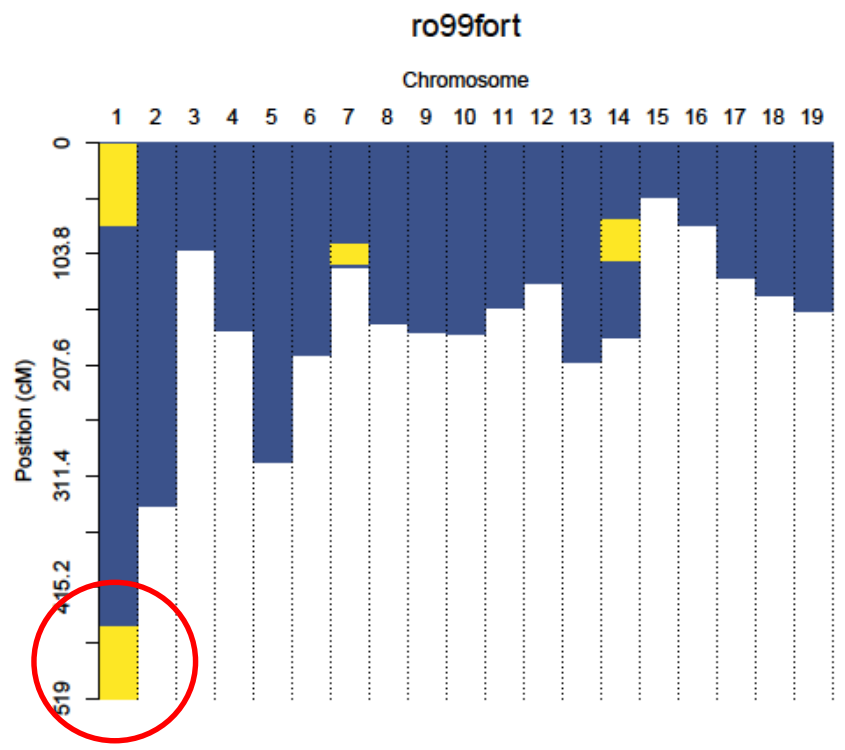
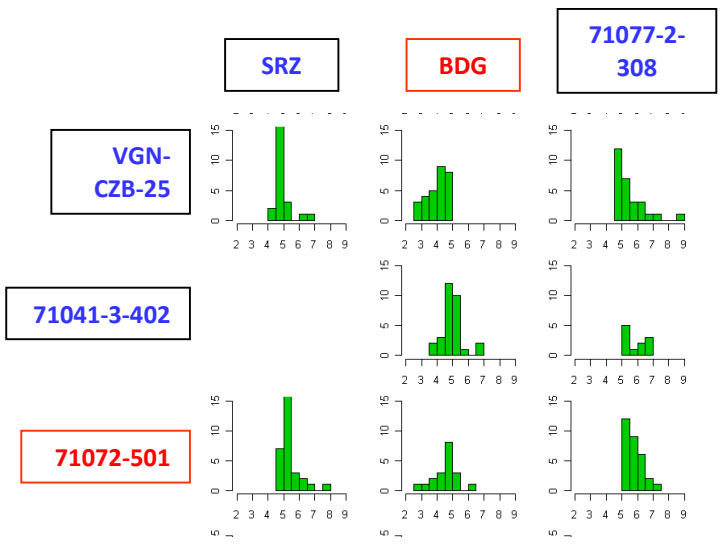


Natural pathosystem

multiparental populations

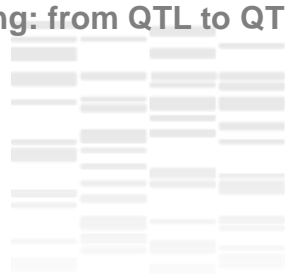
QTL mapping in complex pedigree using FlexQTL (Bink et al. Univ. Wageningen)

Rust scoring in field trial



Previously detected

5. Genetic mapping: from QTL to QTN



Exapted pathosystem

multiparental populations

2 *Mlp* strains

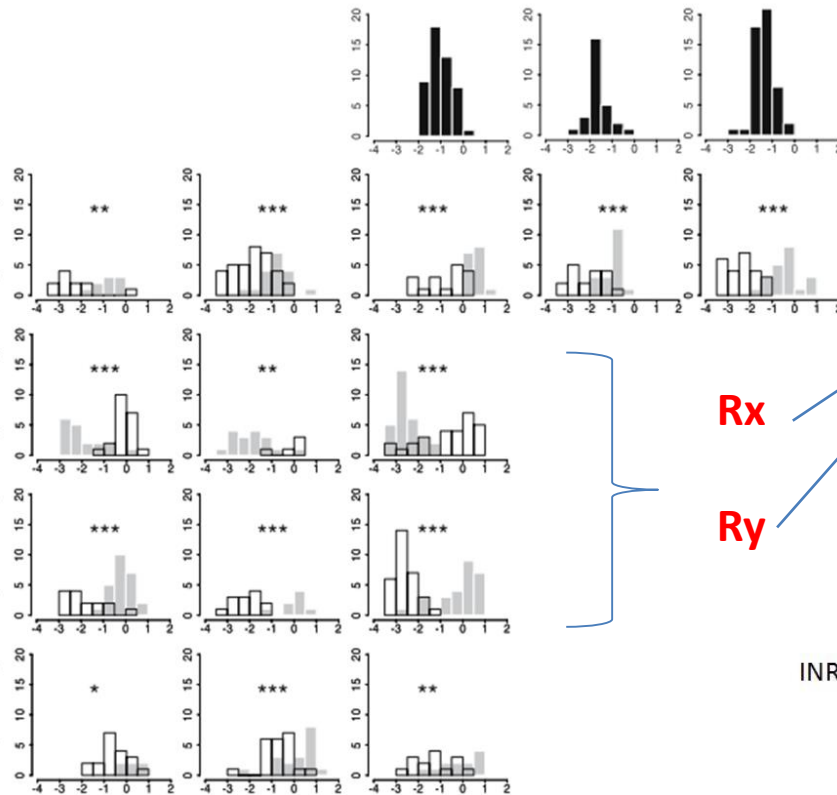
Scaffold_19

P. trichocarpa male parent

36-100 19-77 101-74 03-086 10-302

P. deltoides female parent

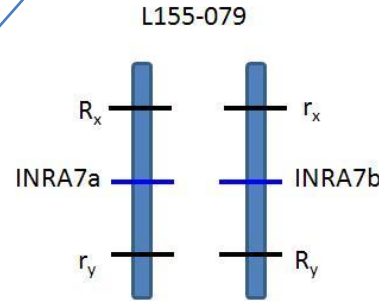
M170-3
73028-62 (93JE3)
L155-079 (93CV1)
(98AG69)
TNS060-42 (93JE3)



R1
(slide 31)

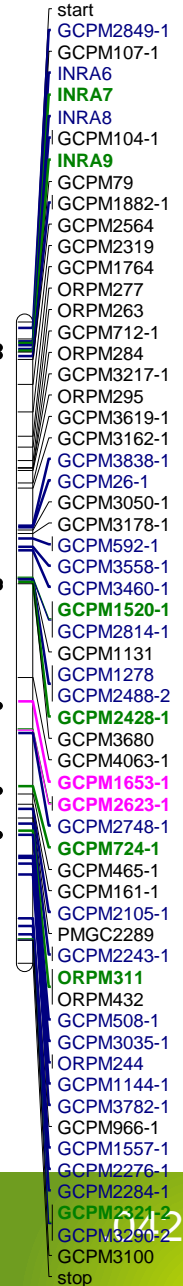
Rx

Ry



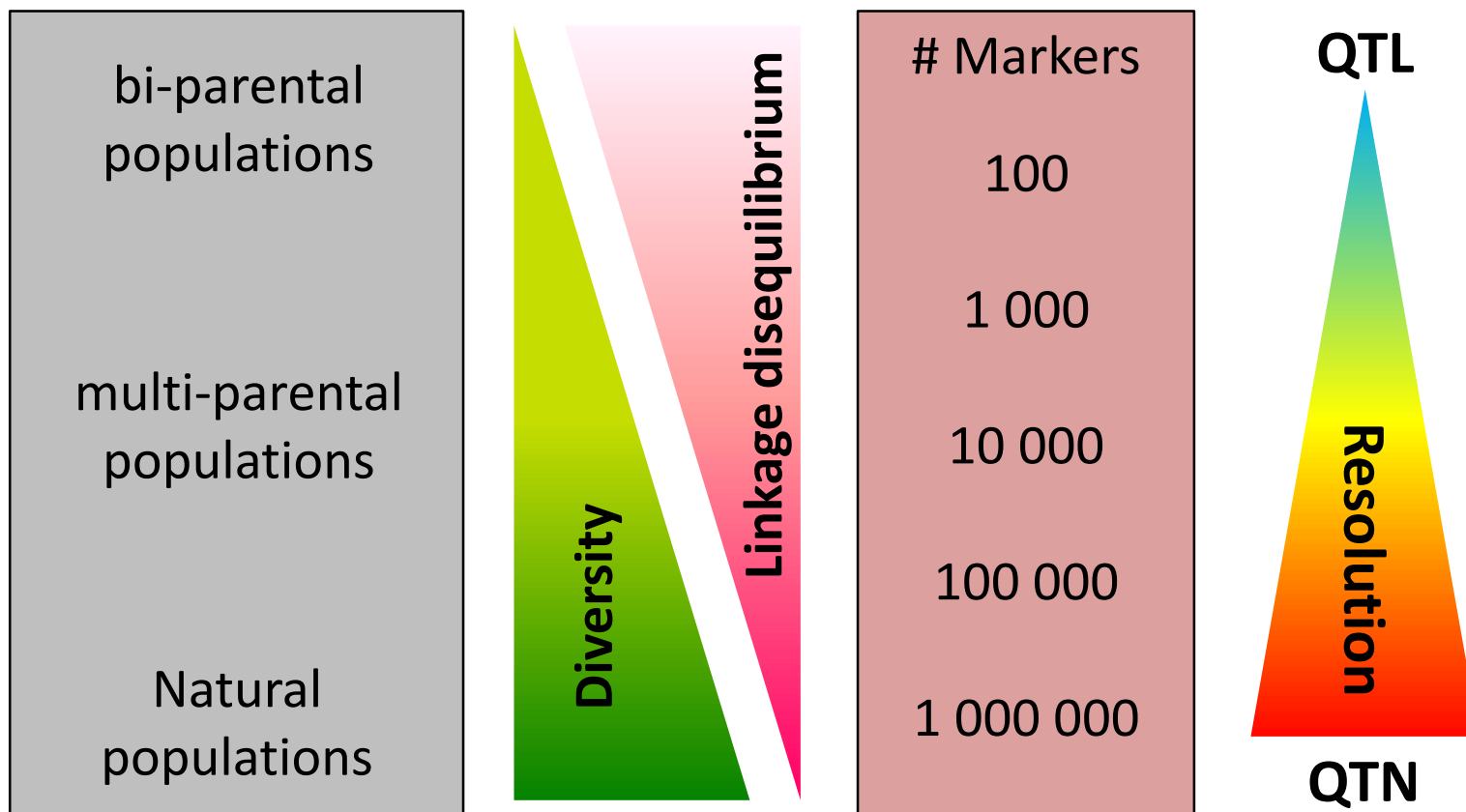
2 additional loci linked in repulsion

- Comp.E4.98A.G6!
- INRA7
- rcomp.E2.93CV1
- INRA9
- GCPM2428-1
- GCPM1520-1
- GCPM1853-1 (GCPM2623-1) (GCPM2623-2)
- ORPM433
- ORPM311
- GCPM724-1



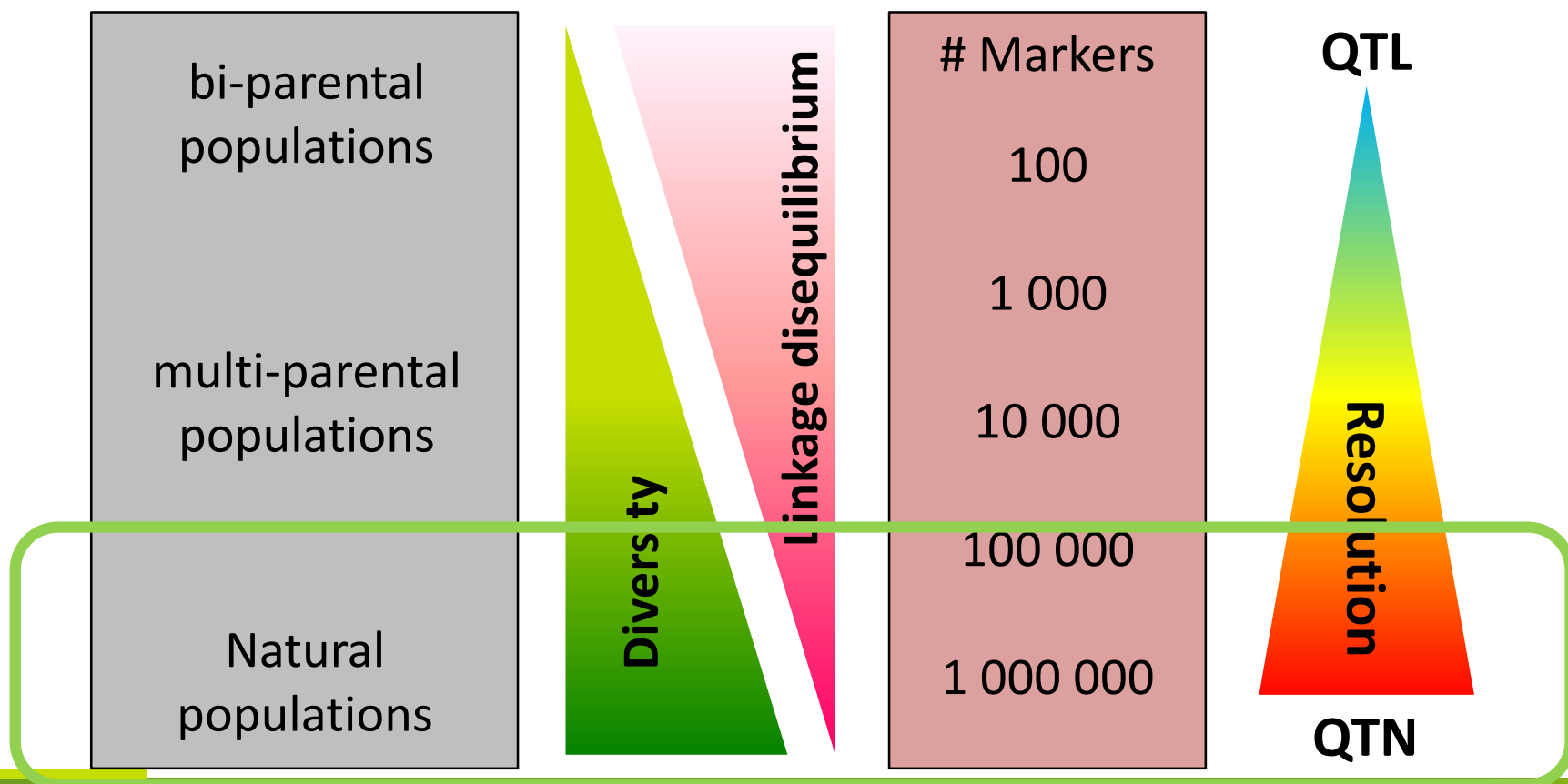
Strategies to study genetic architecture of resistance

From QTLs to QTNs



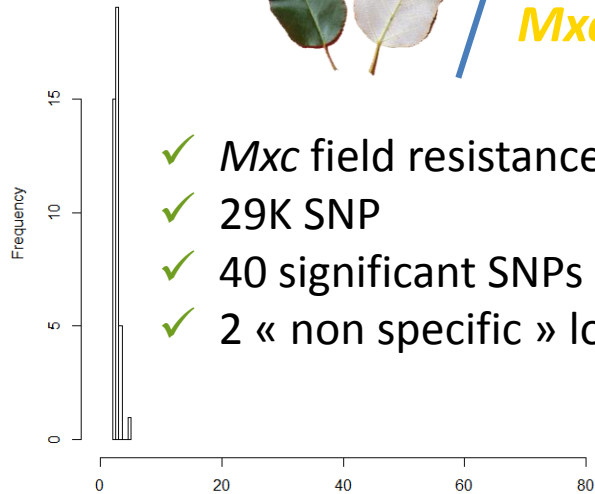
Strategies to study genetic architecture of resistance

From QTLs to QTNs

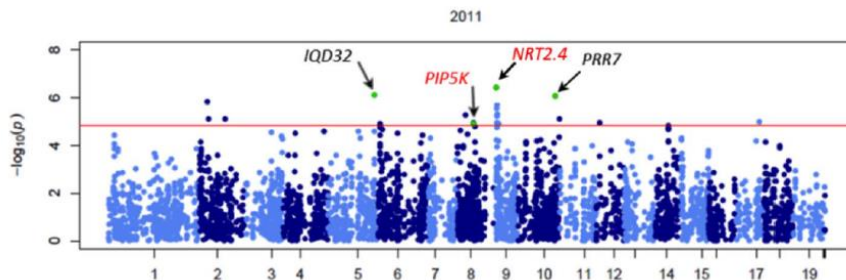


Natural populations GWAS

LaMantia et al. PlosONE 2013



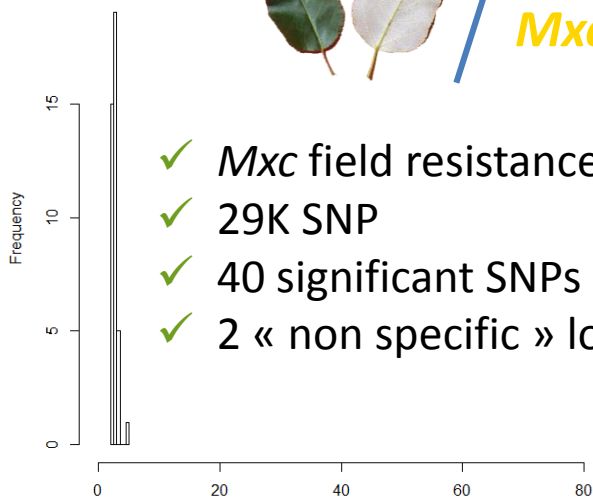
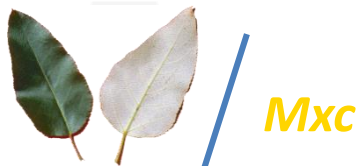
- ✓ *Mxc* field resistance for 412 *P. trichocarpa*
- ✓ 29K SNP
- ✓ 40 significant SNPs
- ✓ 2 « non specific » loci



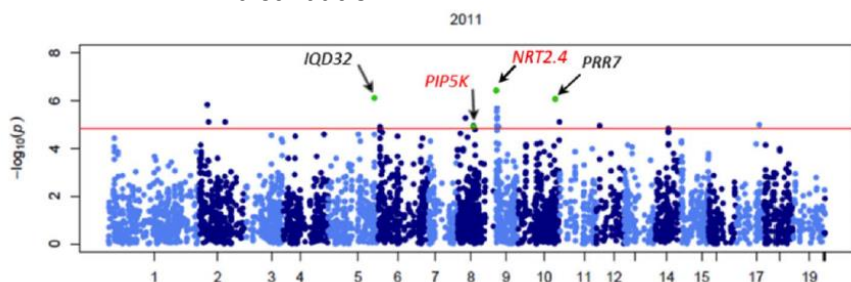
- ✓ 3 sign. SNP match with differentially expressed genes in *P. trichocarpa* x *P. deltoides* cv. Beaupré/*Mlp* interaction

Natural populations GWAS

LaMantia et al. PlosONE 2013



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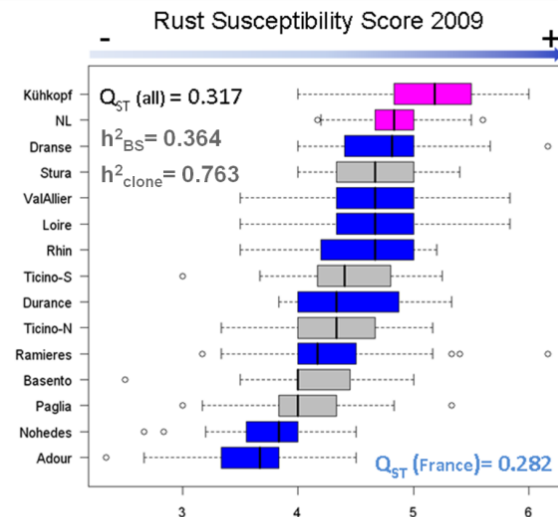


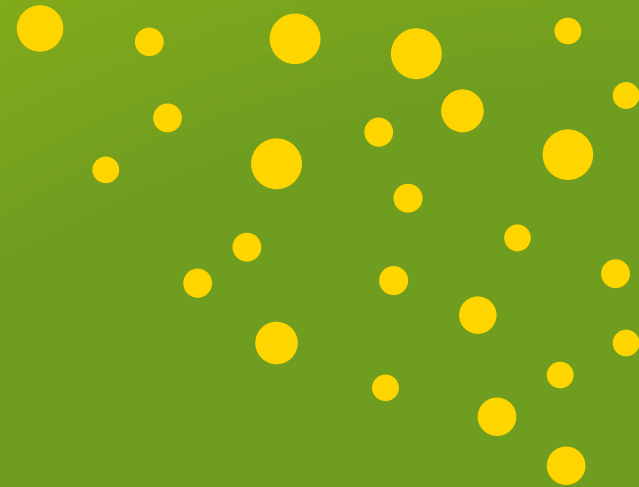
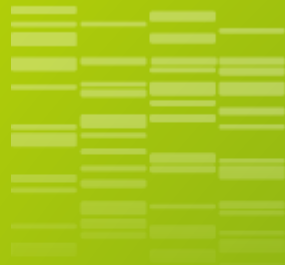
- ✓ 3 sign. SNP match with differentially expressed genes in *P. trichocarpa* x *P. deltoides* cv. Beaupré/*Mlp* interaction

Bastien et al, in prep



- ✓ Lab & Field resistance for 1100 *P. nigra*
- ✓ 8K SNP (focused on genes & candidate regions)
- ✓ To be done ...





6

Comparative genomics



Sum up !

Loci and QTL identification (« Heat map »)

4 mapping pedigrees

Family 331 : TDxTD

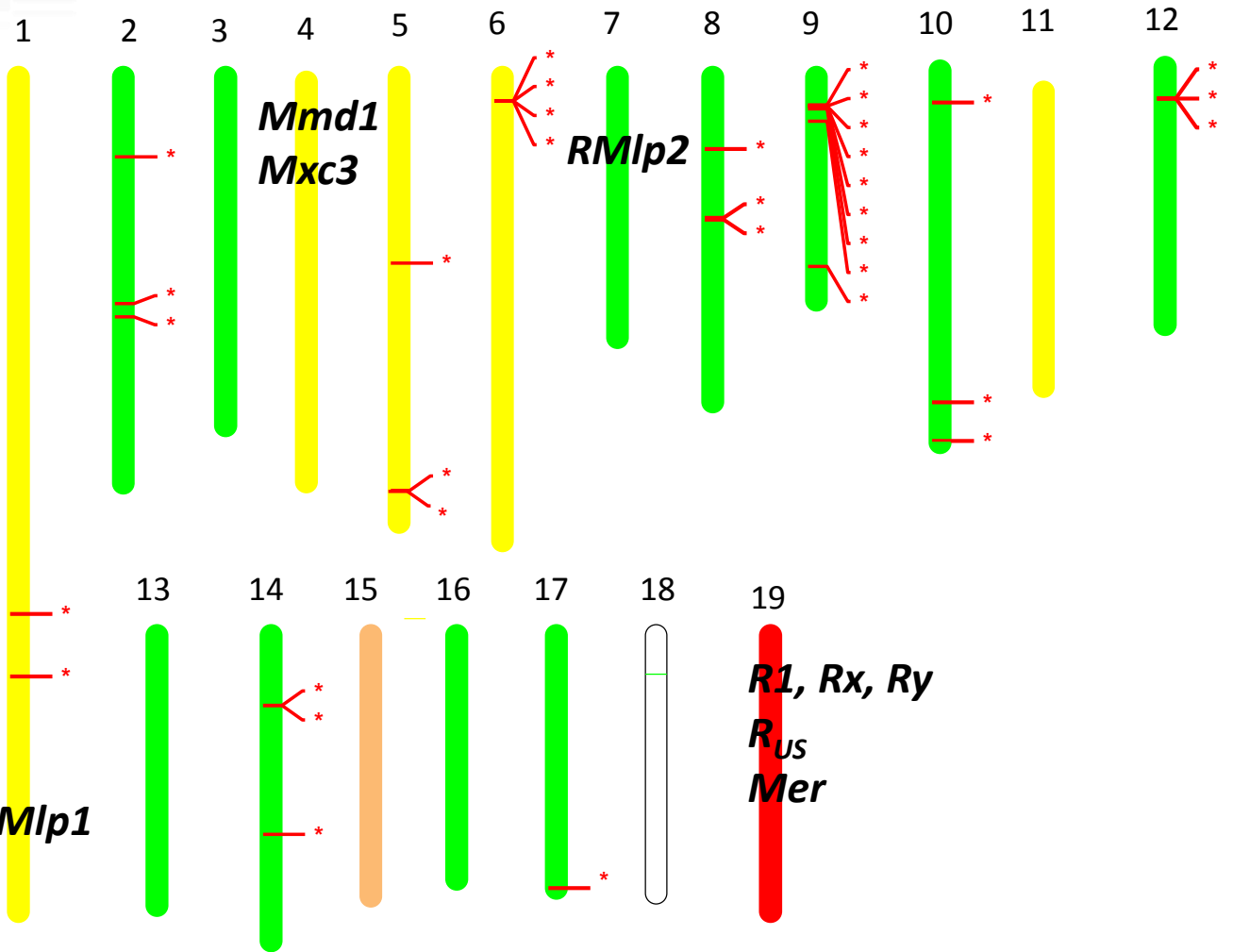
Family 54: DxT

87001,2 : DxN, DxT

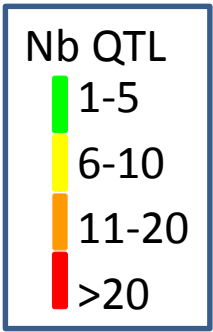
Family 1311: NxN

Factorial

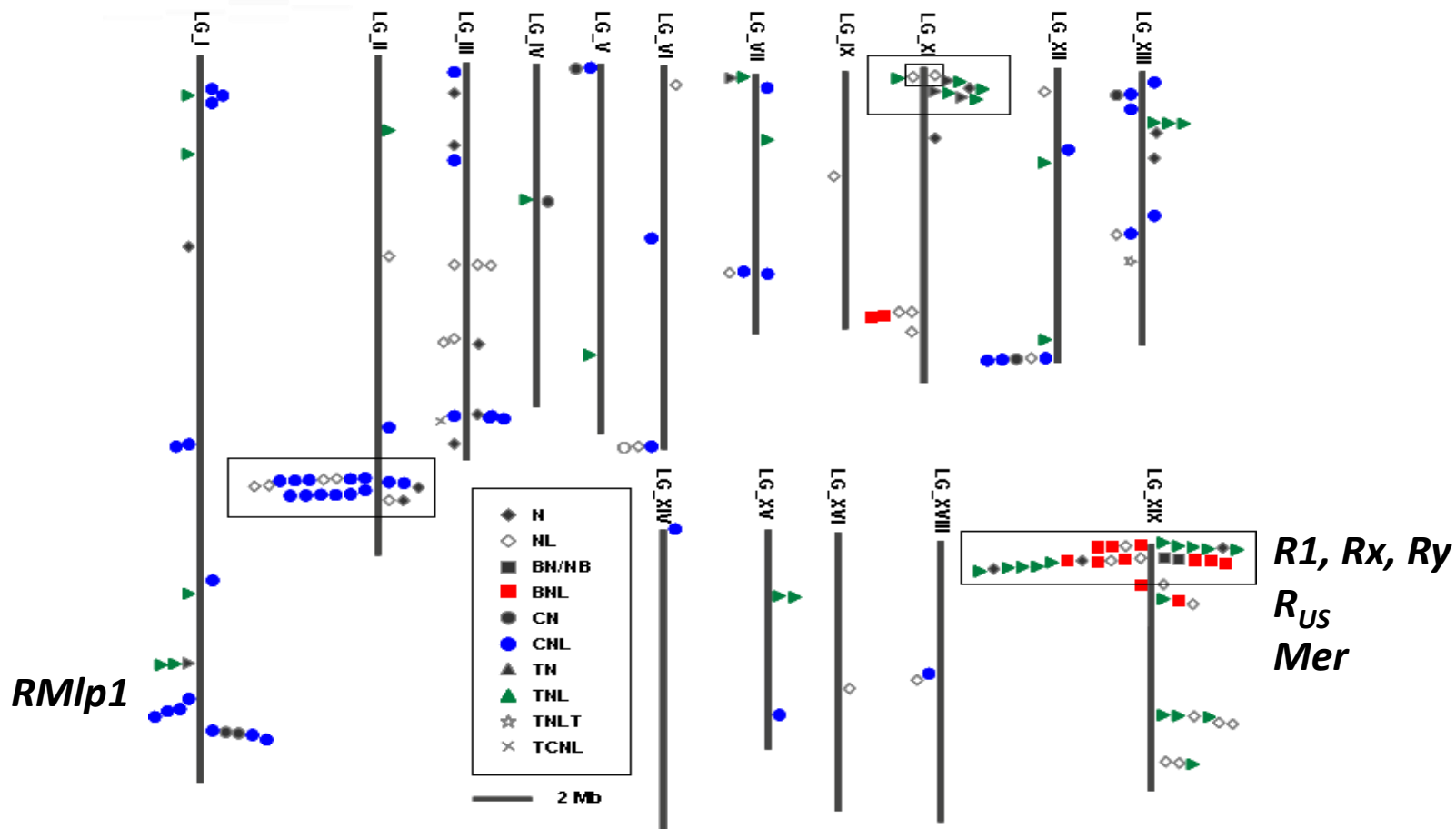
GWAS (*)



- Several components lab & field
- Several strains

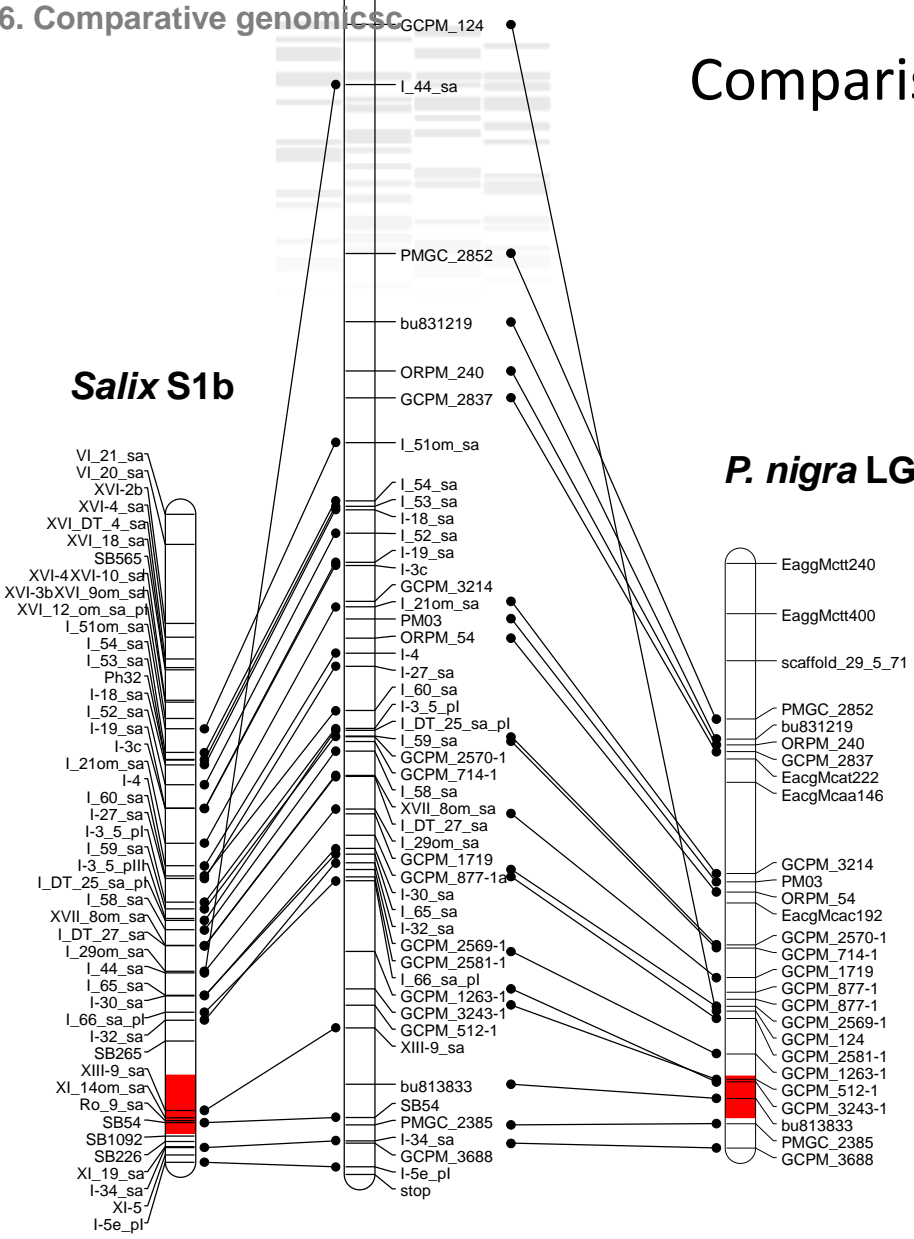


Some RGA clusters co-localise with resistance factors and QTLs described

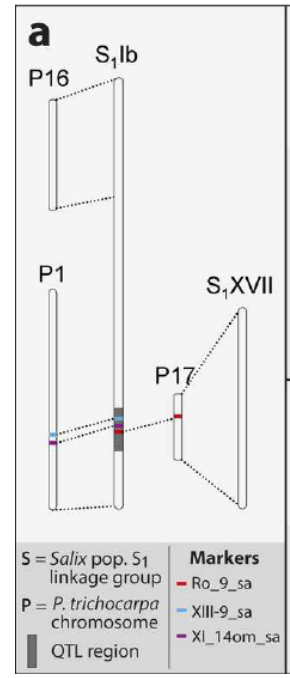


Comparison with *Salix* / *Mle* pathosystem

- Alignment of maps possible thank to co-linearity between *Salix* and *Populus* genomes
- Genetic mapping show co-location
- But physical mapping and cloning not
- Some complex rearrangement between both genus



RMIp1

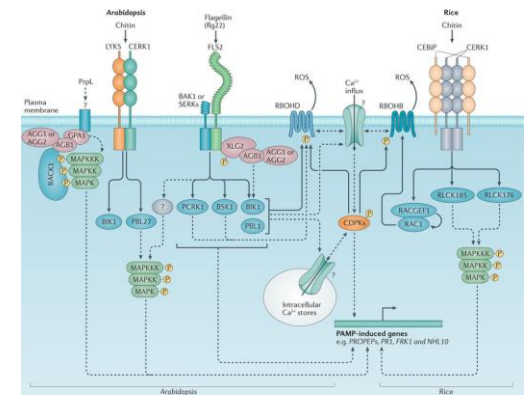


(Samils et al, 2011)
(Bertin et al 2016)

Any pattern of loci identify with natural / exapted classification ?

Major Loci identified	<i>Melampsora occidentalis</i>	<i>Melampsora medusae</i> <i>f.sp. deltoideae</i>	<i>Melampsora larici-populina</i>
<i>Populus trichocarpa</i>	Natural ?	Exapted Mmd1	Exapted Rus,
<i>Populus deltoides</i>	?	Natural ?	Exapted R1, Rx, Ry
<i>Populus nigra</i>	?	Exapted ^a ?	Natural RMlp1, RMlp2

- Both control quantitative / qualitative resistance
- Both showed specificity
- No overlap between loci identified, expected ? =>



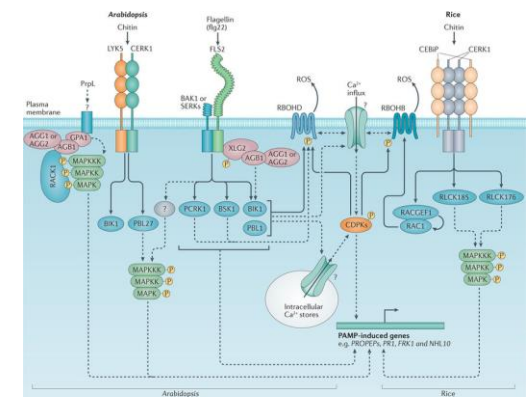
Couto & Zipfel, 2016

Nature Reviews | Immunology

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<i>Populus deltoides</i>	?	Natural ?	Exapted R1, Rx, Ry
<i>Populus nigra</i>	?	Exapted ^a ?	Natural RMlp1, RMlp2

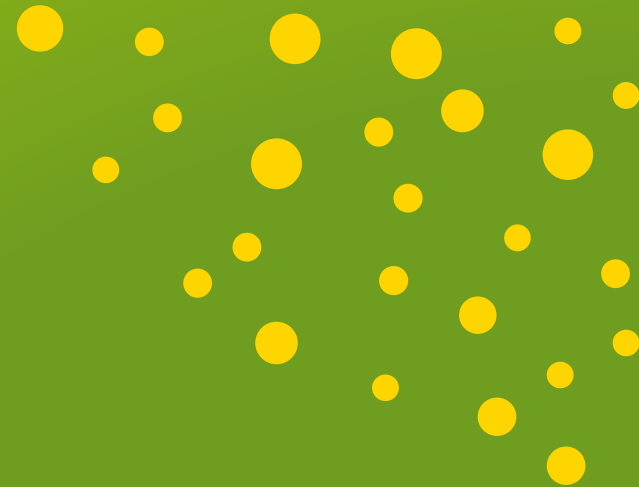
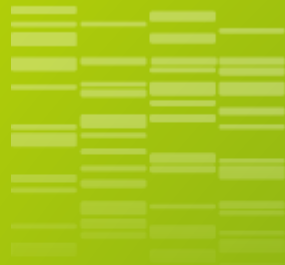
- Both control quantitative / qualitative resistance
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Couto & Zipfel, 2016

Nature Reviews | Immunology

What are the function of exapted resistances in the natural area?



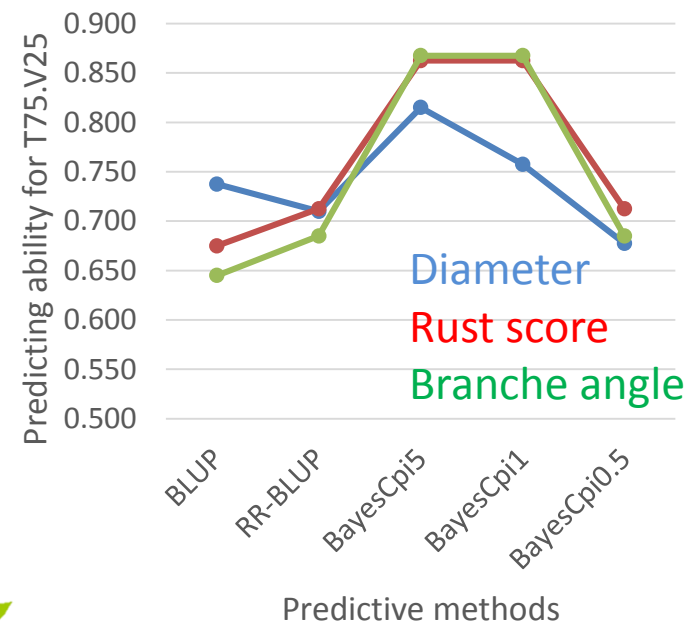
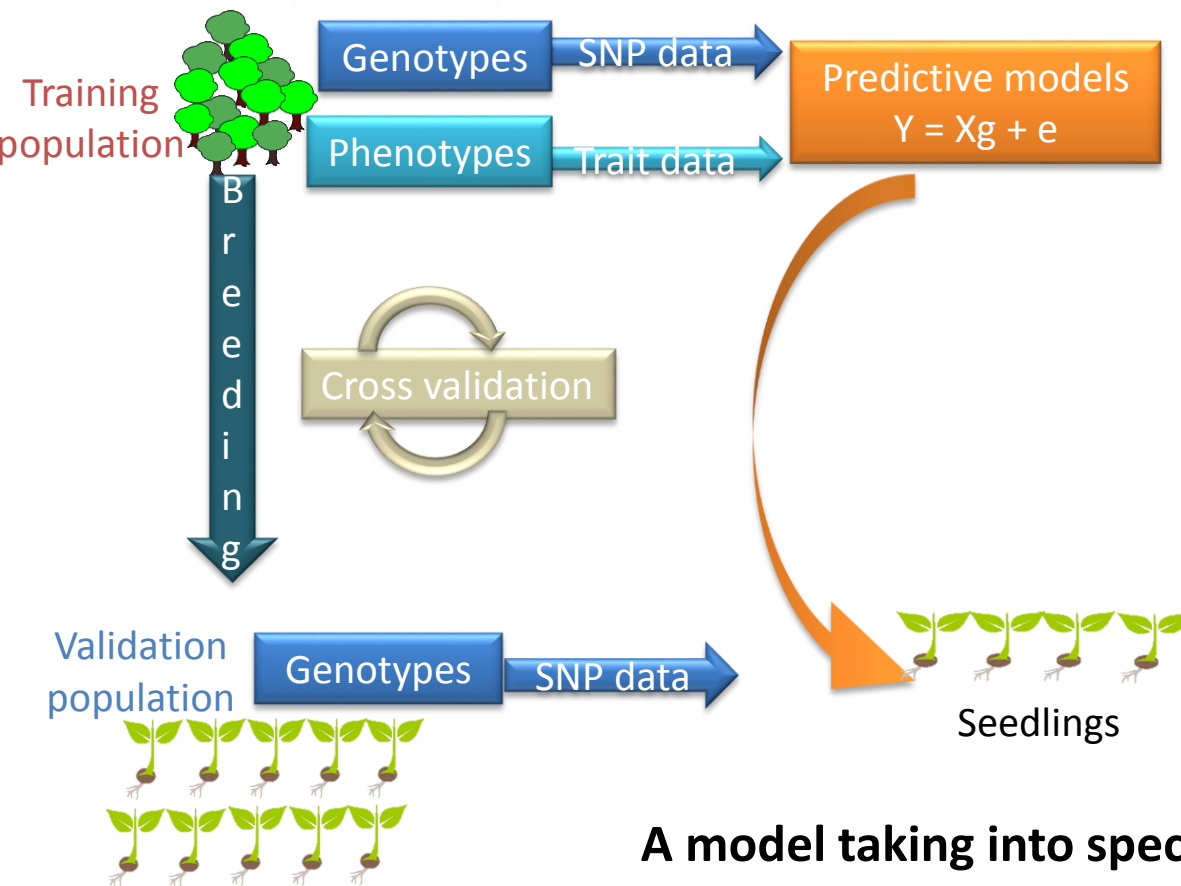
7

Conclusion: potential uses for breeding



A case study of genomic selection in *Populus nigra*

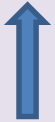
Which is the best predictive model for rust resistance ?



**A model taking into specific marker effects on the trait.
=> Information on genetic determinism is useful!**

Research in Poplar genetics and genomics at INRA
(BioForA-Orleans & URGV-Evry)

Cv 'italica'



M. Villar

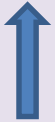
P. nigra



Natural populations

Genetic diversity
conservation
dynamics of natural
ecosystem

Cv 'italica'



M. Villar

P. nigra



Natural populations

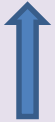
*Genetic diversity
conservation
dynamics of natural
ecosystem*

***Other species and interspecific hybrids
P. deltoides, P. trichocarpa, DxN, DxT***

With focus on :

- *Resistance to Melampora larici-populina*
- *Phenology*
- *Wood properties*

Cv 'italica'



M. Villar

P. nigra



Populus Genomes

genome structure
Whole genome sequencing
SNP identification
HT genotyping
SSR

Molecular polymorphisms

Natural populations

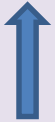
Genetic diversity
conservation
dynamics of natural
ecosystem

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M. Villar

P. nigra



Natural populations

Genetic diversity
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Populus Genomes

genome structure
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Molecular polymorphisms



P. Faivre-Rampant



V. Jorge

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Cv 'italica'



M. Villar

P. nigra



Natural populations

*Genetic diversity
conservation
dynamics of natural
ecosystem*

Populus Genomes

*genome structure
Whole genome sequencing
SNP identification
HT genotyping
SSR*

Molecular polymorphisms



P. Faivre-Rampant



V. Jorge



V. Segura

Genetic Maps and QTL
detection

(F1, factorial mating design)

Association genetics in
natural populations

Other species and interspecific hybrids
P. deltoides, P. trichocarpa, DxN, DxT

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P. nigra



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- *Phenology*
- *Wood properties*

Optimisation of breeding Strategies

Long term management of genetic diversity



L. Sanchez

genetic/genomic prediction

Prediction of heterosis

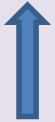


A. Dowkiw

Gene flow
Melampsora- poplar interaction
(R durability, selection pressures)
Wild/Cultivated Interactions



Cv 'italica'



M. Villar

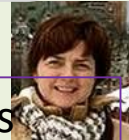
P. nigra



Natural populations

Genetic diversity
conservation
dynamics of natural
ecosystem

Populus Genomes
genome structure
Whole genome sequencing
SNP identification
HT genotyping
SSR
Molecular polymorphisms



P. Faivre-Rampant

Other species and interspecific hybrids
P. deltoides, P. trichocarpa, DxN, DxT

With focus on :

- *Resistance to Melampora larici-populina*
- *Phenology*
- *Wood properties*



V. Jorge



V. Segura

Genetic Maps and QTL
detection
(F1, factorial mating design)

Association genetics in
natural populations

Optimisation of breeding Strategies

Long term management of genetic diversity



L. Sanchez

genetic/genomic prediction
Prediction of heterosis

Research in Poplar genetics and genomics at INRA (BioForA-Orleans & URGV-Evry)



A. Dowkiw

Gene flow
Melampsora- poplar interaction
(R durability, selection pressures)
Wild/Cultivated Interactions



C. Bastien

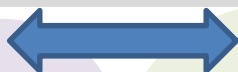
**French national
Breeding Program**
(D, DxN, DxT,)

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M. Villar

P. nigra



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P. Faivre-Rampant

Quantitative Genetics

Other species and interspecific hybrids
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