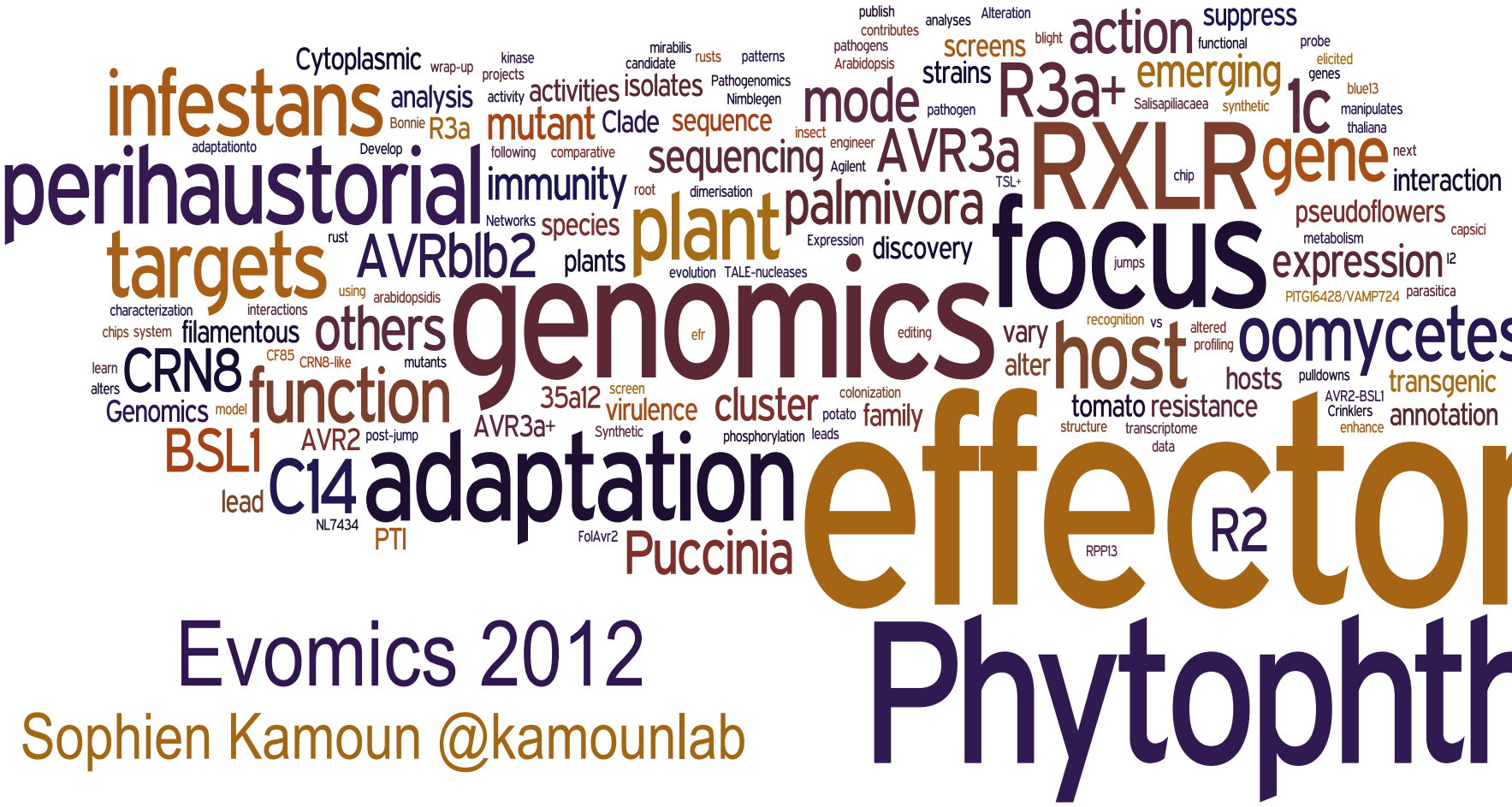


Sebastian Schornack

Mireille van Damme

Joe Win

Krissana Kowitwanich

Liliana Cano

Angela Chaparro

Tolga Bozkurt

Marina Pais

Sylvain Raffaele

Diane Saunders

Maria Segretin

Food crisis: The silent tsunami

- Food and Ag commodity prices at all time highs
- Famine, hunger, food riots
- Chemical control: expensive, environmental damage…
- Crop diseases caused by plant pathogens are a major constraint for food production

Food Export Prices Rise

An index showing what countries around the world pay to import basic foodstuffs rose in January for the seventh consecutive month.

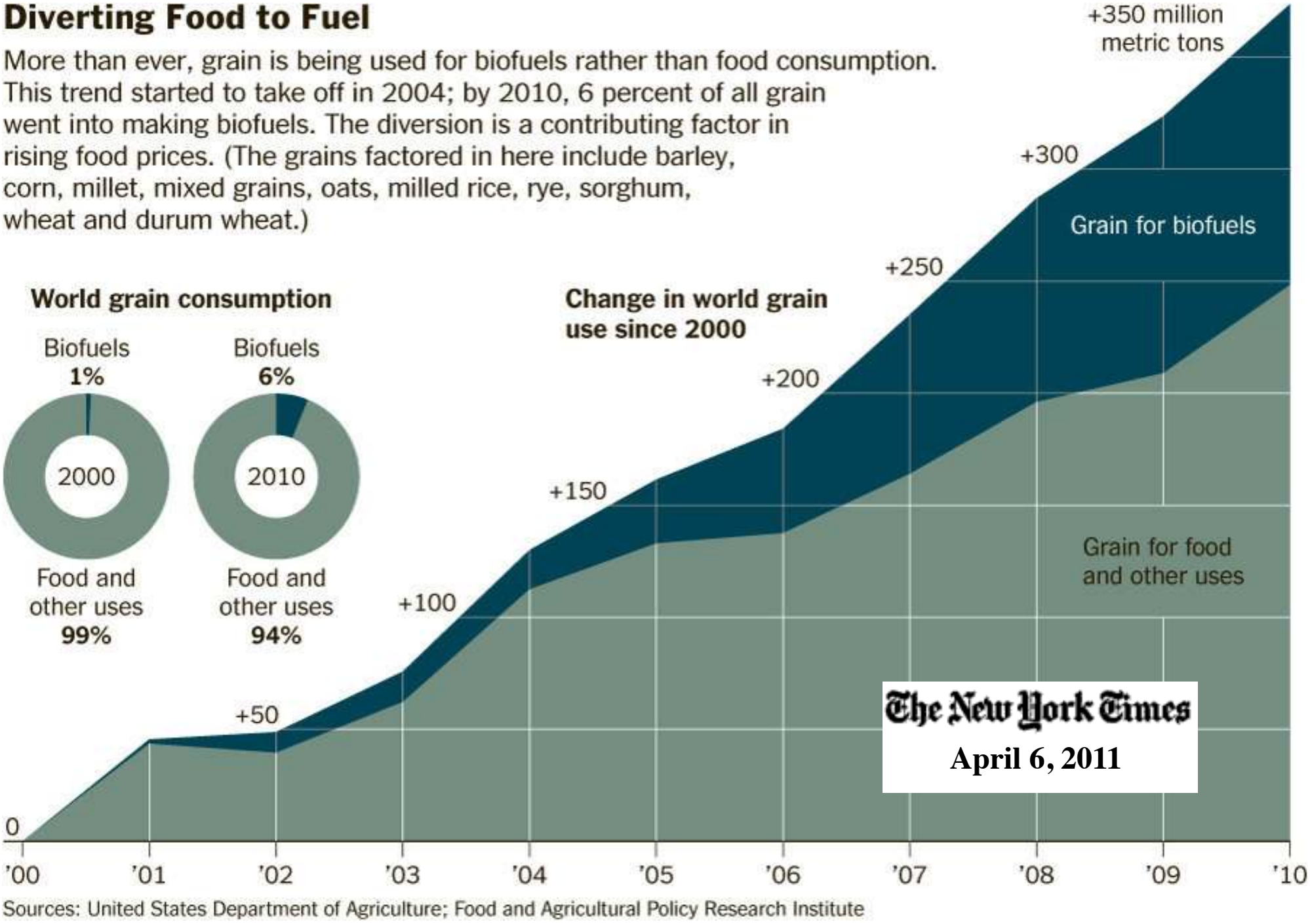
*The adjusted food price index is the unadjusted index deflated by the World Bank Manufactures Unit Value Index (MUV).

Source: Food and Agriculture Organization of the United Nations

The New York Times
February 4, 2011

Diverting Food to Fuel

More than ever, grain is being used for biofuels rather than food consumption. This trend started to take off in 2004; by 2010, 6 percent of all grain went into making biofuels. The diversion is a contributing factor in rising food prices. (The grains factored in here include barley, corn, millet, mixed grains, oats, milled rice, rye, sorghum, wheat and durum wheat.)



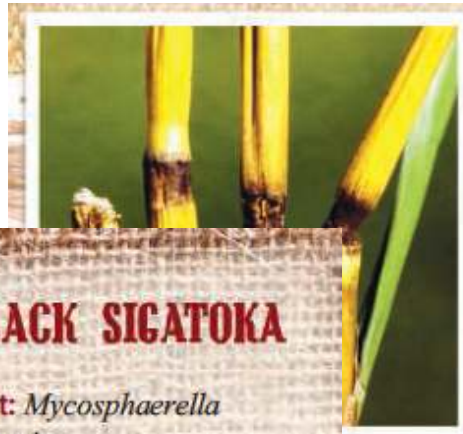
Sources: United States Department of Agriculture; Food and Agricultural Policy Research Institute

The New York Times
April 6, 2011

Armed and Dangerous

BIG 7

These fungi, weeds, and viruses are among the more serious biological threats to food security—so researchers are working hard on countermeasures



RICE BLAST

Pest: *Magnaporthe oryzae*
Crops: Rice, 50 species of grasses and sedges

POTATO BLIGHT

Pest: *Phytophthora infestans*
Crops: Potatoes; also tomatoes and other solanaceous crops

BLACK SIGATOKA

Pest: *Mycosphaerella fijiensis*
Crops: Bananas, plantains
Whereabouts: This fungus, first detected in Fiji in 1964, is now found in 100 countries in the Americas, Africa and South Asia.

ASIAN SOYBEAN RUST

Pest: *Phakopsora pachyrhizi*
Crops: At least 31 legume species, notably soybeans

WHEAT STEM RUST

Pest: *Puccinia graminis* Ug99
Crop: Wheat

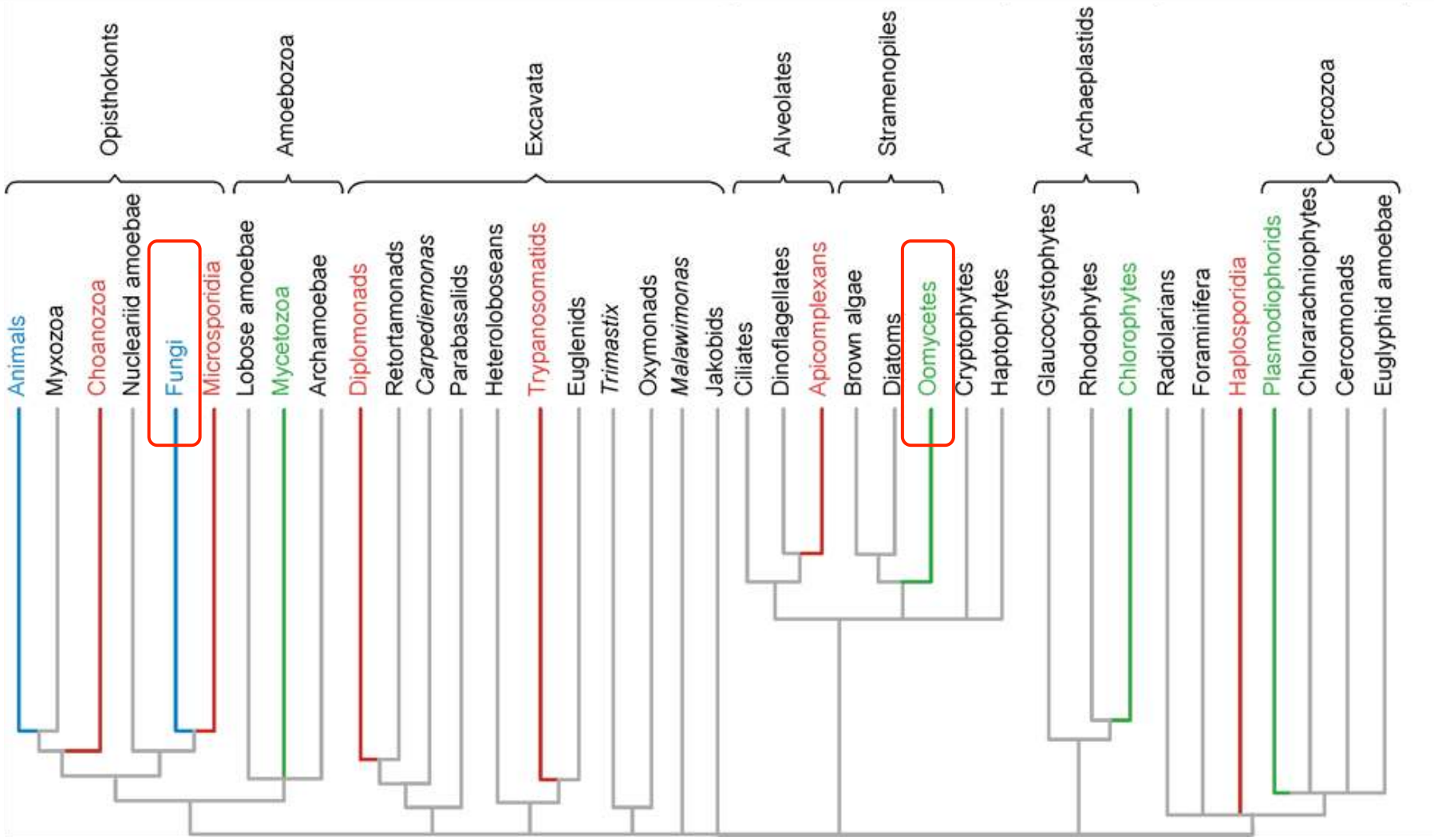
Infection of potato plants by *Phytophthora infestans*

Remco Stam, Univ Dundee

Filamentous plant pathogens (fungi and oomycetes) cause destructive crop diseases

- **Often host-specialized biotrophs** - require living plant cells
- **Highly adaptable -** can rapidly overcome plant resistance
- Large population sizes, mixed asexual and sexual reproduction
- ~30 genome sequences described to date

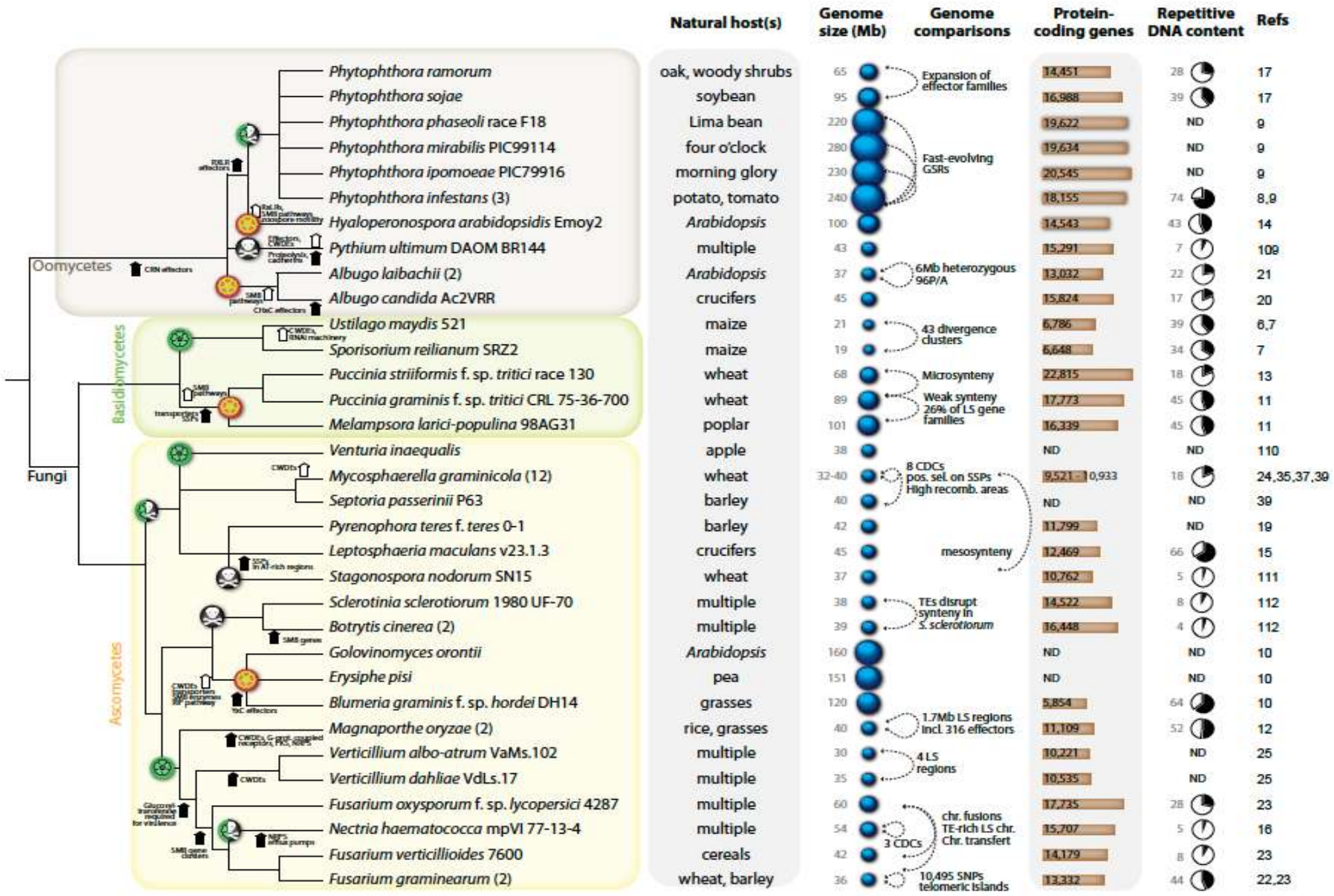
Oomycetes are fungus-like filamentous microbes: a unique group of eukaryotic plant pathogens



Tree adapted from Embley and Martin (2006) Nature 440:623

Animal parasites in red

Plant pathogens in green


Natural host(s)
Genome size (Mb)
Genome comparisons
Protein-coding genes
Repetitive DNA content
Refs
Oomycetes
Basidiomycetes
Ascomycetes
Fungi
Phytophthora ramorum
Phytophthora sojae
Phytophthora phaseoli race F18
Phytophthora mirabilis PIC99114
Phytophthora ipomoeae PIC79916
Phytophthora infestans (3)
Hyaloperonospora arabidopsidis Emoy2
Pythium ultimum DAOM BR144
Albugo laibachii (2)
Albugo candida Ac2VRR
Ustilago maydis 521
Sporisorium reilianum SRZ2
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Golovinomyces orontii
Erysiphe pisi
Blumeria graminis f. sp. hordei DH14
Magnaporthe oryzae (2)
Verticillium albo-atrum VaMs.102
Verticillium dahliae VdLs.17
Fusarium oxysporum f. sp. lycopersici 4287
Nectria haematococca mpVI 77-13-4
Fusarium verticillioides 7600
Fusarium graminearum (2)
oak, woody shrubs
soybean
Lima bean
four o'clock
morning glory
potato, tomato
Arabidopsis
multiple
Arabidopsis
crucifers
maize
maize
wheat
wheat
poplar
apple
wheat
barley
barley
crucifers
wheat
multiple
multiple
Arabidopsis
pea
grasses
rice, grasses
multiple
multiple
multiple
multiple
cereals
wheat, barley
65
95
220
280
230
240
100
43
37
45
21
19
68
89
101
38
32-40
40
42
45
37
38
39
160
151
120
40
30
35
60
54
42
36
Expansion of effector families
Fast-evolving GSRs
6Mb heterozygous 96P/A
43 divergence clusters
Microsynteny
Weak synteny
26% of LS gene families
8 CDCs
pos. sel. on SSPs
High recomb. areas
mesosynteny
TEs disrupt synteny in S. sclerotiorum
1.7Mb LS regions
Incl. 316 effectors
4 LS regions
chr. fusions
TE-rich LS chr.
Chr. transfert
3 CDCs
10,495 SNPs
telomeric islands
14,451
16,988
19,622
19,634
20,545
18,155
14,543
15,291
13,032
15,824
6,786
6,648
22,815
17,773
16,339
ND
9,521 - 10,933
ND
11,799
12,469
10,762
14,522
16,448
ND
ND
5,854
11,109
10,221
10,535
17,735
15,707
14,179
13,332
28
39
ND
ND
ND
74
43
7
22
17
39
34
18
45
45
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18
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ND
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5
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ND
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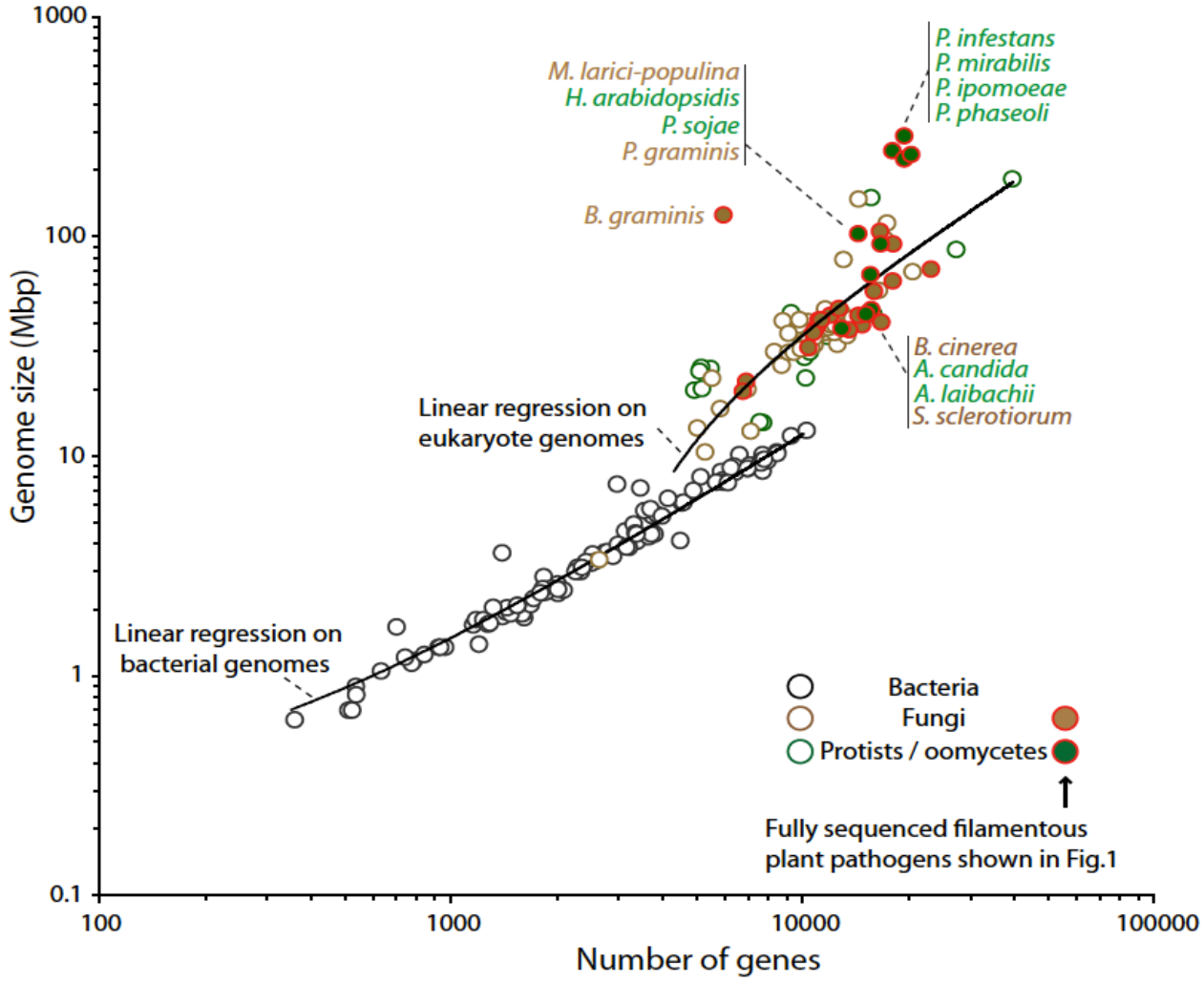
11
110
24,35,37,39
39
19
15
111
112
112
10
10
10
12
25
25
23
16
23
22,23
obligate biotroph;
biotroph;
hemibiotroph;
necrotroph.
gene/pathways losses
gene gain or gene families expansion
non-repetitive
repetitive

Expanded filamentous plant pathogen genomes are enriched in noncoding DNA



Sylvain Raffaele

Genomes of host-specific filamentous plant pathogens – *The bigger the better!*

- Typically, larger genomes than non-parasitic relatives
- Extreme repeat-driven expansions in distinct lineages:
  - *Phytophthora infestans*: 240 Mb, 74% repeats
  - Rust fungi: 68-100 Mb, 45% repeats
  - Powdery mildew fungi: 120-160 Mb, 65% repeats
- In sharp contrast to many parasites and symbionts that tend to evolve small compact genomes

Reduction and Compaction in the Genome of the Apicomplexan Parasite *Cryptosporidium parvum*

Parasites genomes are often considered to be "reduced" or "degenerate," but exactly what do these terms mean? How various are the forces that affect genome size and density, and how do their effects differ in different parasites?

The genome of *Tetranychus urticae* reveals herbivorous pest adaptations

At 90 megabases *T. urticae* has the smallest sequenced arthropod genome.

Extreme genome reduction in symbiotic bacteria

John P. McCutcheon[1] and Nancy A. Moran[2]

Sequence and genetic map of *Meloidogyne hapla*: A compact nematode genome for plant parasitism

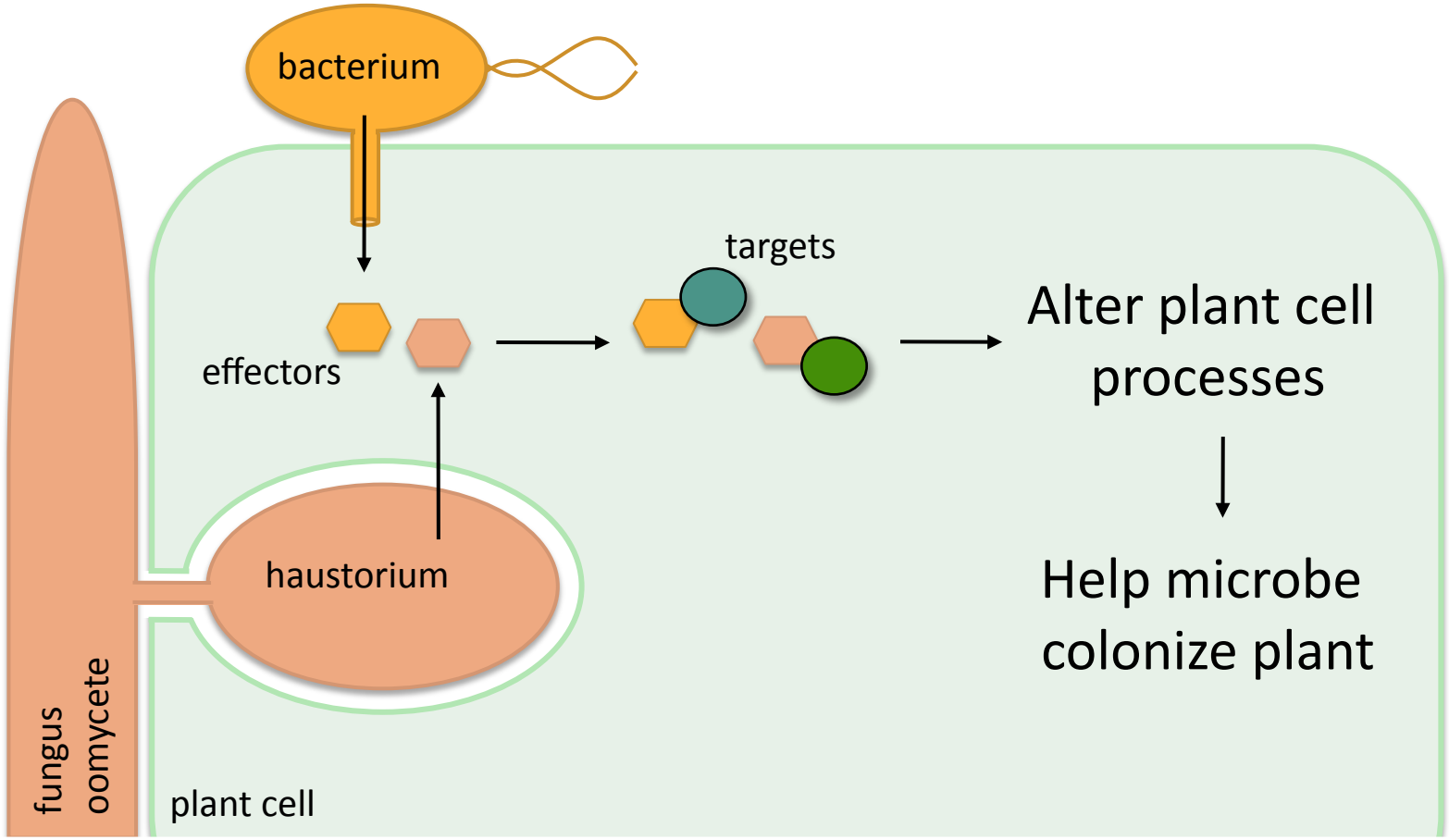
Charles H. Opperman[a,b,c], David M. Bird[a,b], Valerie M. Williamson[d], Dan S. Rokhsar[e], Mark Burke[a], Jonathan Cohn[a], John Cromer[a], Steve Diener[a,f], Jim Gajan[a], Steve Graham[a], T. D. Houfek[a,g], Qingli Liu[d,h], Therese Mitros[i], Jennifer Schaff[a,j], Reenah Schaffer[a], Elizabeth Scholl[a], Bryon R. Sosinski[k,l], Varghese P. Thomas[d], and Eric Windham[a]

- Why is bigger better in filamentous plant pathogens?
- Which evolutionary tradeoffs counterbalance the cost of the larger genomes?

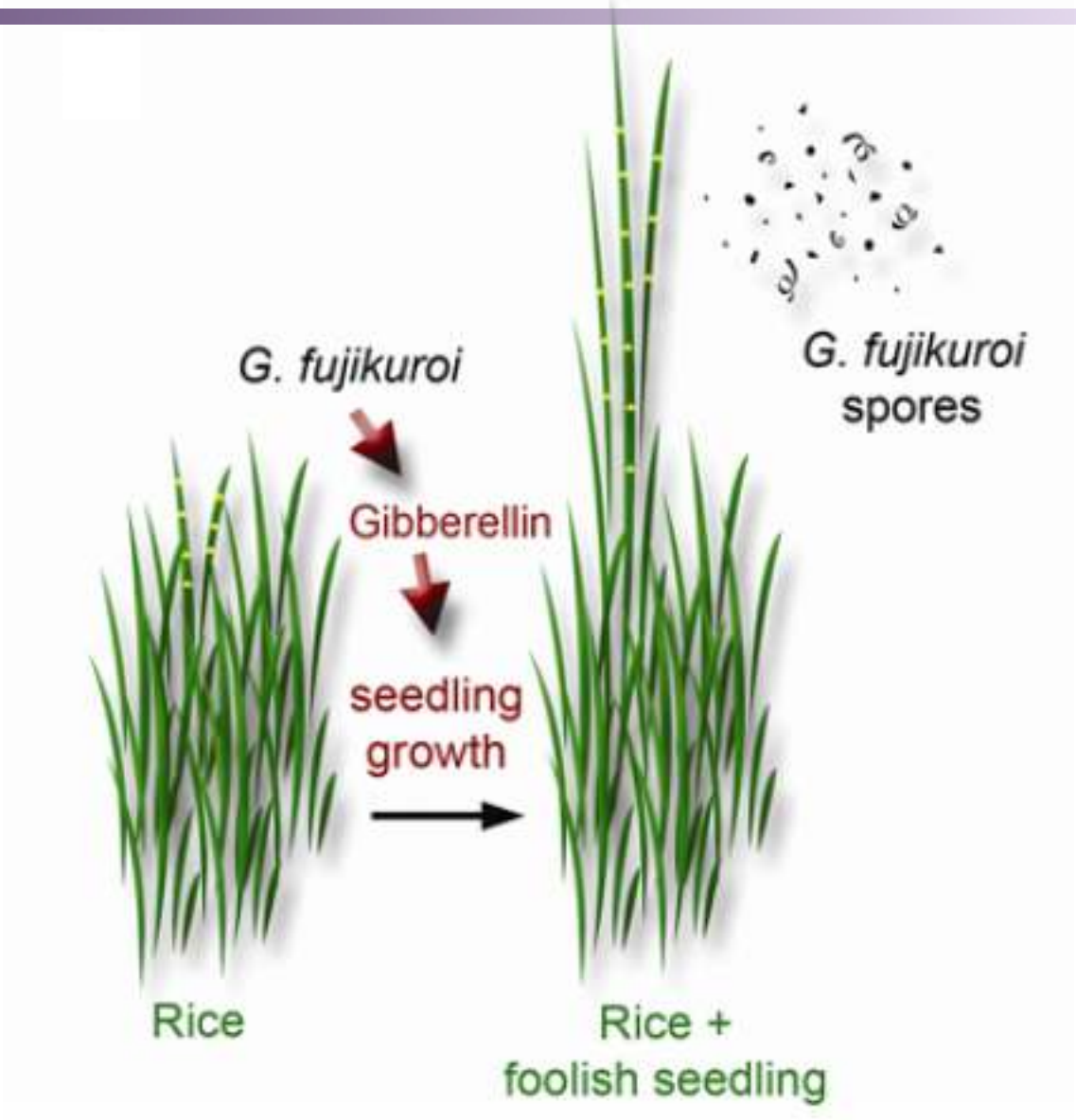
Effectors – secreted pathogen molecules that perturb plant processes

- **Effectors** – described in parasitic bacteria, oomycetes, fungi, nematodes, and insects
- Encoded by genes in pathogen genomes but function in (inside) plant cells – **operate as plant proteins**
- **Target of natural selection** in the context of coevolutionary arms race between pathogen and plant
- **Current paradigm** – effector activities are key to understanding parasitism

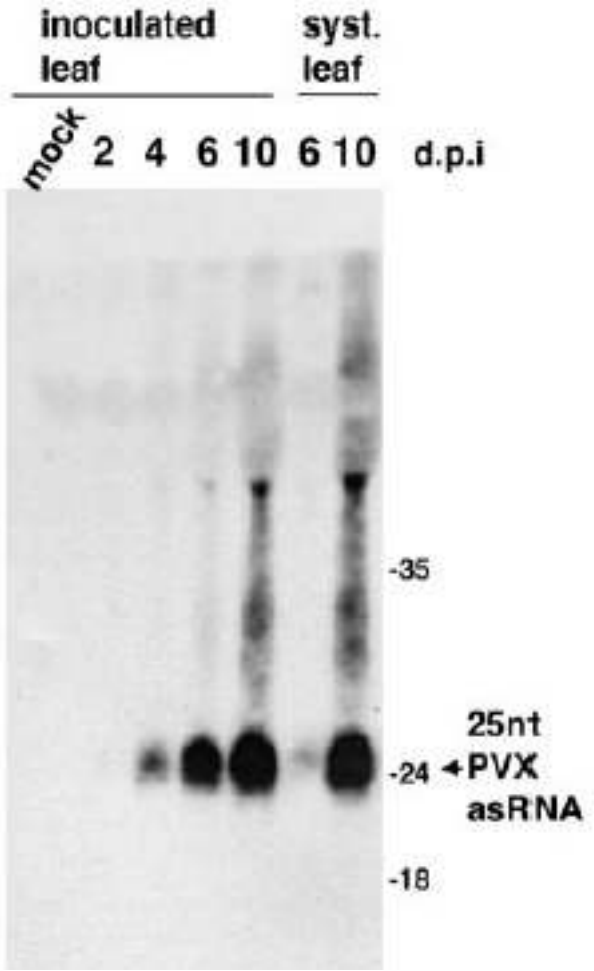
Microbes alter plant cell processes by secreting a diversity of effector molecules



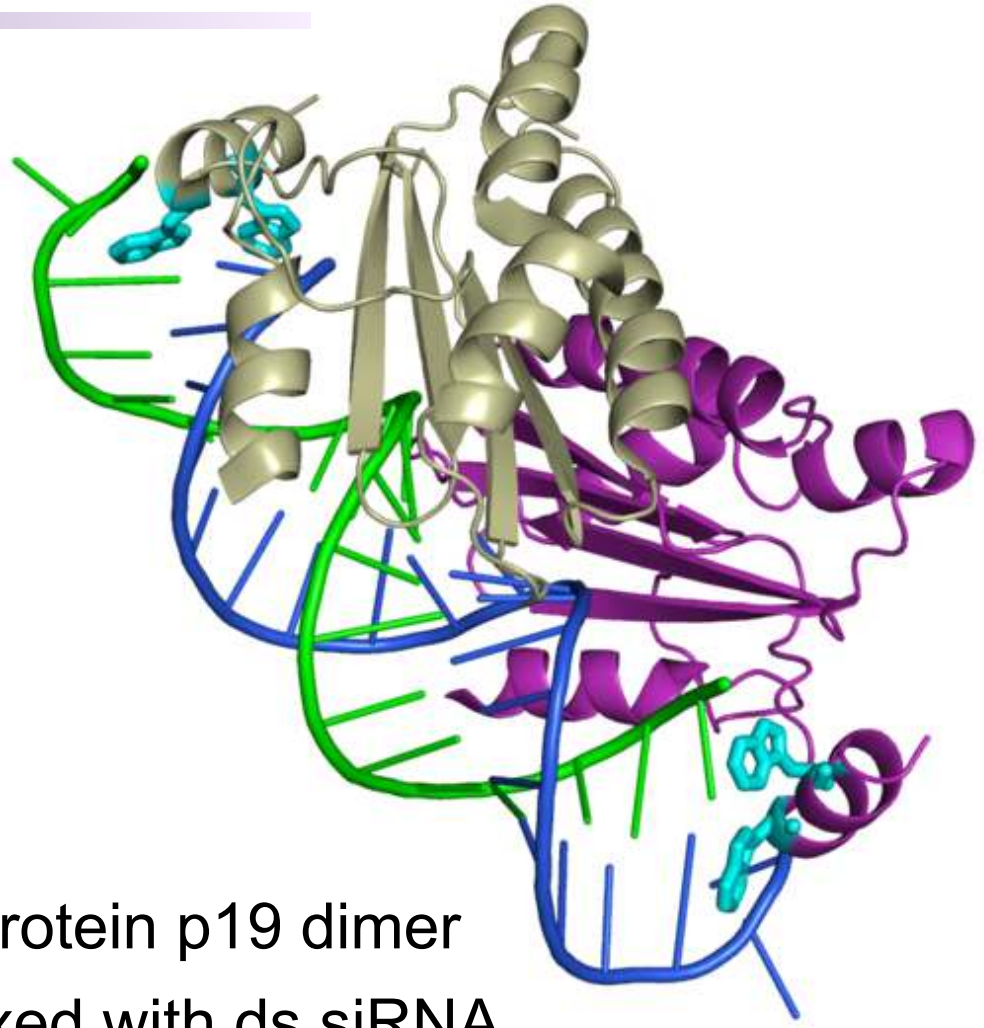
Bakanae (バカナエ) – “foolish seedling” disease caused by *Gibberella fujikuroi*



Suppression of post-translational gene silencing (PTGS) by plant virus effectors



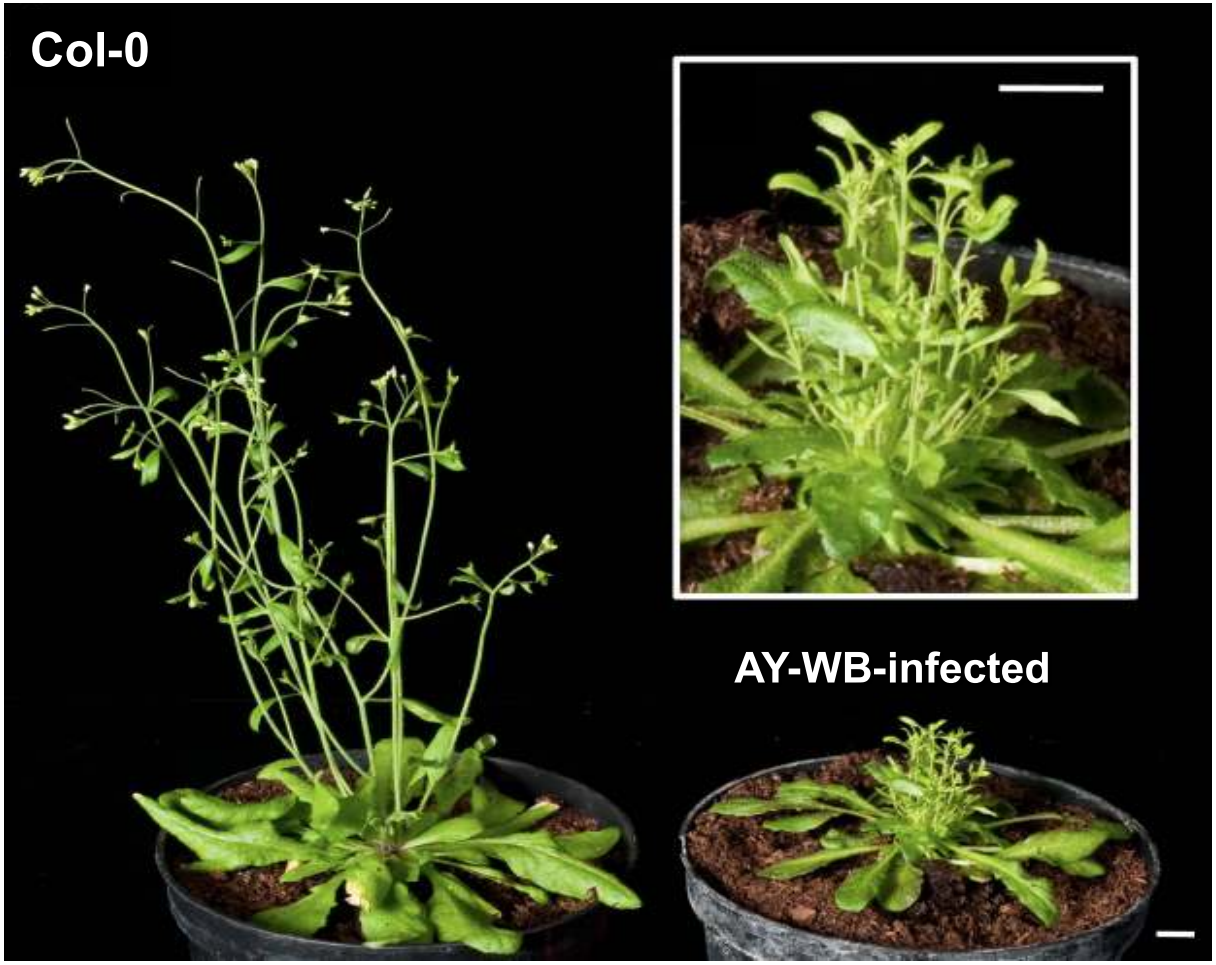
Hamilton and Baulcombe
Science 1999

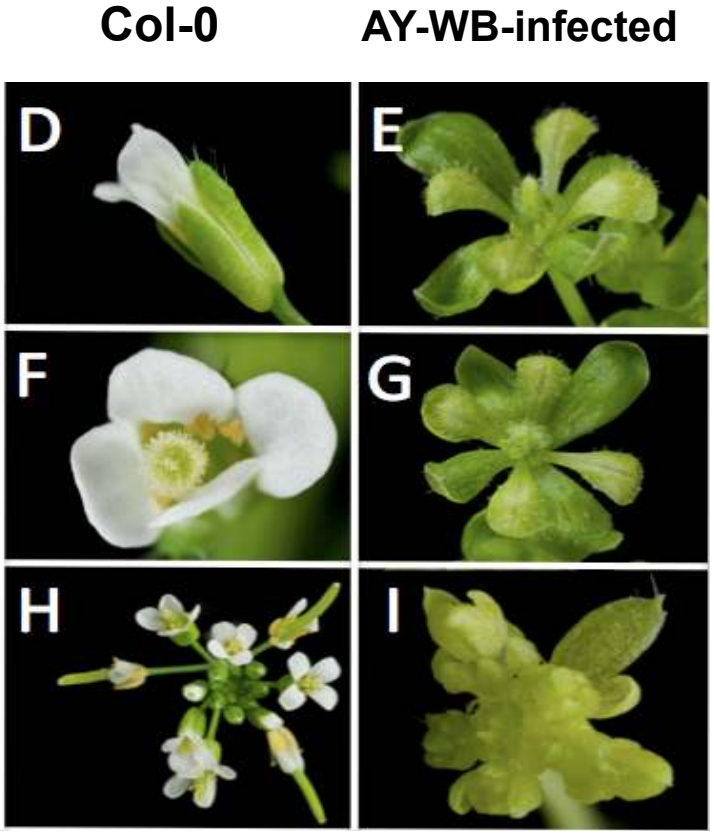


Viral protein p19 dimer complexed with ds siRNA

www.proteopedia.org

AY-WB phytoplasma induces witches' broom symptoms in Arabidopsis





MacLean *et al.* Plant Phys 2011; Saskia Hogenhout's lab

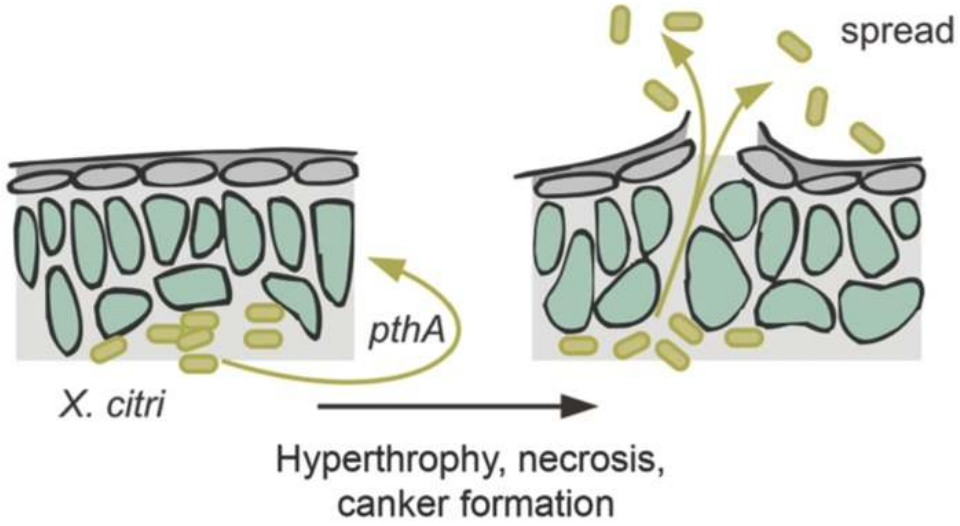
The phytoplasma effector protein SAP54 induces shoot formation from flowers

Phytoplasma-infected Arabidopsis

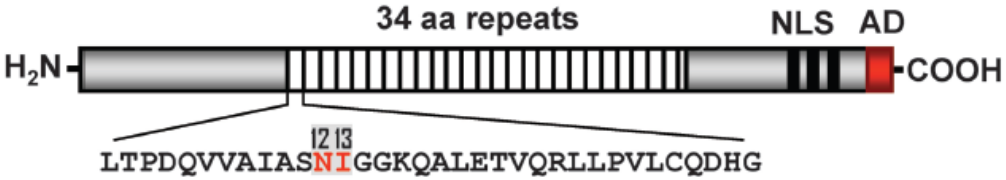
35S:SAP54

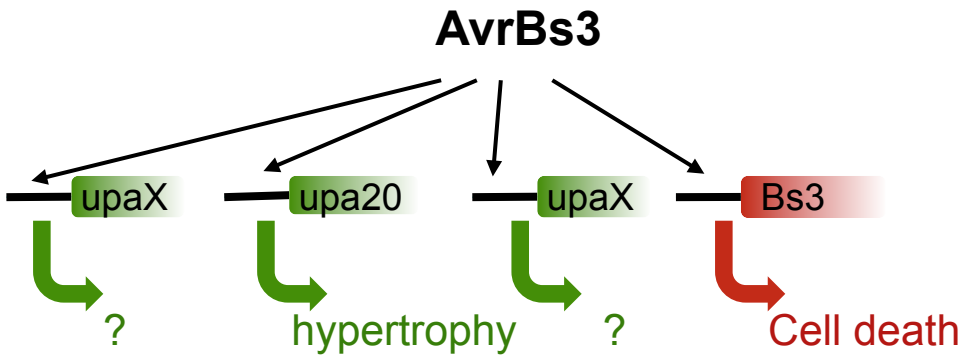
MacLean *et al.* Plant Phys 2011; Saskia Hogenhout's lab

Xanthomonas TAL effectors: DNA binding proteins with an amino acid to nucleotide specificity code



TAL effectors –
Designer DNA binding proteins



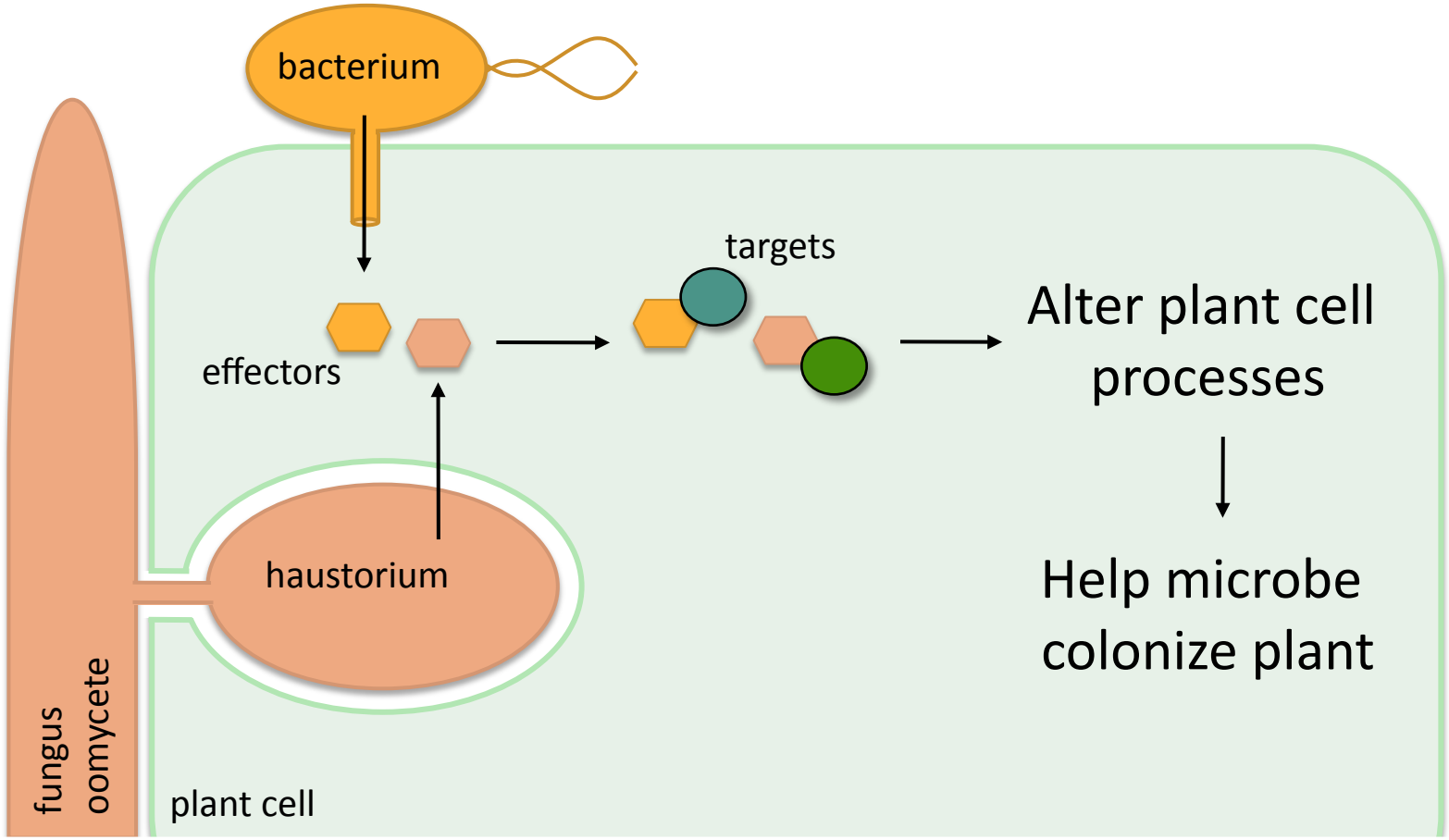


Hypervariable residues: **NI HD HG NG**

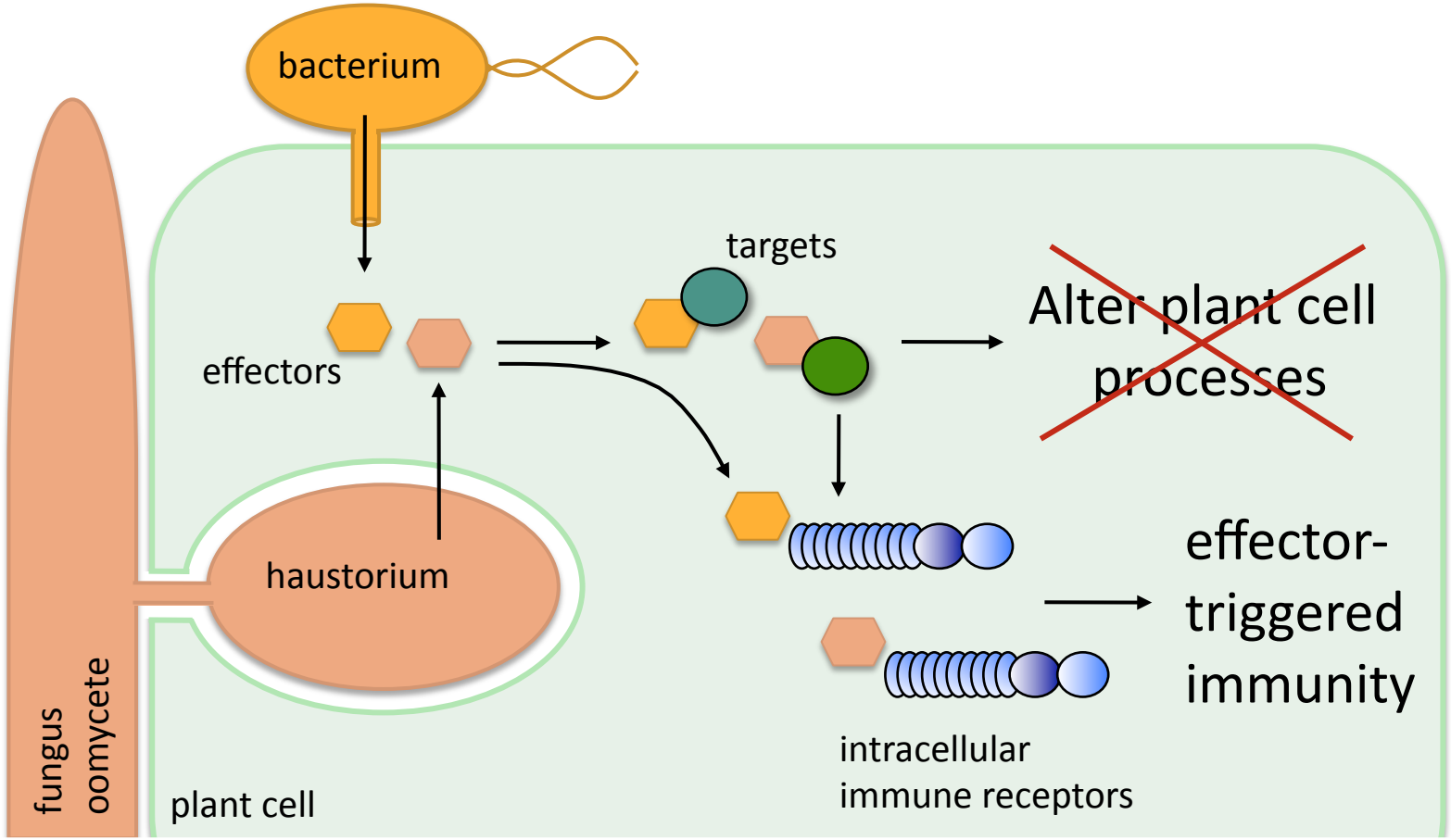
Target base: **A C G T**

Moscou *et al.*; Boch *et al.* Science 2009

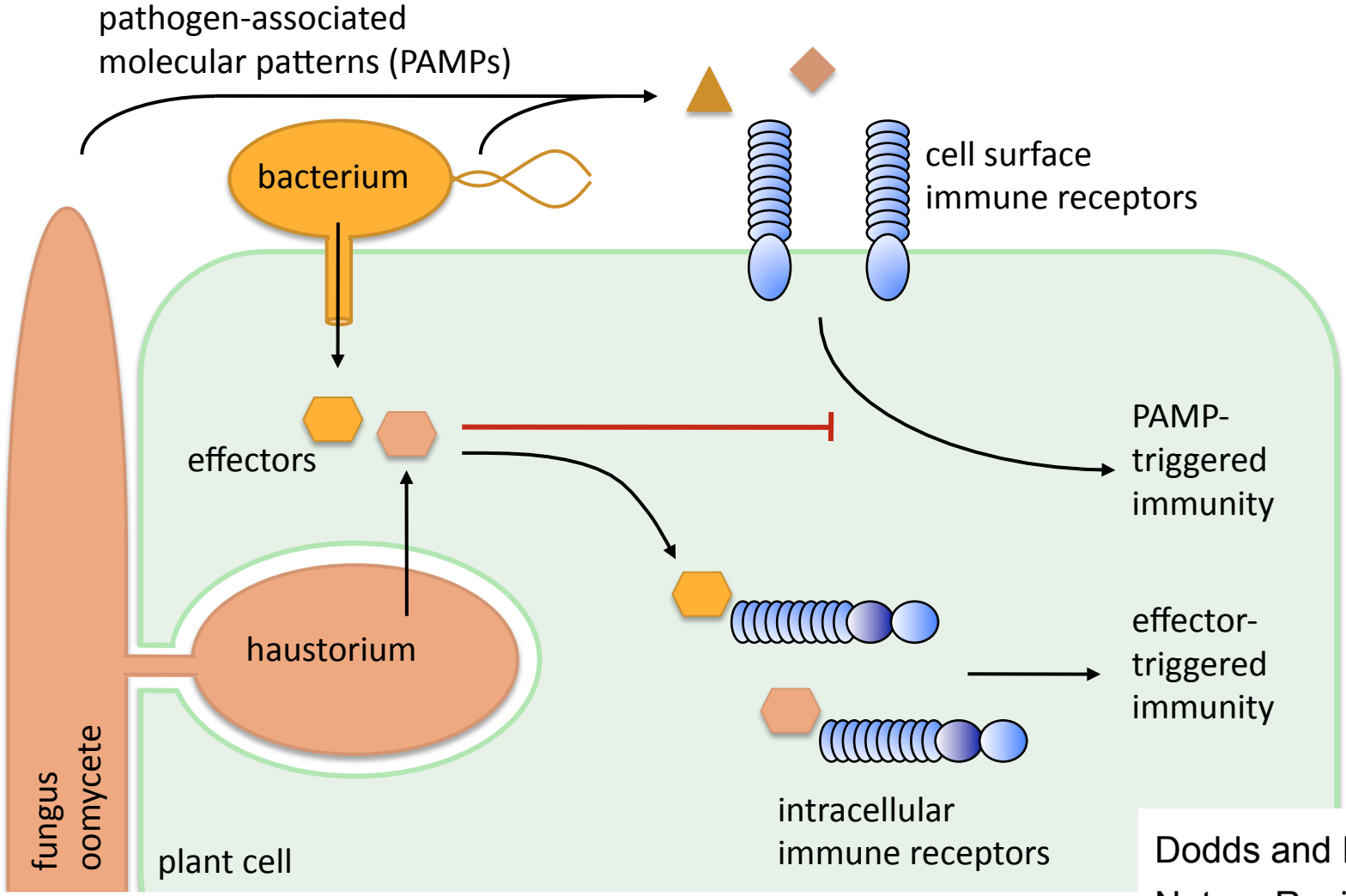
Microbes alter plant cell processes by secreting a diversity of effector molecules



Some effectors “trip on the wire” and activate immunity in particular plant genotypes

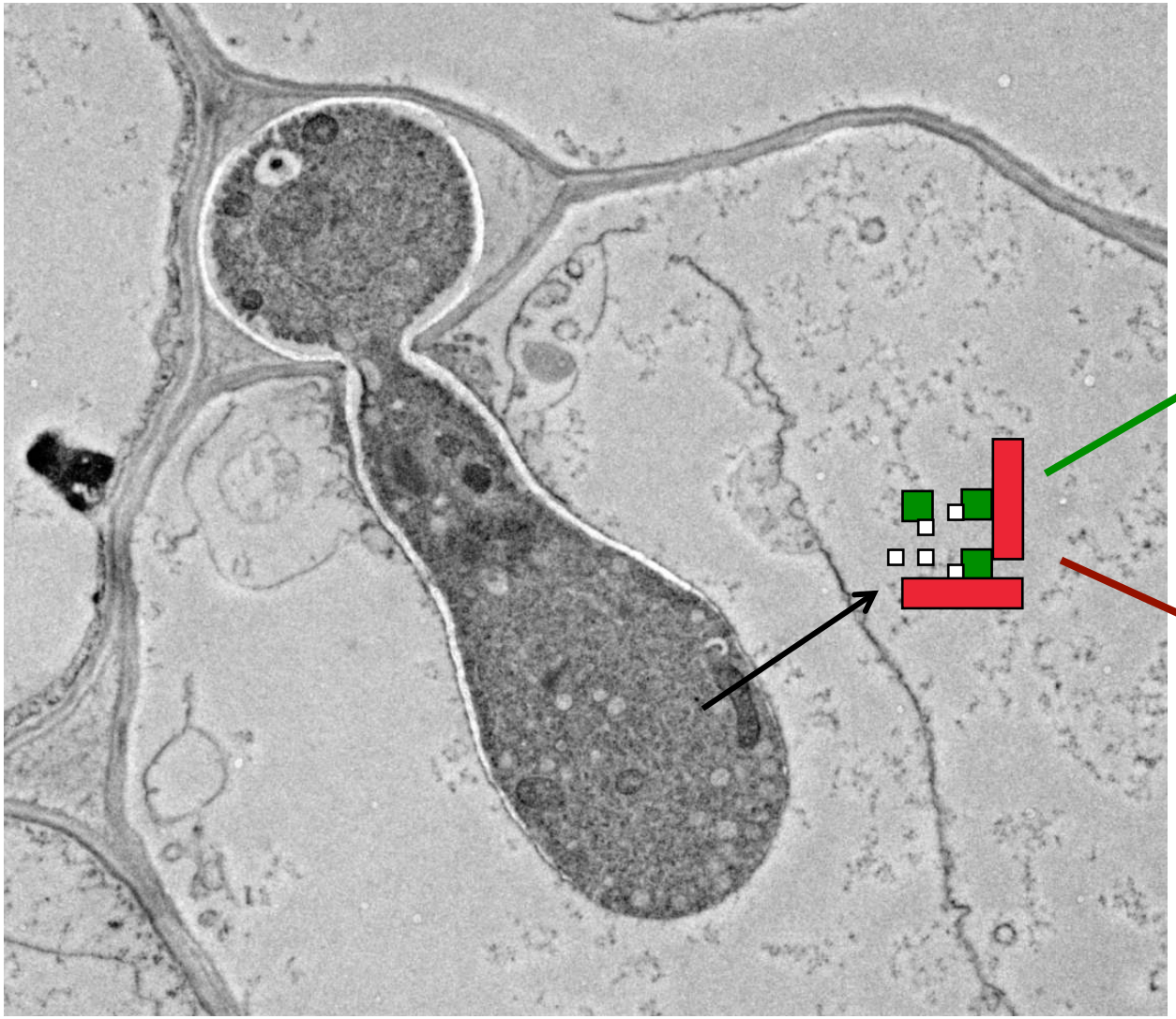


Surface receptors mediate basal immunity – often suppressed by effectors



Dodds and Rathjen 2010
Nature Reviews Genetics

P. infestans delivers effectors inside host cells to suppress or activate immunity



Suppress immunity

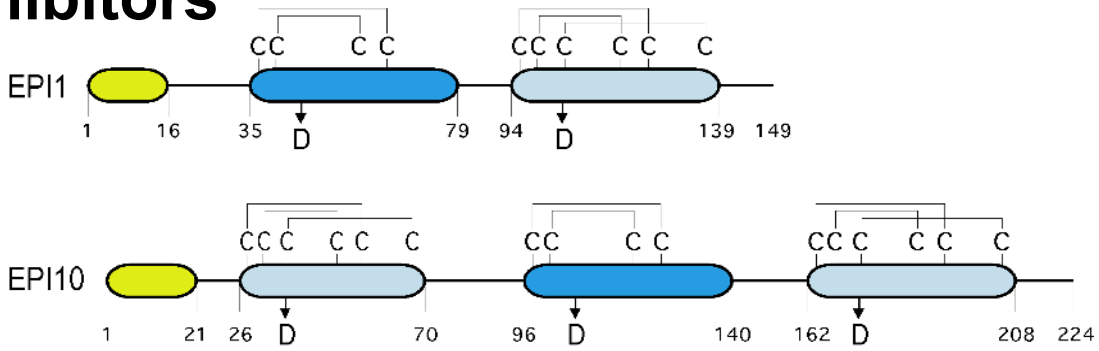
Trigger immunity

The diverse effectors of *Phytophthora infestans*

Protease inhibitors

Number

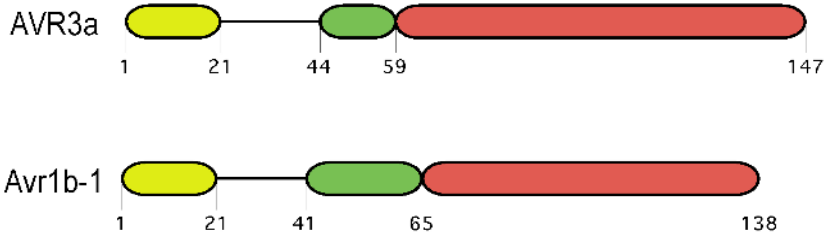
~38

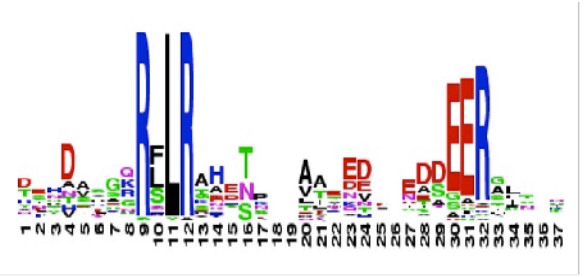


Apoplastic

RXLR

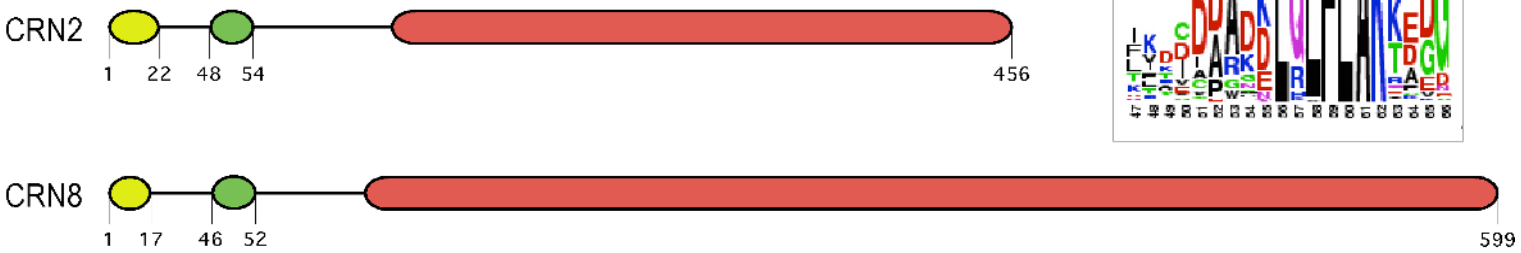
Host-translocated

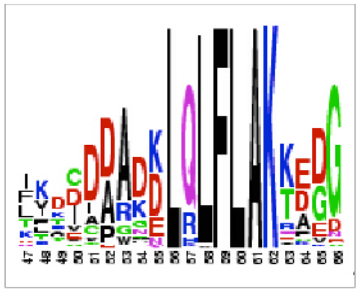




~550

Crinklers

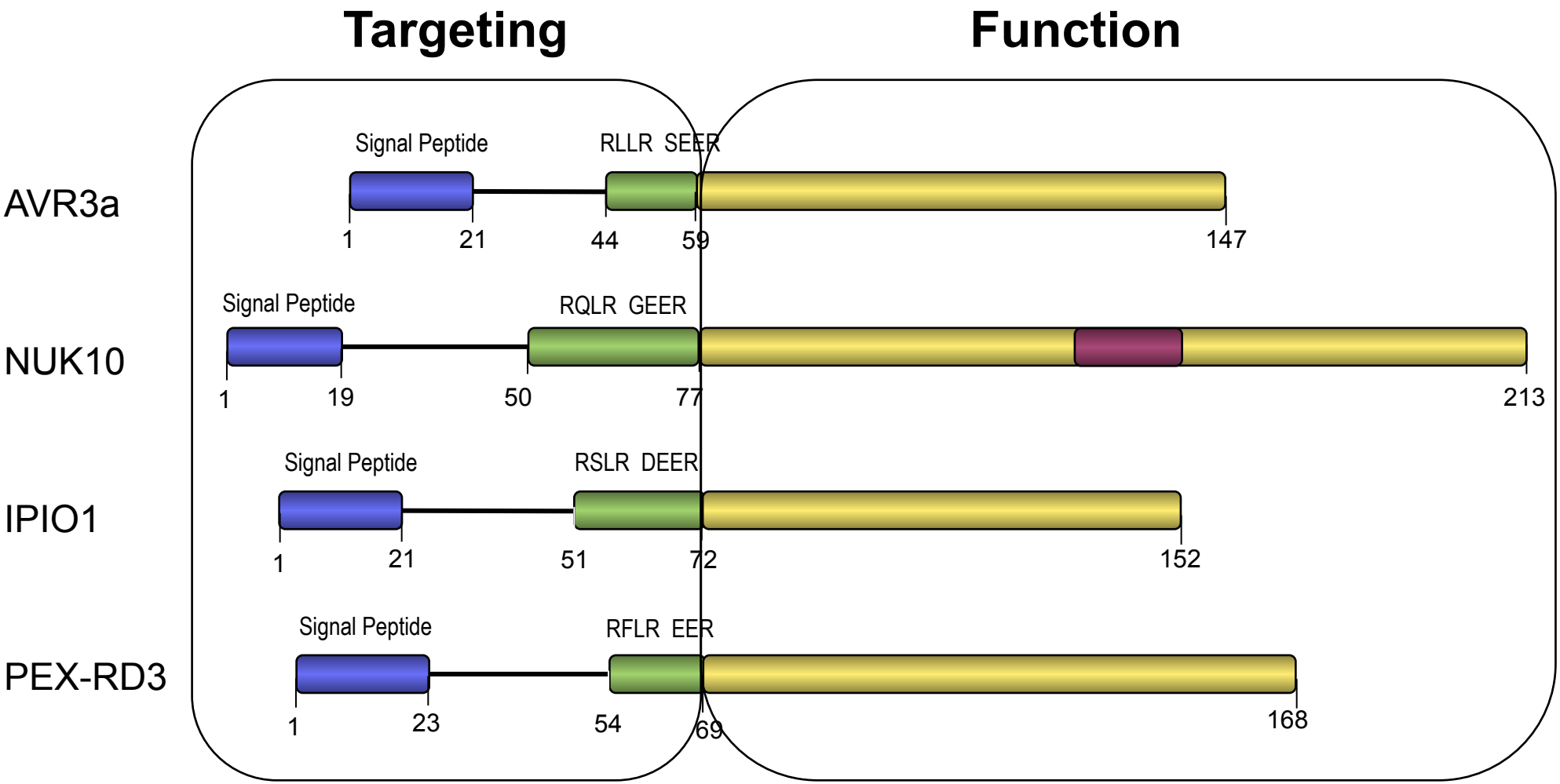




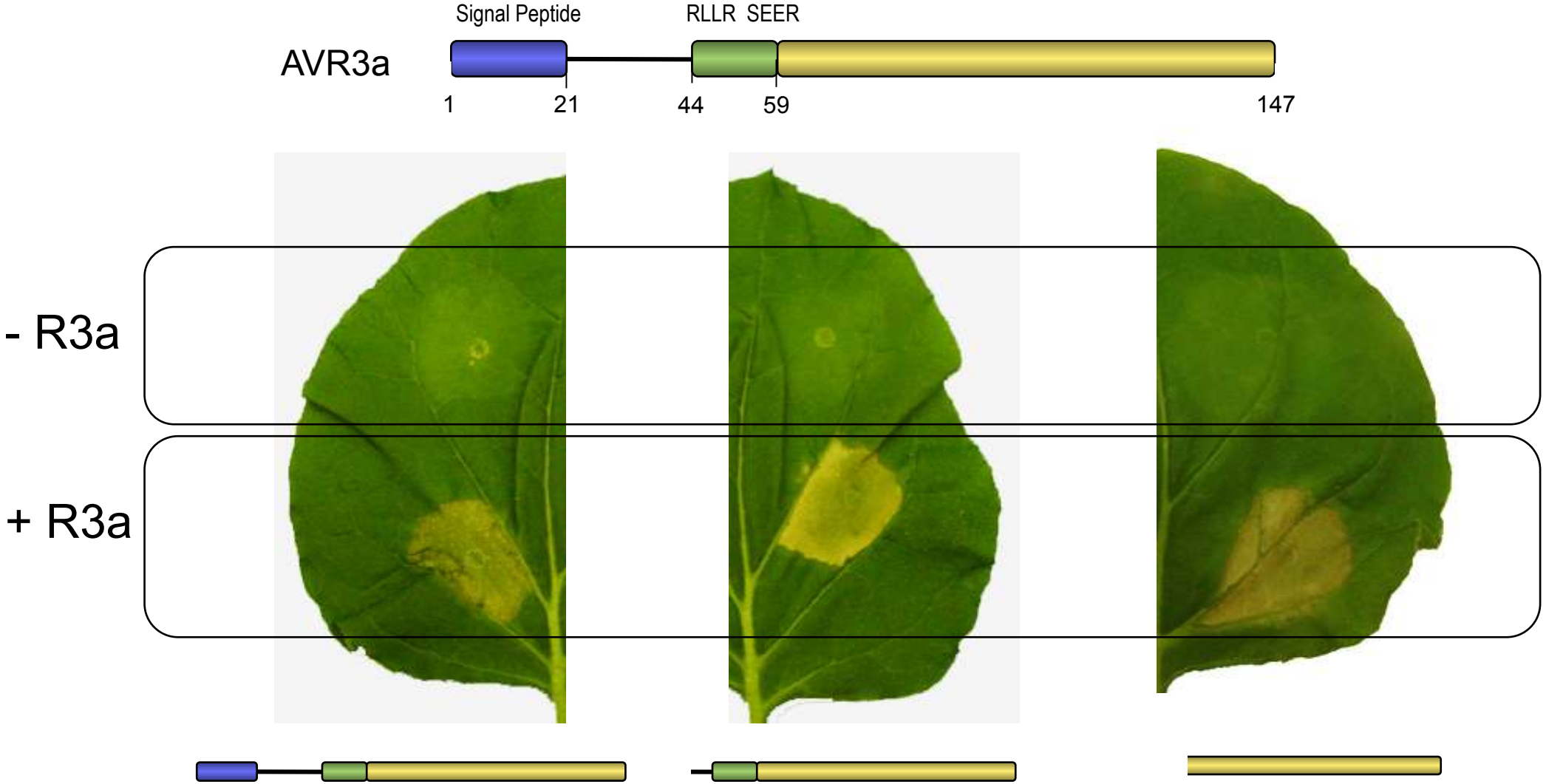
~200

~250ψ

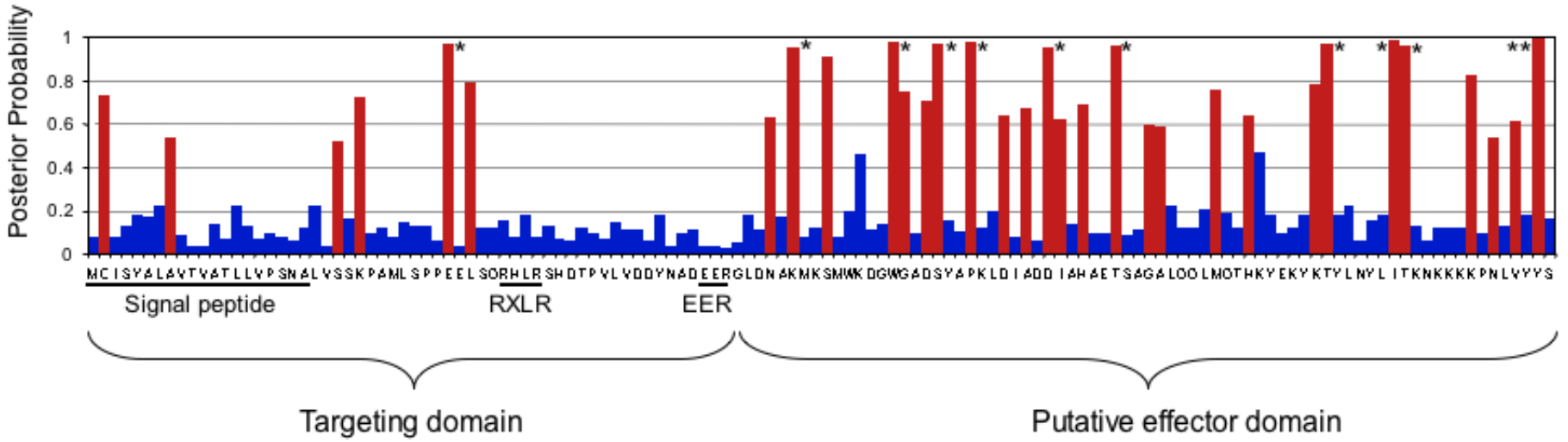
Modular structure of RXLR effectors



The C-terminal region of Avr3a is sufficient for triggering R3a dependent HR



Positive selection has targeted the C terminal domain of RXLR effectors (ML method in paml)




```
                                20                  40                  60                  80                 100                 120
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PiPGG1_4  ........................T.......E.....................................................T.......S.....................................
PiPGG1_1  .C.....A.............S.K.......E.L.........................N.K..S..K..WG.DS..P..D.A.D..H..T...A.......HK....KT.....IT.......N.V.Y.
PiPGG1_2  .......A.............S.K.......E.........................N.K..S..K..W..DN..P....A.D..H..T...A....T..HK....KT.....IT.....Q.N.V.Y.
```
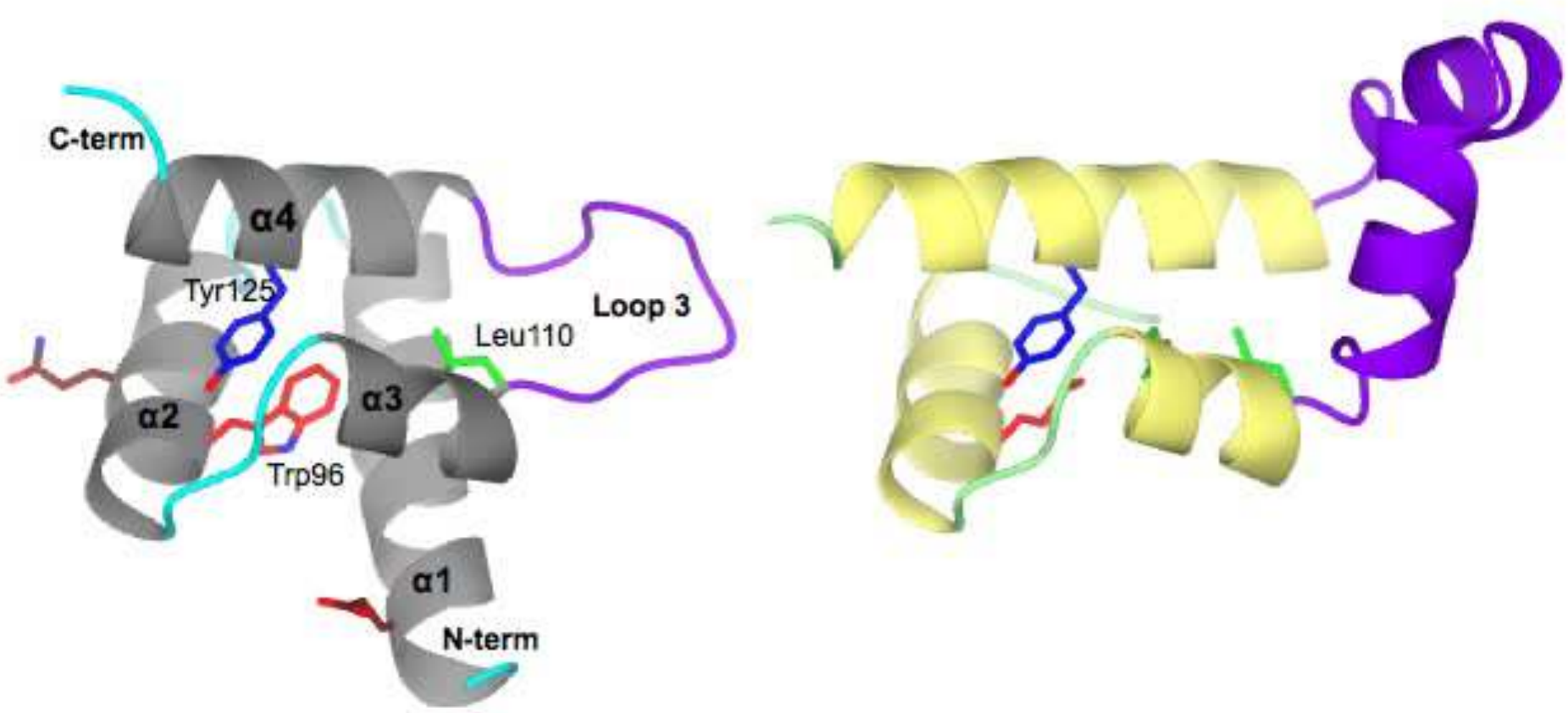

- Consistent with the view that RXLR effectors are modular

Win et al. Plant Cell, 2007

RXLR effector proteins have conserved but adaptable structures



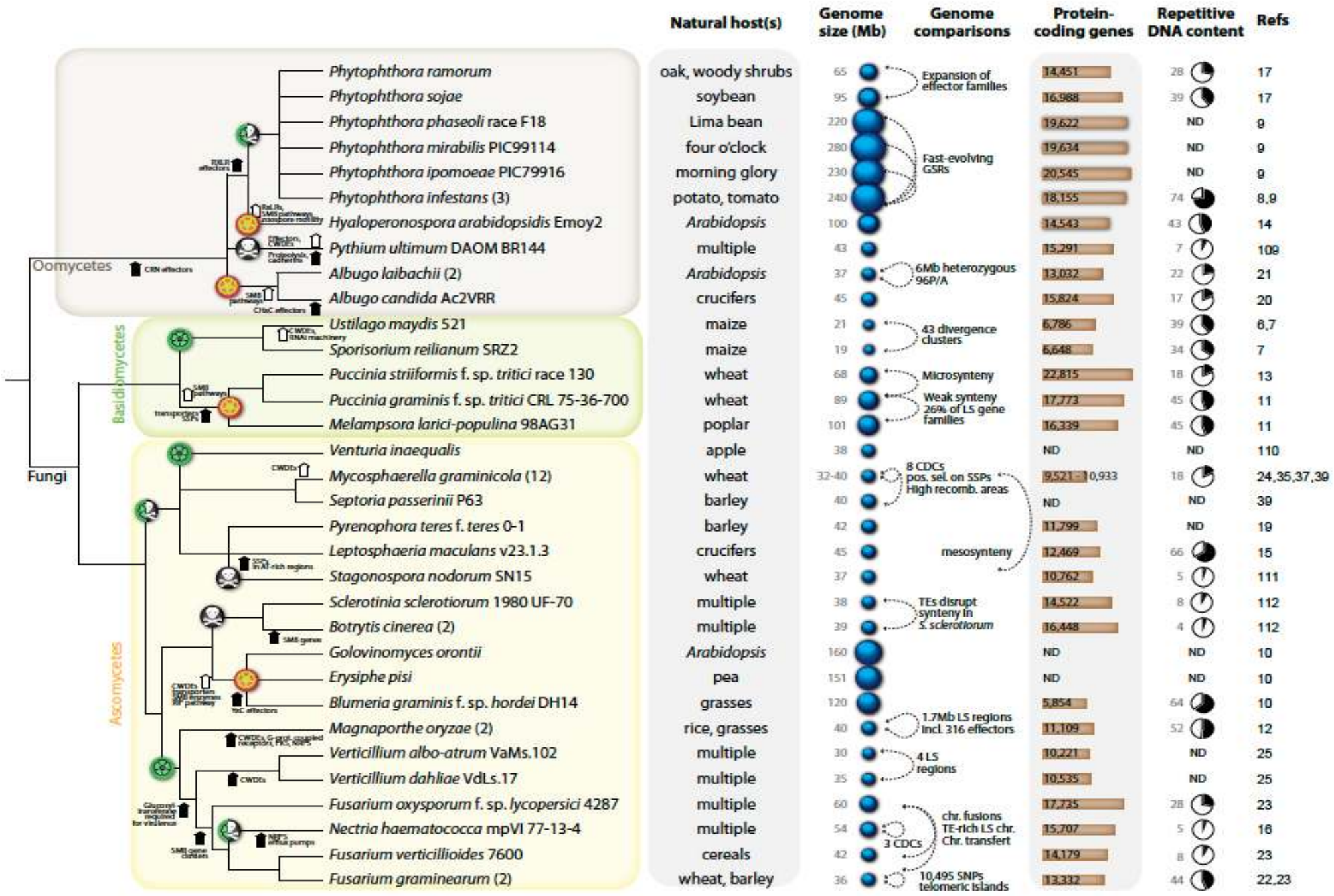
Mark Banfield Lab @ John Innes Centre

Boutemy et al. JBC 2011

Win et al. PLoS Pathogens 2012

Questions driving oomycete effector research

- How do effectors traffic inside host cells?
- How do they vary within and between pathogen species? How do they evolve?
- How do they function? What are their host targets? How do they perturb plant processes?
- How are effectors recognized by plant immune receptors? How can this be exploited to develop resistant crops?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oak, woody shrubs
soybean
Lima bean
four o'clock
morning glory
potato, tomato
Arabidopsis
multiple
Arabidopsis
crucifers
maize
maize
wheat
wheat
poplar
apple
wheat
barley
barley
crucifers
wheat
multiple
multiple
Arabidopsis
pea
grasses
rice, grasses
multiple
multiple
multiple
multiple
cereals
wheat, barley
65
95
220
280
230
240
100
43
37
45
21
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68
89
101
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32-40
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37
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36
Expansion of effector families
Fast-evolving GSRs
6Mb heterozygous 96P/A
43 divergence clusters
Microsynteny
Weak synteny
26% of LS gene families
8 CDCs
pos. sel. on SSPs
High recomb. areas
mesosynteny
TEs disrupt synteny in S. sclerotiorum
1.7Mb LS regions
Incl. 316 effectors
4 LS regions
chr. fusions
TE-rich LS chr.
Chr. transfert
3 CDCs
10,495 SNPs
telomeric islands
14,451
16,988
19,622
19,634
20,545
18,155
14,543
15,291
13,032
15,824
6,786
6,648
22,815
17,773
16,339
ND
9,521 - 10,933
ND
11,799
12,469
10,762
14,522
16,448
ND
ND
5,854
11,109
10,221
10,535
17,735
15,707
14,179
13,332
28
39
ND
ND
ND
74
43
7
22
17
39
34
18
45
45
ND
18
ND
ND
66
5
8
4
ND
ND
64
52
ND
ND
28
5
8
44
17
17
9
9
9
8,9
14
109
21
20
6,7
7
13
11
11
110
24,35,37,39
39
19
15
111
112
112
10
10
10
12
25
25
23
16
23
22,23
obligate biotroph;
biotroph;
hemibiotroph;
necrotroph.
gene/pathways losses
gene gain or gene families expansion
non-repetitive
repetitive

The genome sequence of *Phytophthora infestans*

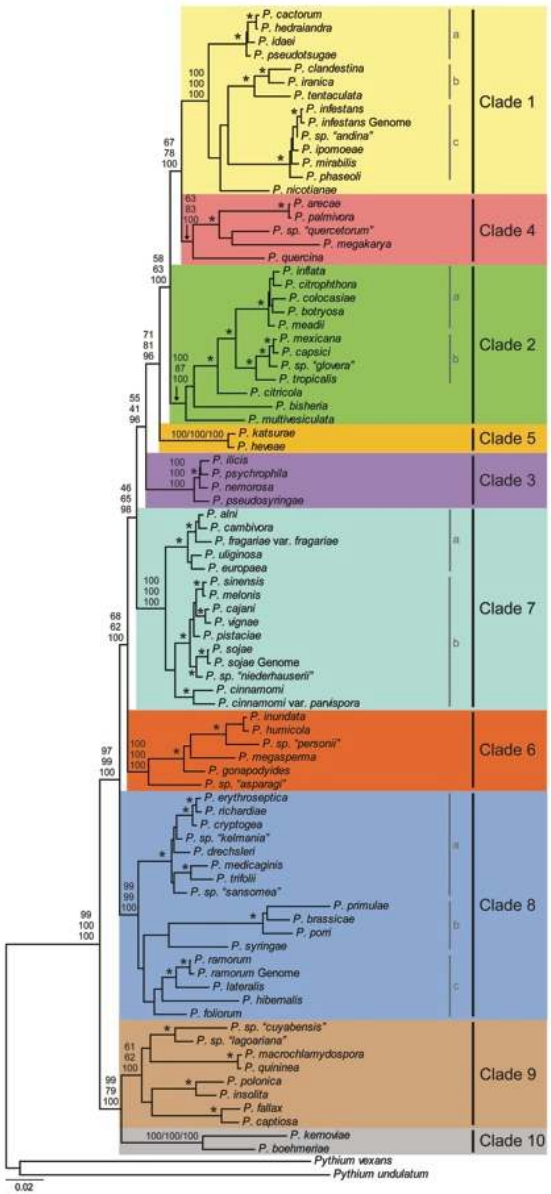
Brian Haas, Mike Zody, and Chad Nusbaum @ Broad Institute

NSF

NRI
Knowledge For Tomorrow's Solutions

BROAD INSTITUTE

Oomycete genome sequences from divergent species



- *Phytophthora infestans* (240 Mbp) - *Solanum* spp.
- *P. capsici* (65 Mbp) - pepper, tomato, cucurbits
- *P. sojae* (95 Mbp) - soybean
- *P. ramorum* (65 Mbp) - various woody plants
- *Hyalop. arabidopsidis* (100 Mbp) - Arabidopsis
- *Pythium ultimum* (50 Mbp) - various dicots

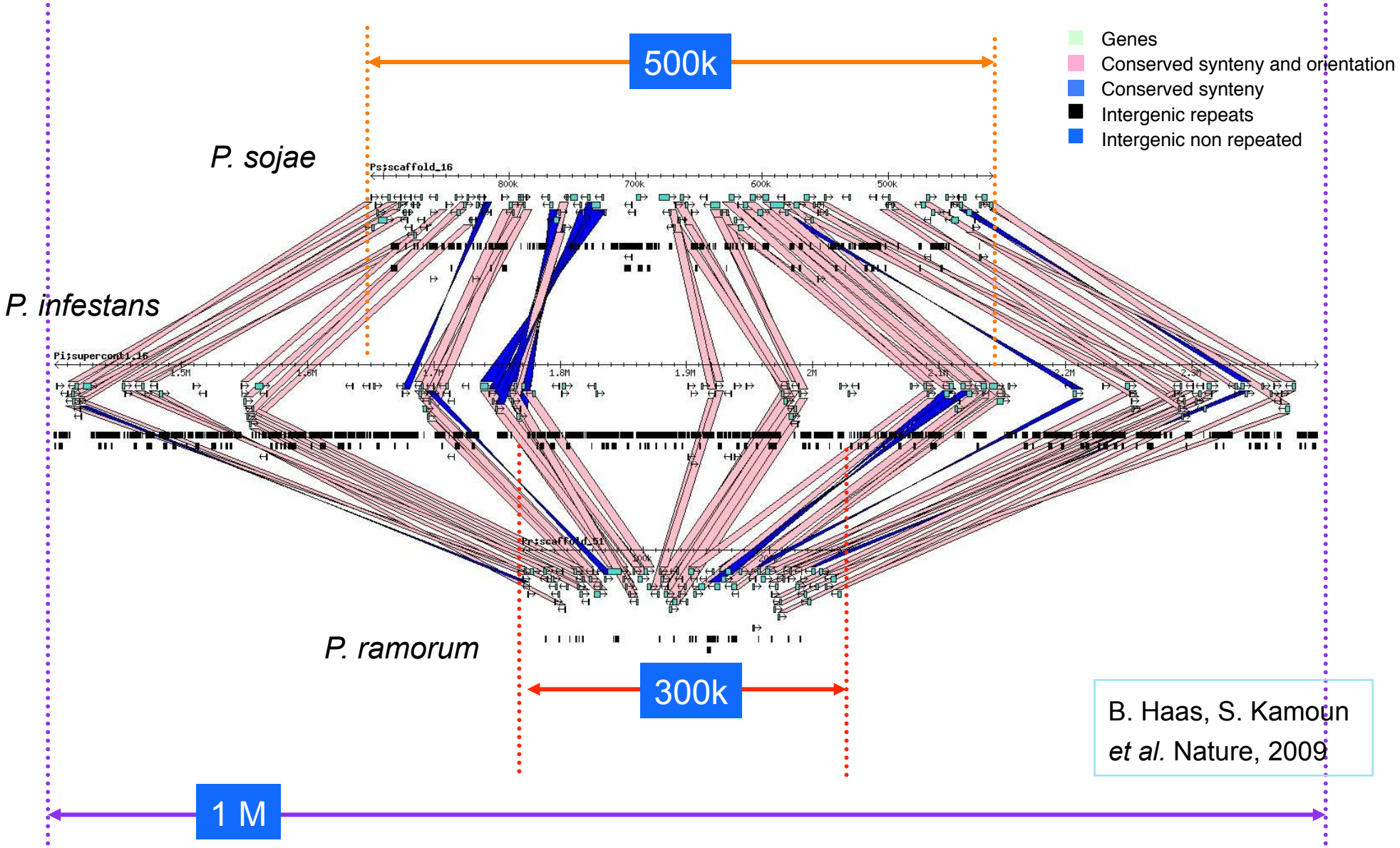
multilocus phylogeny of *Phytophthora* from Blair et al. 2008 Fungal Genet Biol

Major features of the genome of *P. infestans*

	P. infestans	*P. sojae*	*P. ramorum*
Estimated genome size	240 Mbp	95 Mbp	65 Mbp
Number of genes	17,887	16,988	14,451
Orthologous genes	11,893	12,427	12,136
Colinear blocks	85 Mbp	52 Mbp	37 Mbp
Repeats	74%	39%	28%
Repeats in colinear blocks	57%	28%	13%
Repeats outside colinear	86%	60%	56%

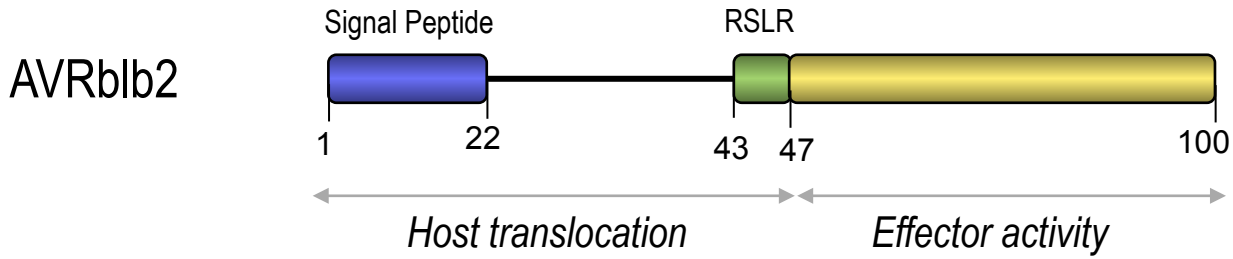
• Repeat driven expansion of the *P. infestans* genome

Significant 1:1:1 orthology and colinearity between *P. infestans*, *P. sojae* and *P. ramorum*



B. Haas, S. Kamoun *et al.* Nature, 2009

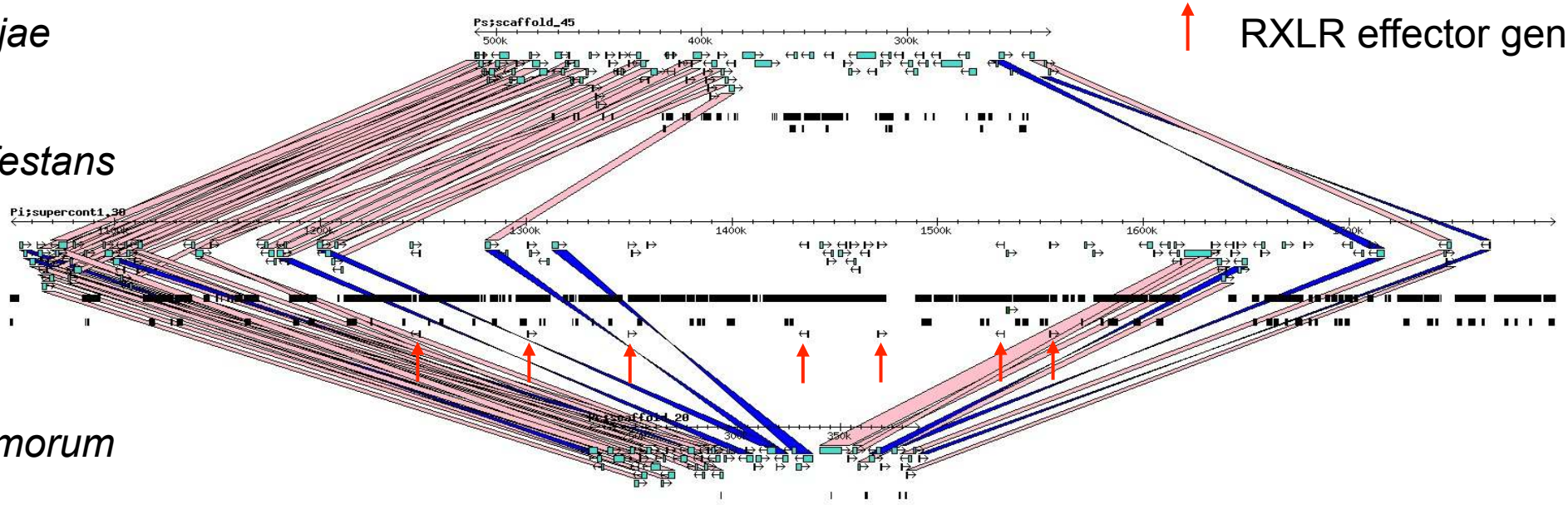
RXLR effectors typically occur in expanded, repeat-rich and gene-poor loci



P. sojae

P. infestans

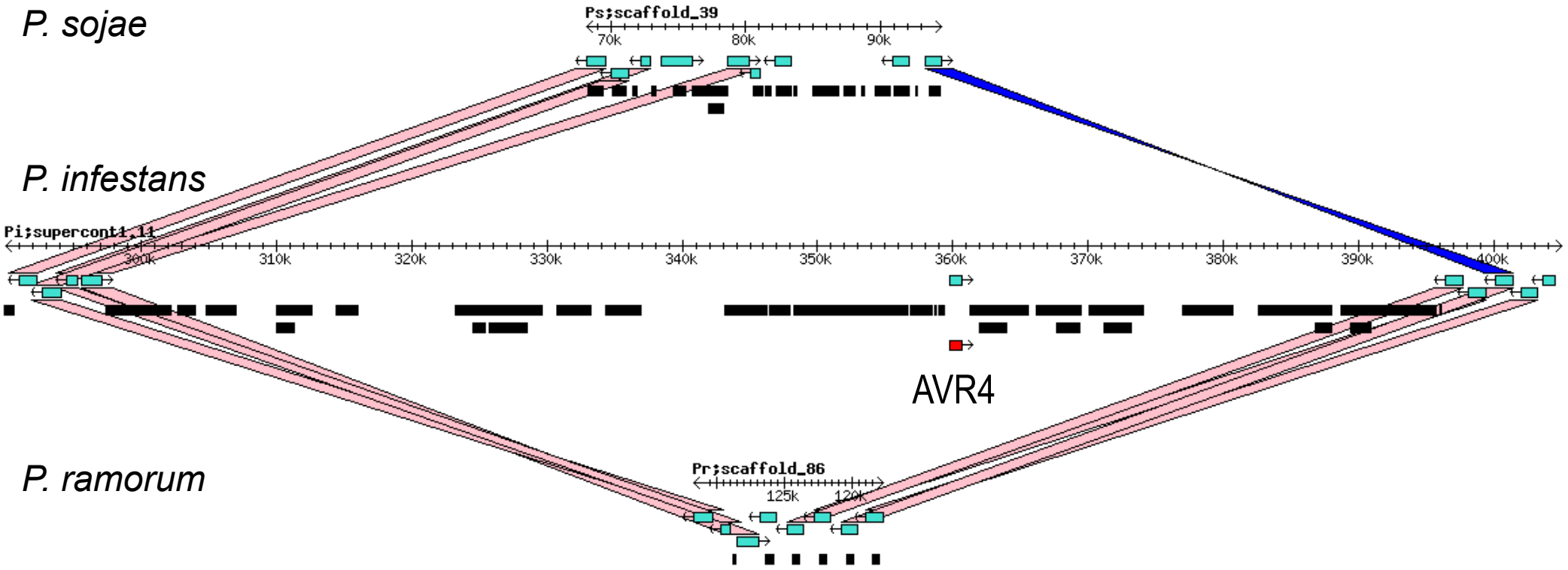
P. ramorum



RXLR effector gene

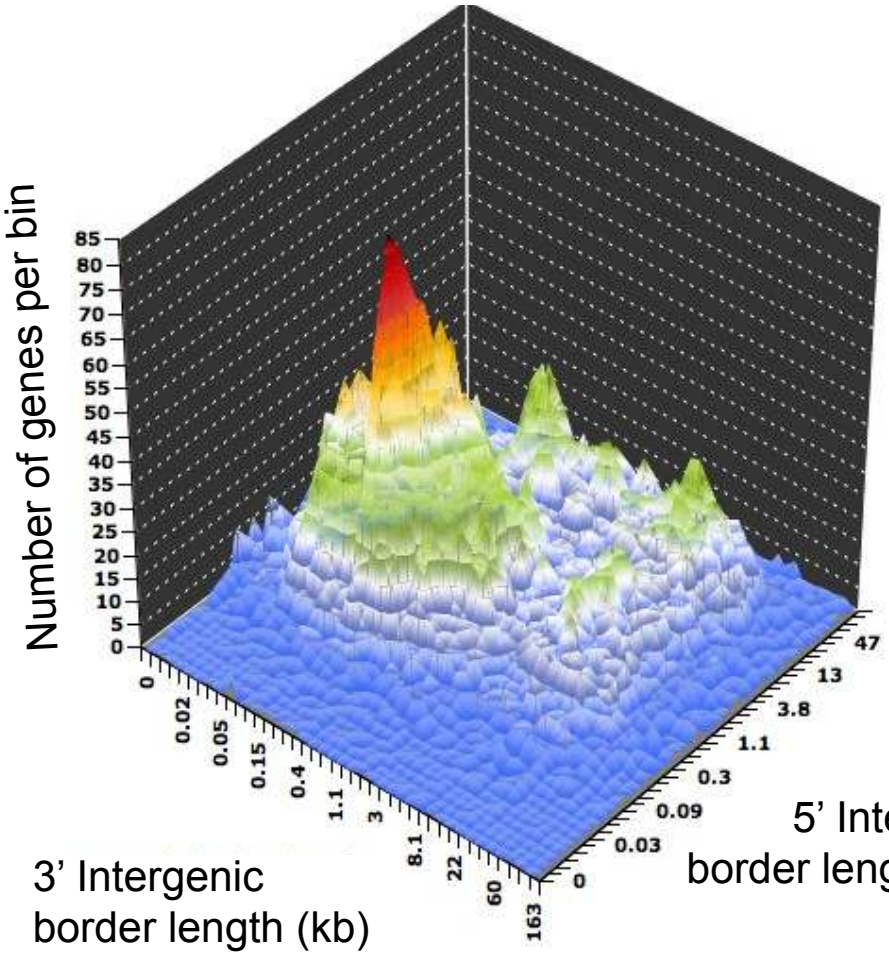
B. Haas, S. Kamoun *et al.* Nature, 2009

AVR4: a single gene in a repeat-rich expanded ~100 kb locus

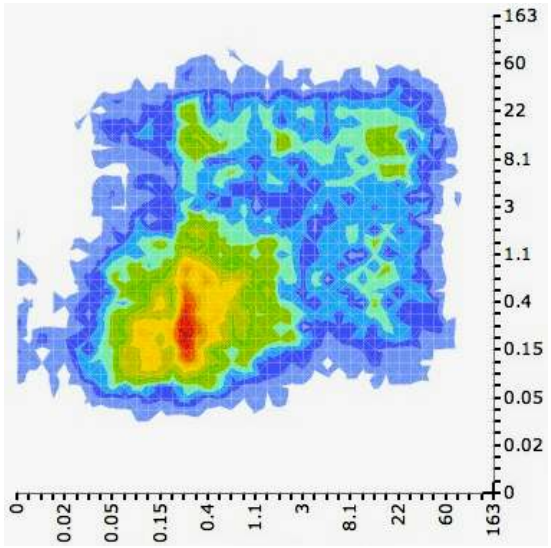


P. infestans genome shows an unusual variability in intergenic region length (gene density)

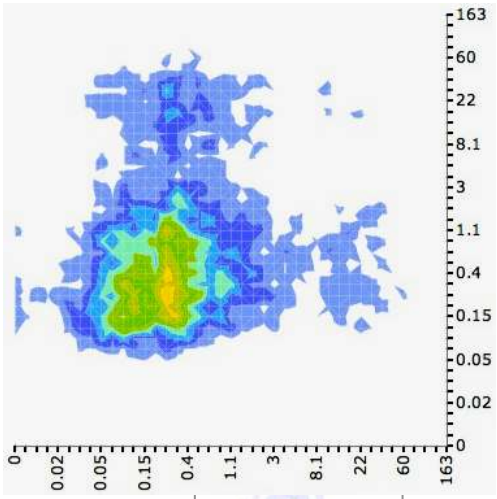
P. infestans (16442 genes)



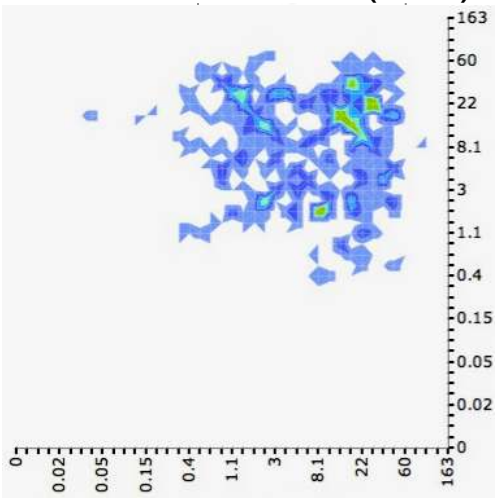
P. infestans (16442)



Core orthologs (7580)

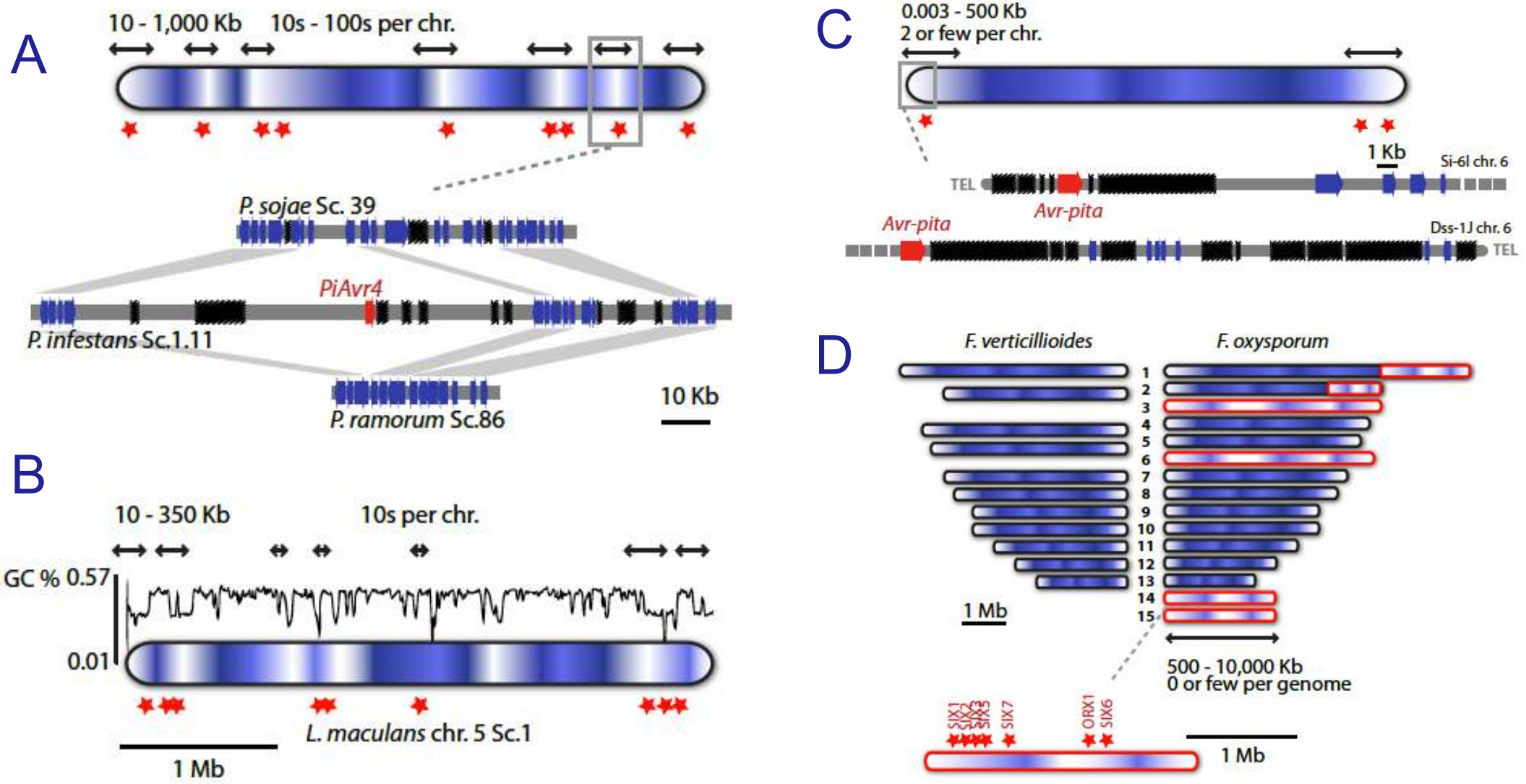


RXLR effectors (520)

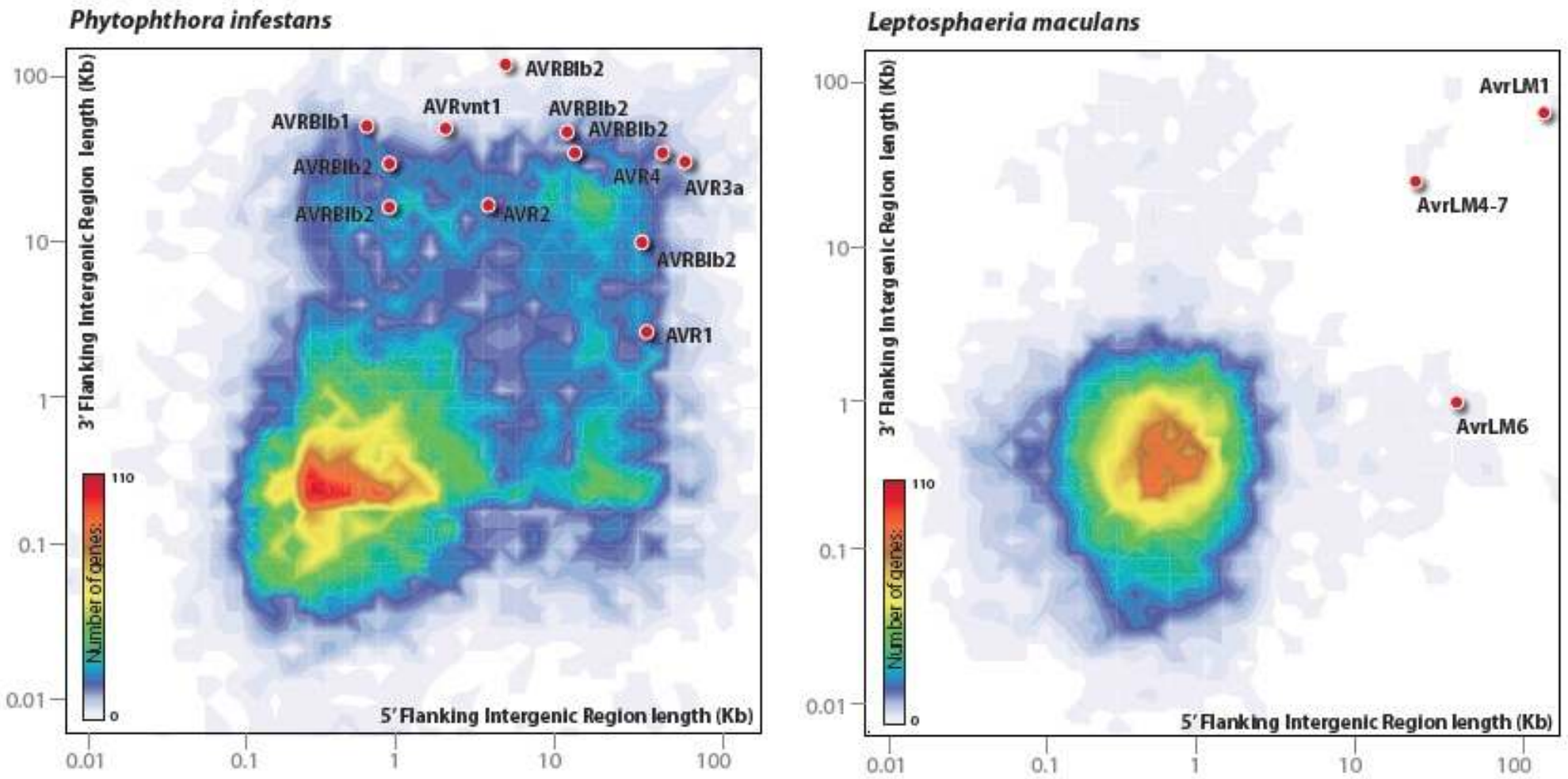


Sylvain Raffaele, Brian Haas

Effector genes populate plastic regions of filamentous plant pathogen genomes

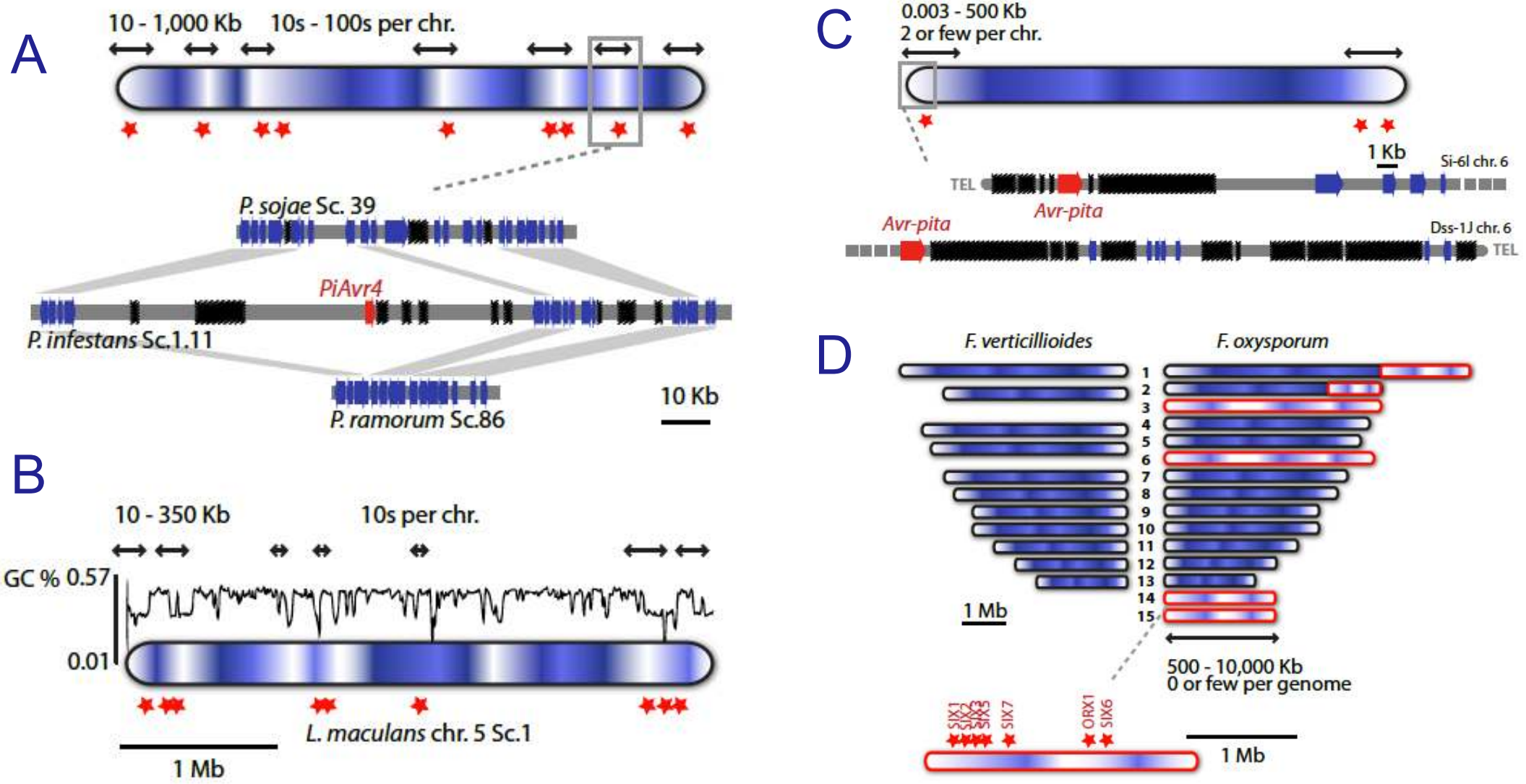


P. Infestans gene-sparse vs *L. maculans* isochore-like regions



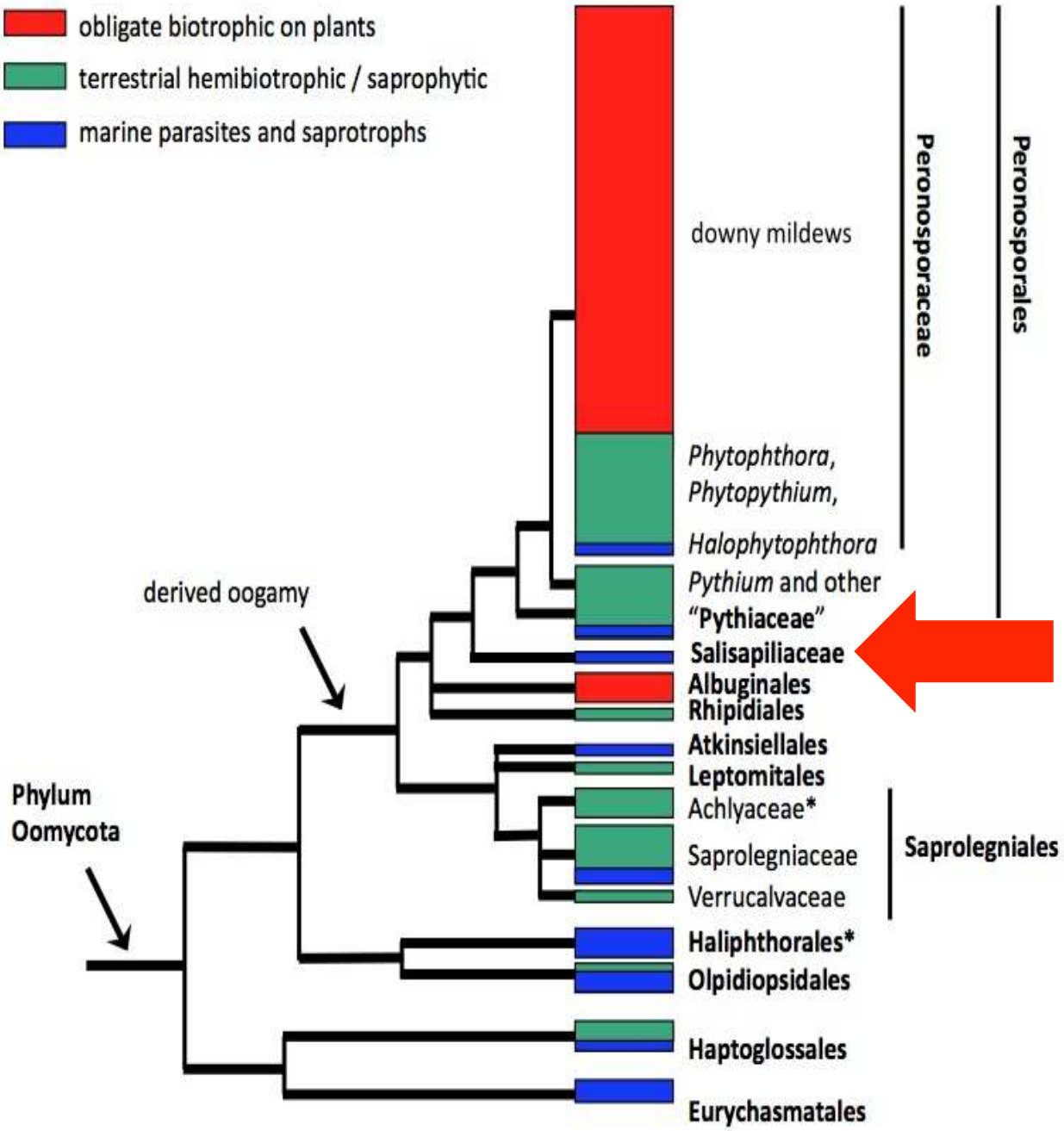
Sylvain Raffaele; with thanks to Thierry Rouxel

Effector genes populate plastic regions of filamentous plant pathogen genomes

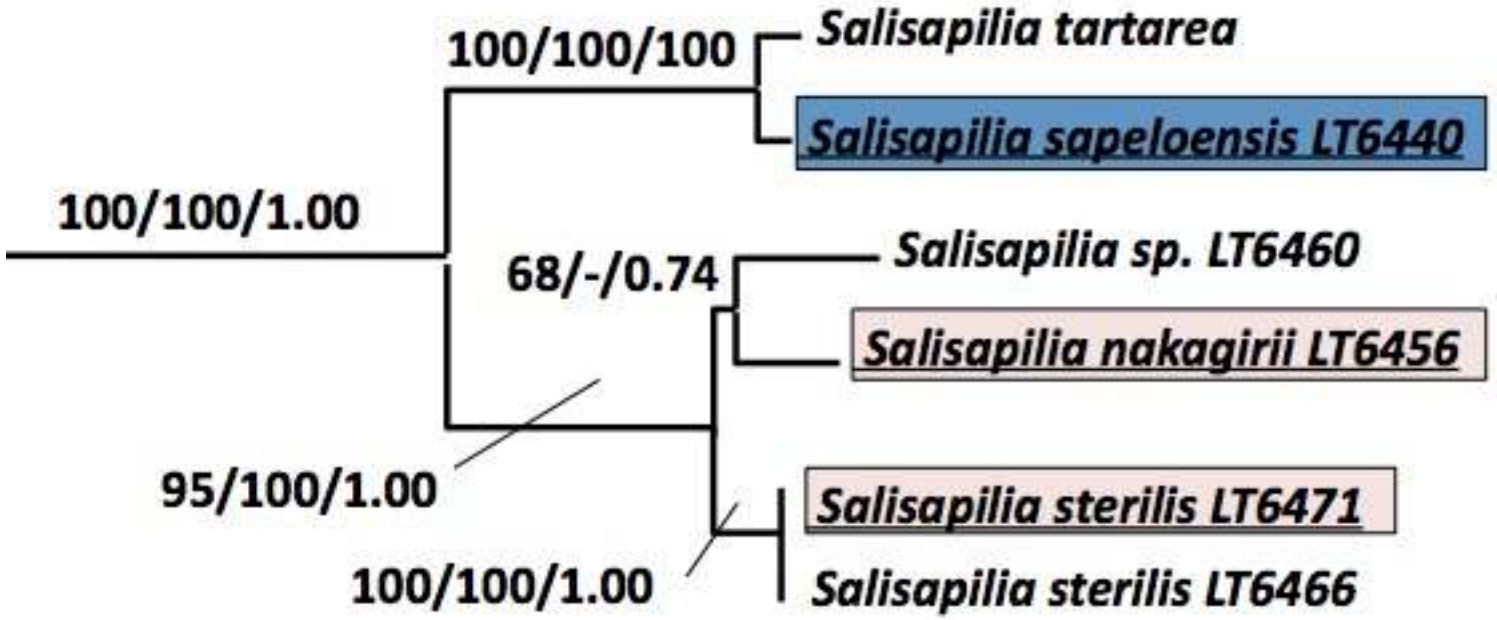


Salisapiliaceae: a new family of salt march saprophytes

Hulvey *et al*. Persoonia 2010



Salisapilia genomes are significantly reduced relative to other oomycetes



Species	Total No contigs	Average length	Longest contig	Number of bases assembled (Mb)	N50
S. sapeloensis LT6440	4363	5305.1	176061	23.1	29926
S. nakagirii LT6456	2020	13812.4	281703	27.9	71080
S. sterilis LT6471	2430	8544.3	283395	20.8	47392

Diane Saunders

Reduction and Compaction in the Genome of the Apicomplexan Parasite *Cryptosporidium parvum*

Parasites genomes are often considered to be "reduced" or "degenerate," but exactly what do these terms mean? How various are the forces that affect genome size and density, and how do their effects differ in different parasites?

The genome of *Tetranychus urticae* reveals herbivorous pest adaptations

At 90 megabases *T. urticae* has the smallest sequenced arthropod genome.

Extreme genome reduction in symbiotic bacteria

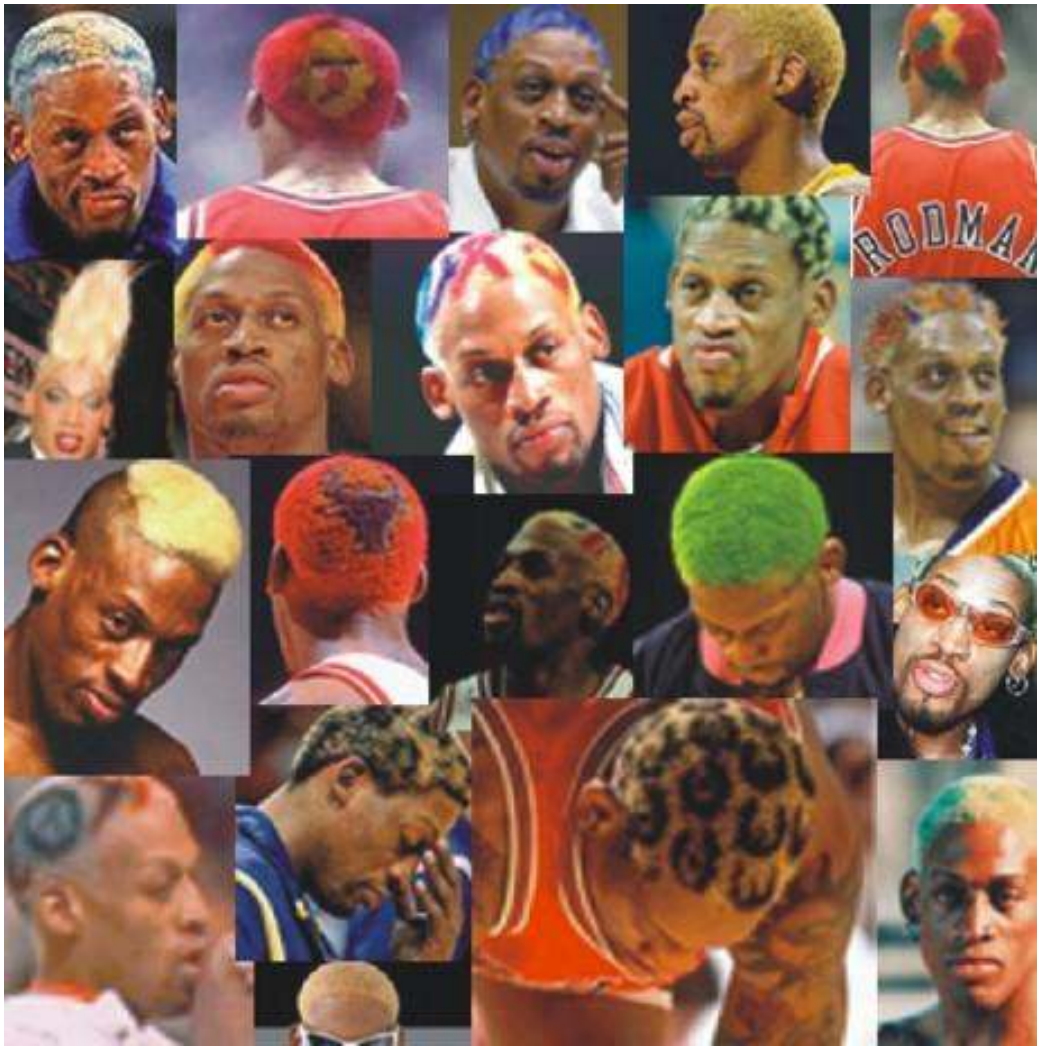
John P. McCutcheon[1] and Nancy A. Moran[2]

Sequence and genetic map of *Meloidogyne hapla*: A compact nematode genome for plant parasitism

Charles H. Opperman[a,b,c], David M. Bird[a,b], Valerie M. Williamson[d], Dan S. Rokhsar[e], Mark Burke[a], Jonathan Cohn[a], John Cromer[a], Steve Diener[a,f], Jim Gajan[a], Steve Graham[a], T. D. Houfek[a,g], Qingli Liu[d,h], Therese Mitros[i], Jennifer Schaff[a,j], Reenah Schaffer[a], Elizabeth Scholl[a], Bryon R. Sosinski[k,l], Varghese P. Thomas[d], and Eric Windham[a]

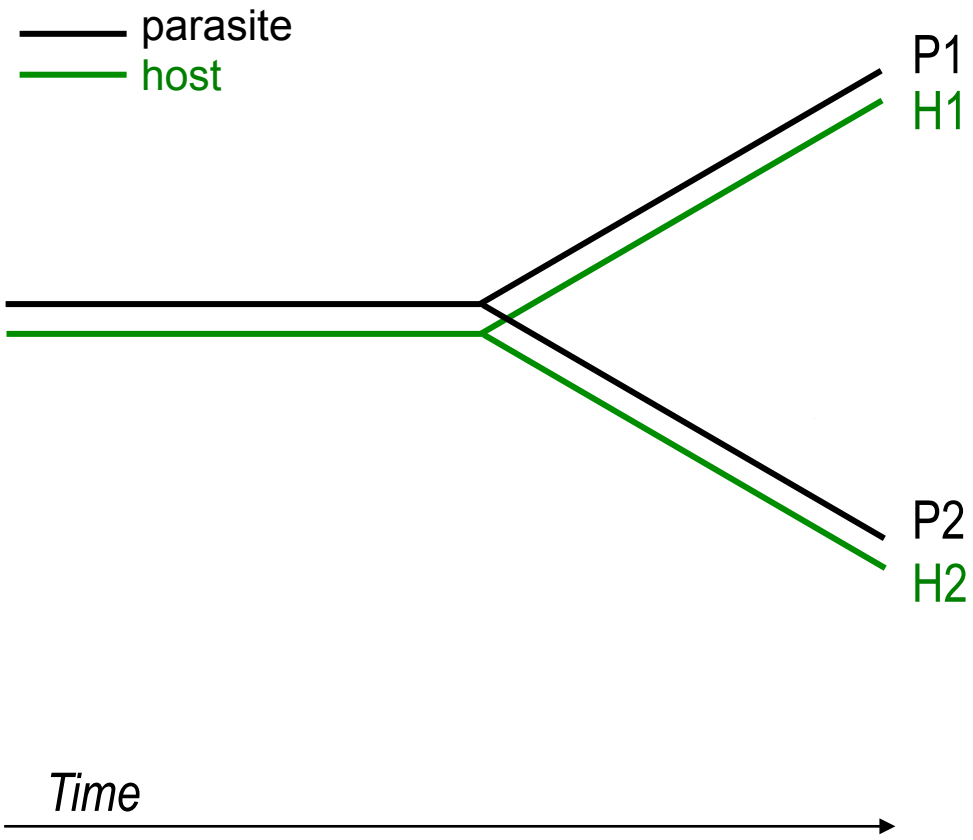
- Why is bigger better in filamentous plant pathogens?
- Which evolutionary tradeoffs counterbalance the cost of the larger genomes?

How do pathogens adapt to environmental change?
How does environmental change impact genome evolution?

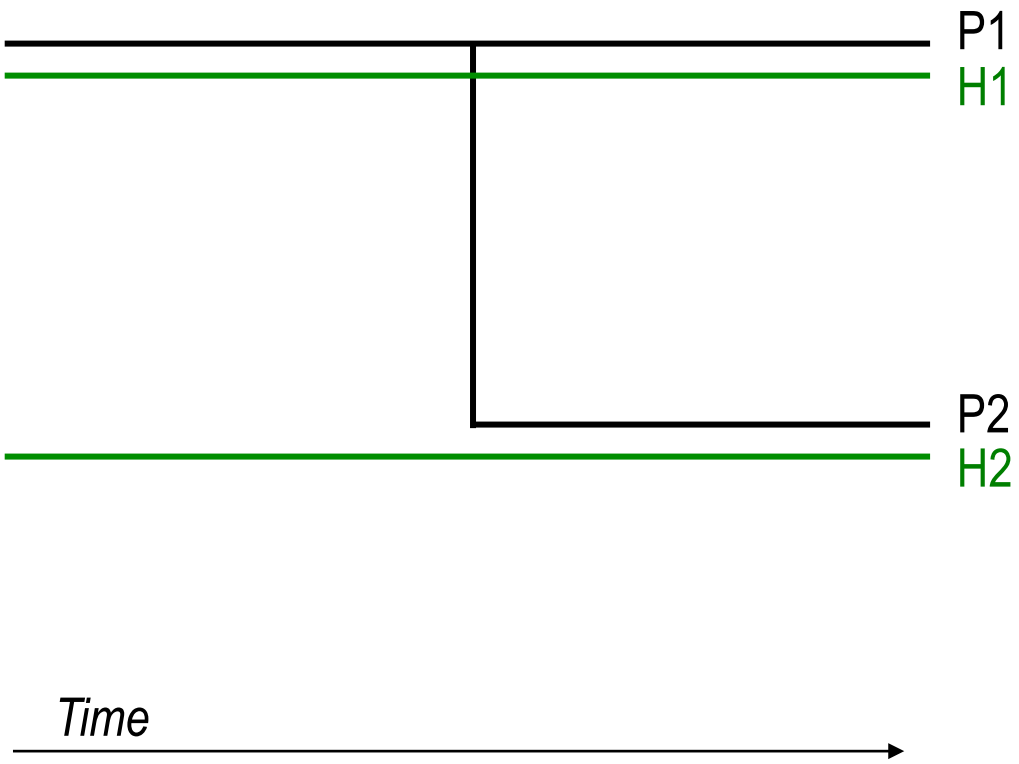


Models of host-parasite evolution

coevolution / cospeciation

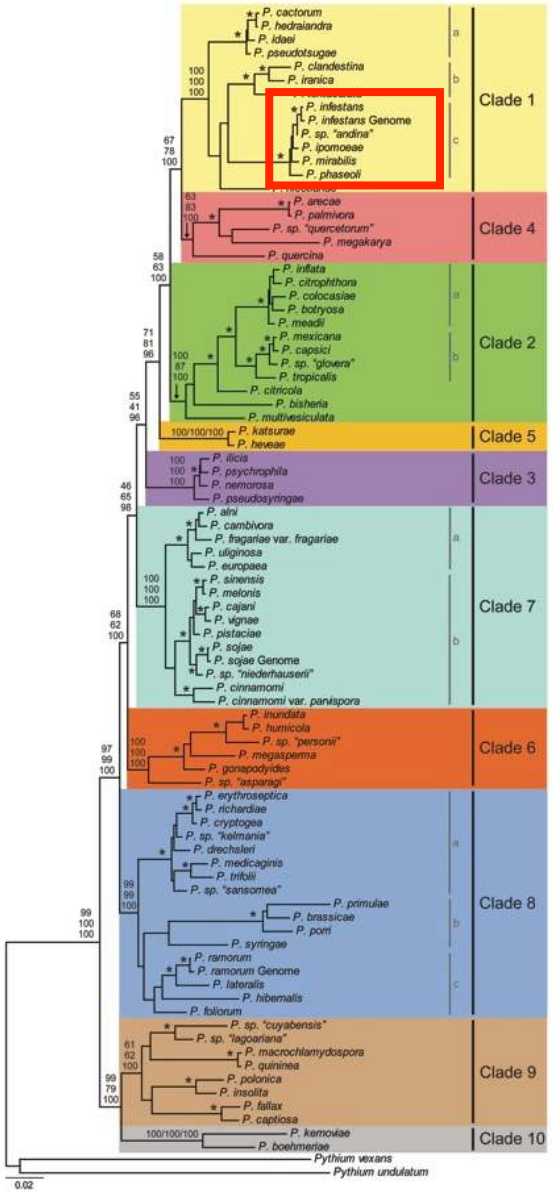


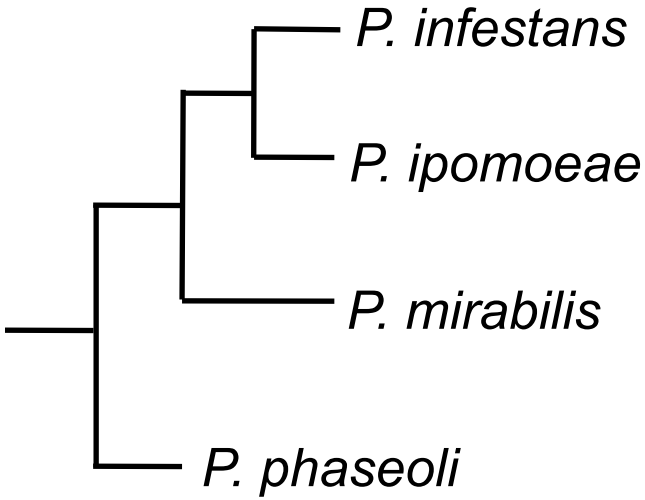
host-jumps / host-shifts

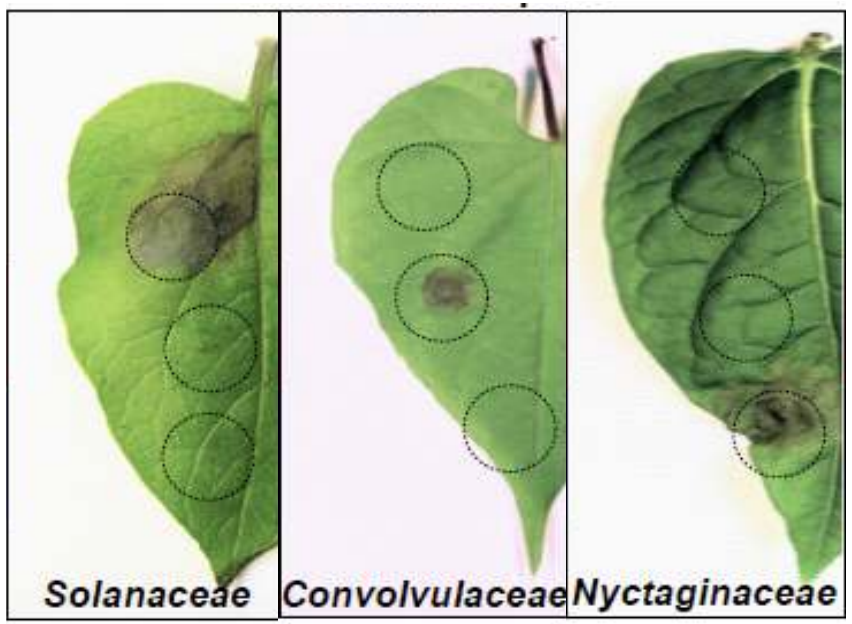


BA Roy, Evolution 2001

Species in the *Phytophthora infestans* lineage (clade 1c) evolved by host jumps



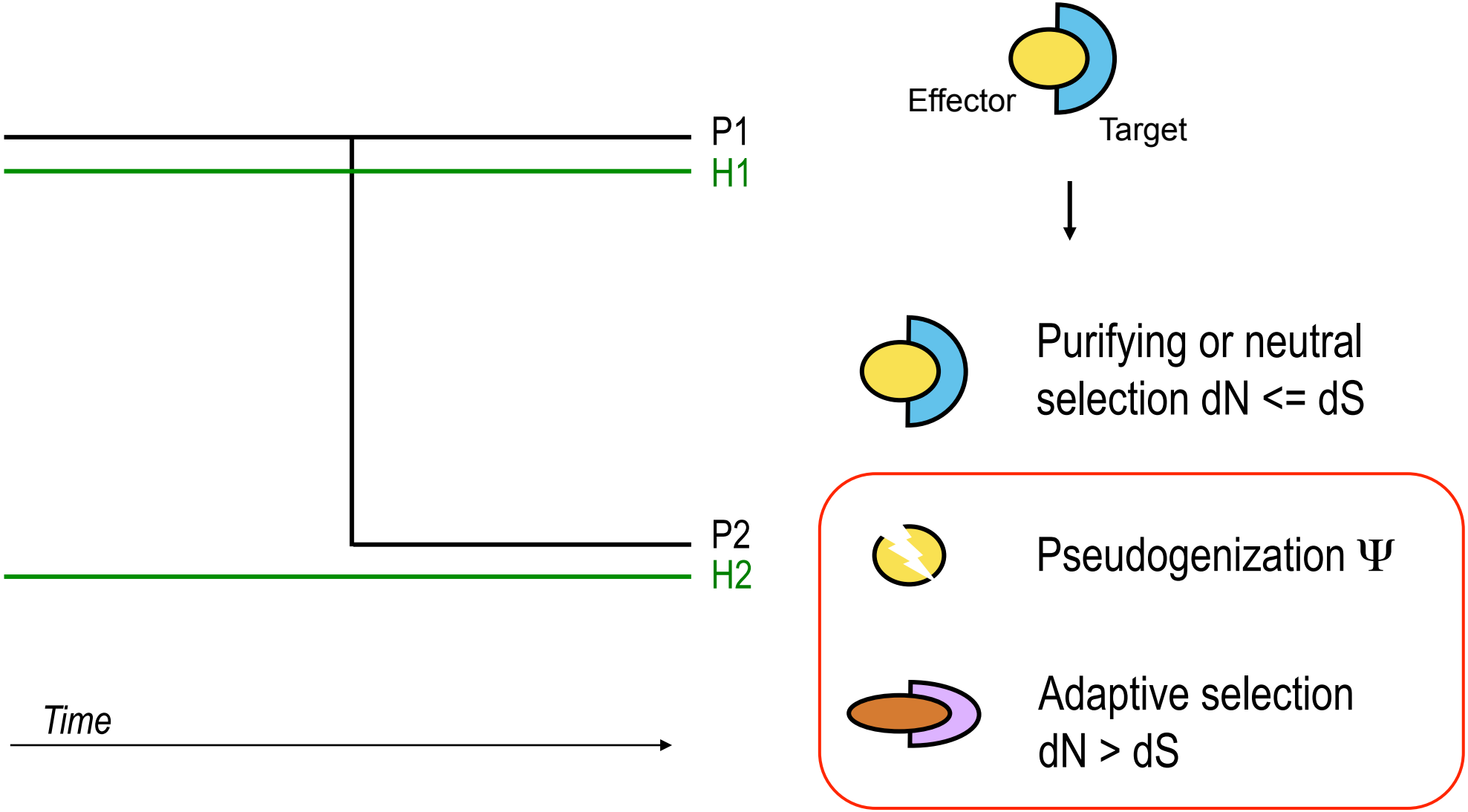




- "Recently" diverged: 99.9% identical in ITS
- Three species naturally co-occur in Toluca, Mexico
- Specialized on their respective hosts

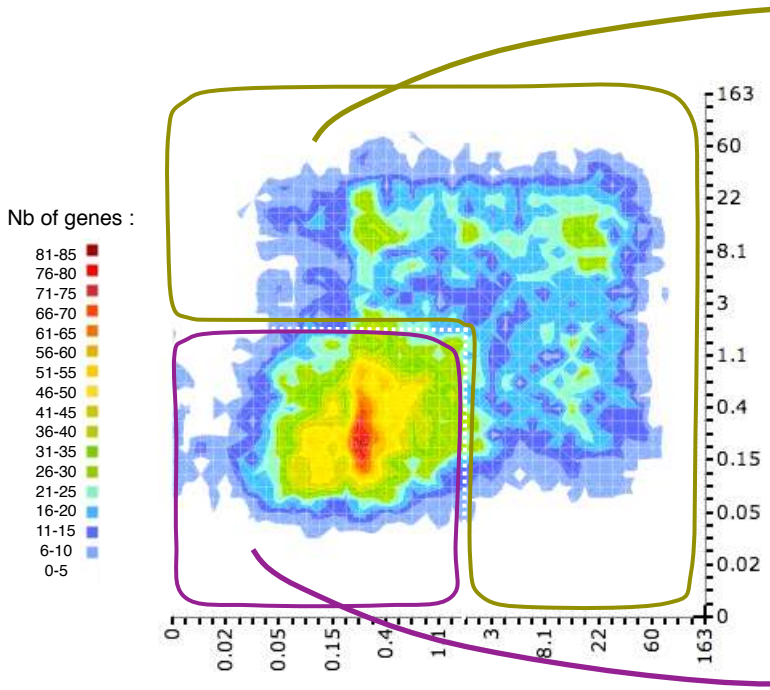
multilocus phylogeny of *Phytophthora* from Blair et al. 2008 Fungal Genet Biol

Host jumps must have a dramatic impact on effector evolution

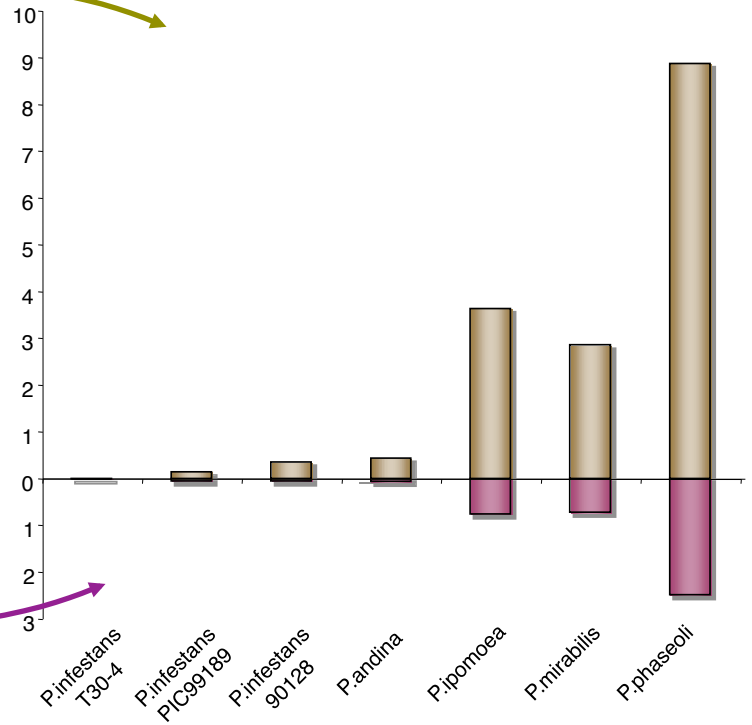


Genes in repeat-rich regions are more likely to be missing in sister species: 4X faster turnover

Length of intergenic regions (Kb)

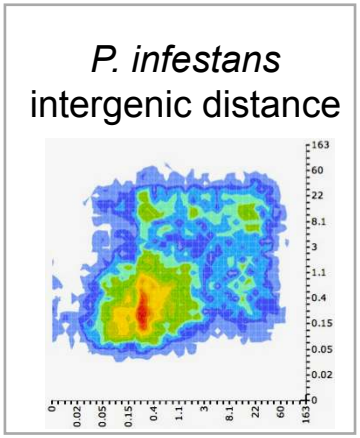


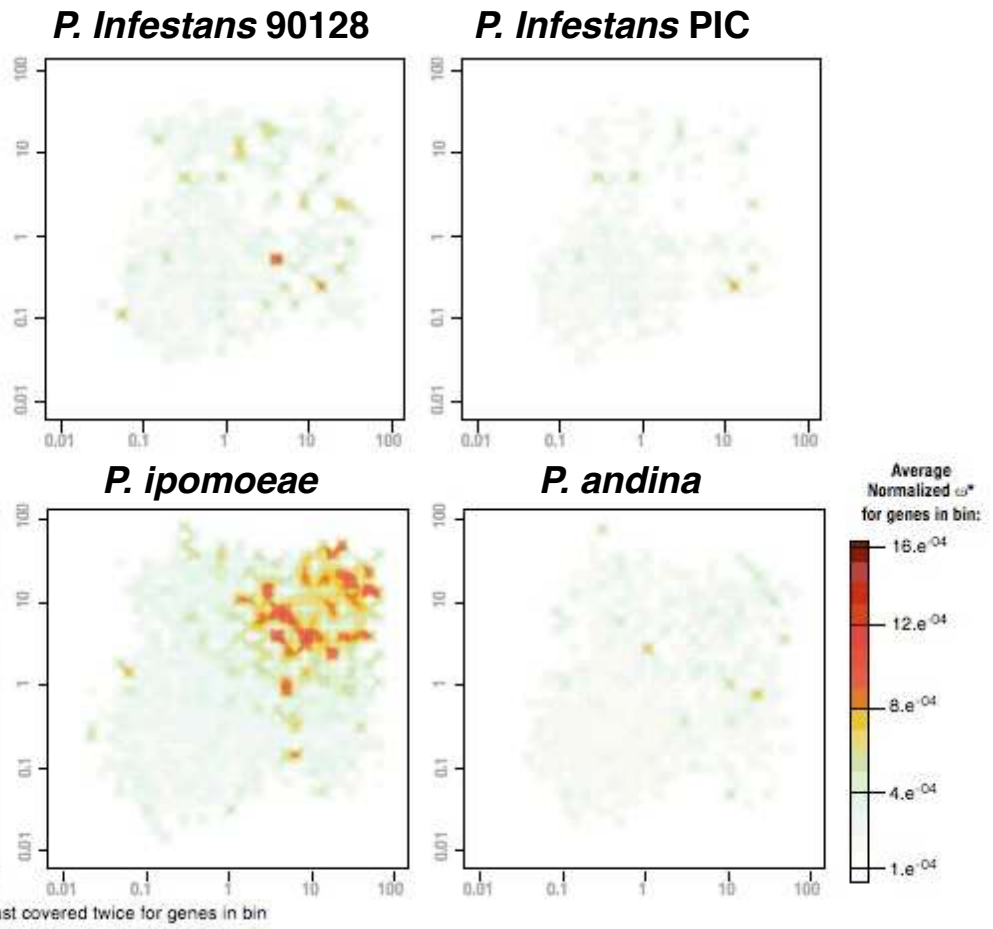
% of gene class with 0% coverage



Rhys Farrer, Sylvain Raffaele

Genes in repeat-rich regions are more likely to be under positive selection (ω = dN/dS > 1)

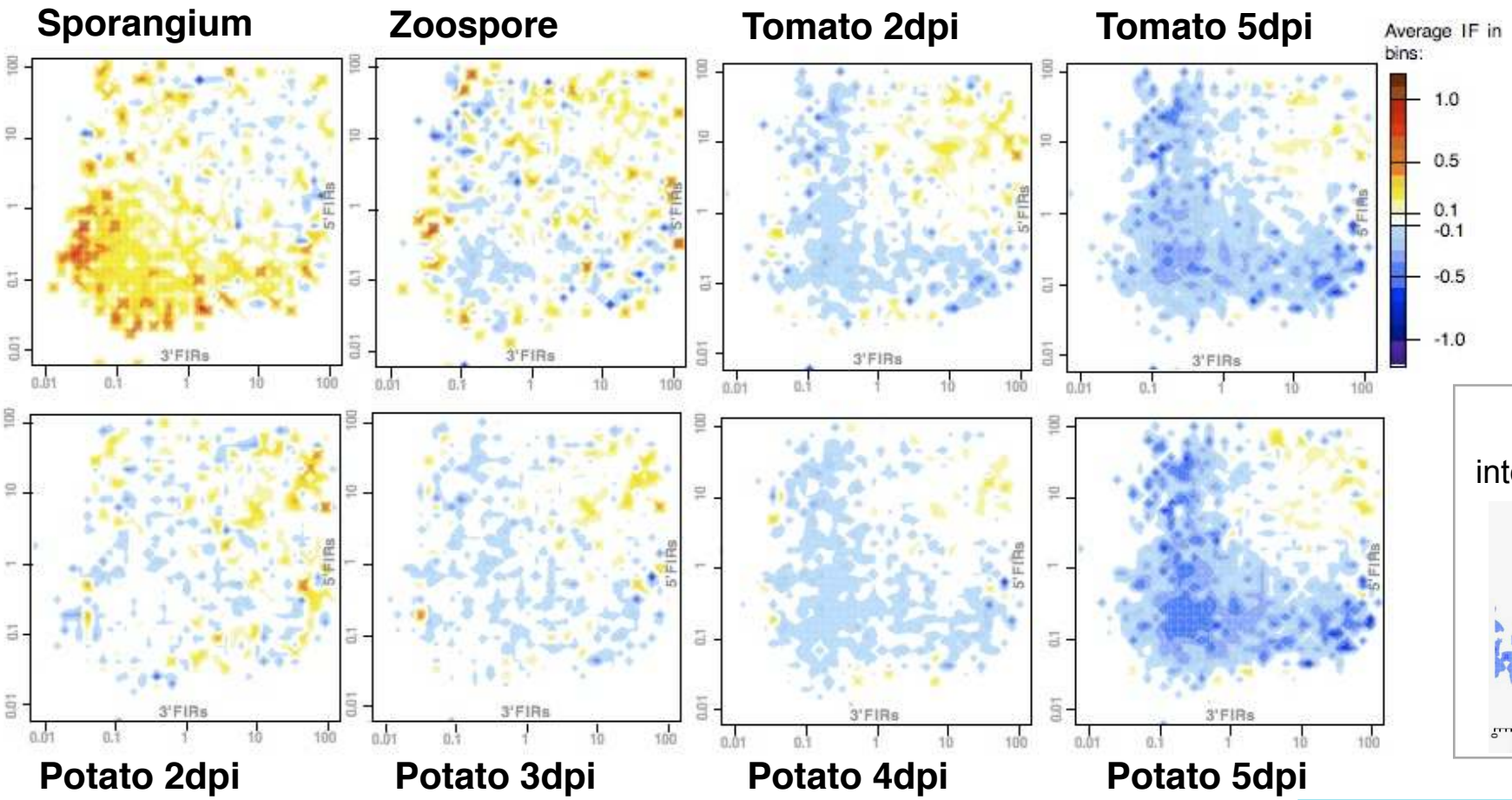




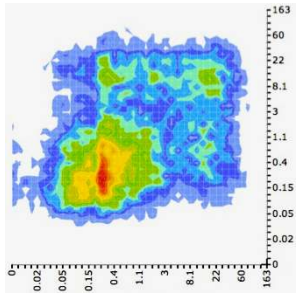
Rhys Farrer, Sylvain Raffaele

Repeat-rich regions are highly enriched in genes induced during colonization of tomato and potato

Average Induction Fold (Log2 T/T_0) in bins (n=3 min)



P. infestans intergenic distance



Sylvain Raffaele, Liliana Cano

Summary - The two-speed genome of *Phytophthora infestans*

- **The core genome** - high gene density, low repeat content, carries the core ortholog genes
- **The 'plastic' genome** - low gene density, high repeat content, highly enriched in secreted protein and effector genes
- Higher rates of gene turnover and positive selection in the 'plastic' genome
- Niches in the genome that enable rapid effector evolution and adaptation to host plants

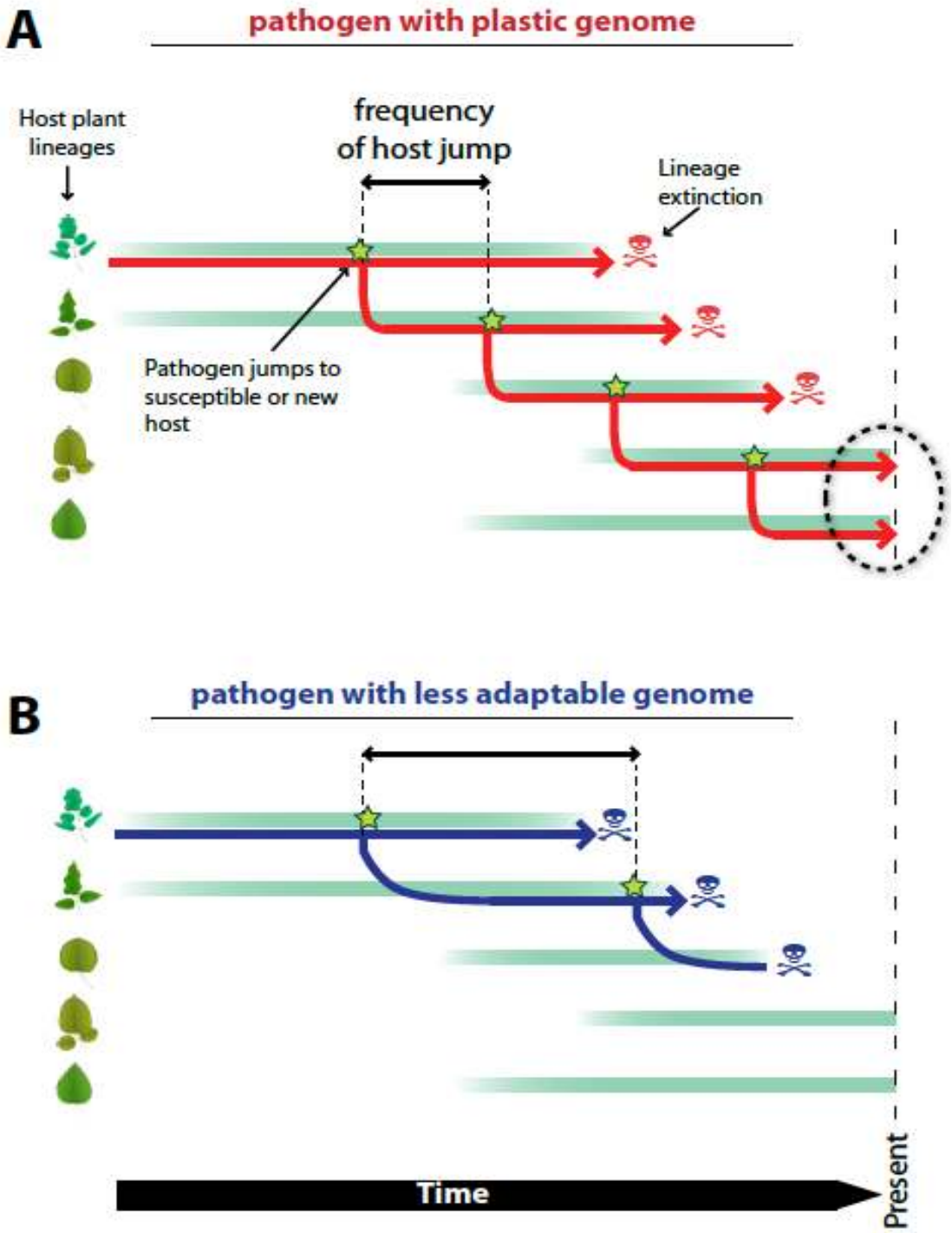
Why bigger is better?

- Convergent evolution of large genomes infested with repetitive elements in deep lineages of host-specific plant pathogens
- Which trade offs drive this evolutionary trend and counterbalance the cost of maintaining these large genomes?
- TEs are thought to enhance plasticity and evolutionary potential of pathogens, but this creates a conundrum because natural selection cannot maintain genes for future use
- Conundrum is solved by the evolutionary concept of clade selection (species selection) put forward by Georges C. Williams

Clade selection

- Lineages that produce new species at a high frequency and, therefore, are better at avoiding extinction, will dominate the biota compared to lineages that are prone to extinction
- Explains major evolutionary trends (sexual reproduction etc.)
- Our model is that clade selection opposes the advantages conferred by smaller, compact genomes and underlies the evolutionary trend towards larger plastic genomes
- Lineages with compact genomes have an increased probability of extinction, they suffer a macroevolutionary disadvantage

Jump or die! Lineages with less adaptable genomes suffer higher extinction rates



Raffaele and Kamoun, submitted

GC Wlliams (1992) Oxford Uni Press

Prospects for blight resistance

ANNUAL REVIEWS IN ADVANCE

Understanding and Exploiting Late Blight Resistance in the Age of Effectors

Vivianne G.A.A. Vleeshouwers,[1] Sylvain Raffaele,[2] Jack Vossen,[1] Nicolas Champouret,[1] Ricardo Oliva,[2] Maria E. Segretin,[2] Hendrik Rietman,[1] Liliana M. Cano,[2] Anoma Lokossou,[1] Geert Kessel,[3] Mathieu A. Pel,[1] and Sophien Kamoun[2]

[1]Wageningen UR Plant Breeding, 6700 AJ, Wageningen, The Netherlands; email: vivianne.vleeshouwers@wur.nl, jack.vossen@wur.nl, nicolas.champouret@sainsbury-laboratory.ac.uk, hendrik.rietman@wur.nl, Anoma.Lokossou@syngenta.com, m.pel@enzazaden.nl

[2]The Sainsbury Laboratory, Norwich Research Park, Norwich, NR4 7UH, United Kingdom; email: sylvain.raffaele@sainsbury-laboratory.ac.uk, ricardo.oliva@sainsbury-laboratory.ac.uk, maria.segretin@sainsbury-laboratory.ac.uk, liliana.cano@sainsbury-laboratory.ac.uk, sophien.kamoun@sainsbury-laboratory.ac.uk

[3]Plant Research International, 6700 AA, Wageningen, The Netherlands; email: geert.kessel@wur.nl

Recent potato and tomato blight epidemics

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Last Updated: Tuesday, 31 July 2007, 08:38 GMT 09:38 UK

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Helicopter tackles potato blight

Potato growers in the north of Scotland have hired a helicopter to spray their crops in an effort to control blight.

Farmers have blamed a long spell of poor weather for the

Slow Food USA™ Supporting Good, Clean, and Fair Food

A Midsummer Nightmare: Tomato Blight

Posted on *Wed, July 29, 2009* by *Brian Sinderson*
2 Comments | Categories: Biodiversity, Contaminated Food, Farms and Farming, News, Current Events,

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by Winnie Yang

It's the moment we've all been w
eagerly awaited by produce lover
finally here, and the farmers' mar
beans, and tom — Wait. Where a

As you may have heard (**here**, fo
widespread outbreak of late bligh
from plants in garden stores to ba
the *New York Times*. A rainy June
windy weather."

The Washington Post

washingtonpost.com > Metro > Maryland

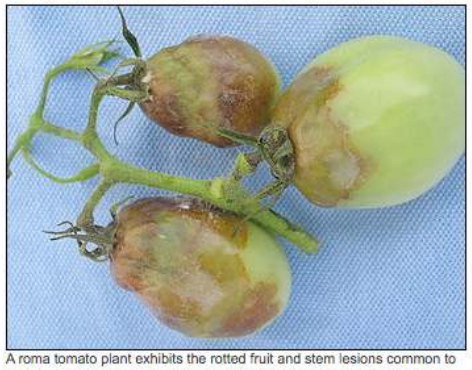
POSTLOCAL Click for news, weather, entertainment, more.

HORTICULTURE

Late Blight Comes Early, Hitting Tomatoes Hard, Experts Say

By Adrian Higgins
Washington Post Staff Writer
Friday, July 10, 2009

Plant scientists are asking home
check their
e that could
ar's crop.



A roma tomato plant exhibits the rotted fruit and stem lesions common to the late blight that scientists say is striking tomato plants early this year. (Courtesy Of Cornell University Department Of Plant Pathology And Plant-microbe Biology)

BREAKING NEWS | Philip R. F. Anderer

CURSE OF POTATO BLIGHT

| Sunday Mirror, Sep 7, 2008

1 2 Next

THE Irish Famine, known as the Great Hunger, began in 184
ravaged with blight.

At the time, the poorest third of the population were depen
staple diet.

These rural tenant farmers were the hardest hit by the bligh
five years.

At the Famine's height, in 'Black 47', a vicious winter and a
increased the misery of already starving population Cholera
following two years.

A million Irish filled the coffin ships and another million peri
shiploads of food day were exported Ireland to Britain unde

disease affects both tomatoe
mid-1800s) and is so infectio
ning, spraying and deeply bu
ne gardeners should pull pla

FARMERS WEEKLY INTERACTIVE

MAKING THE FARMING CONNECTION

Enter Search term SE

New blight strain demands extra vigilance

Charles Abel
Sunday 05 April 2009 08:00

With aggressive potato blight strain A2-Blue13 now dominant, skill is again needed to strike the right balance between effective control and acceptable fungicide use.

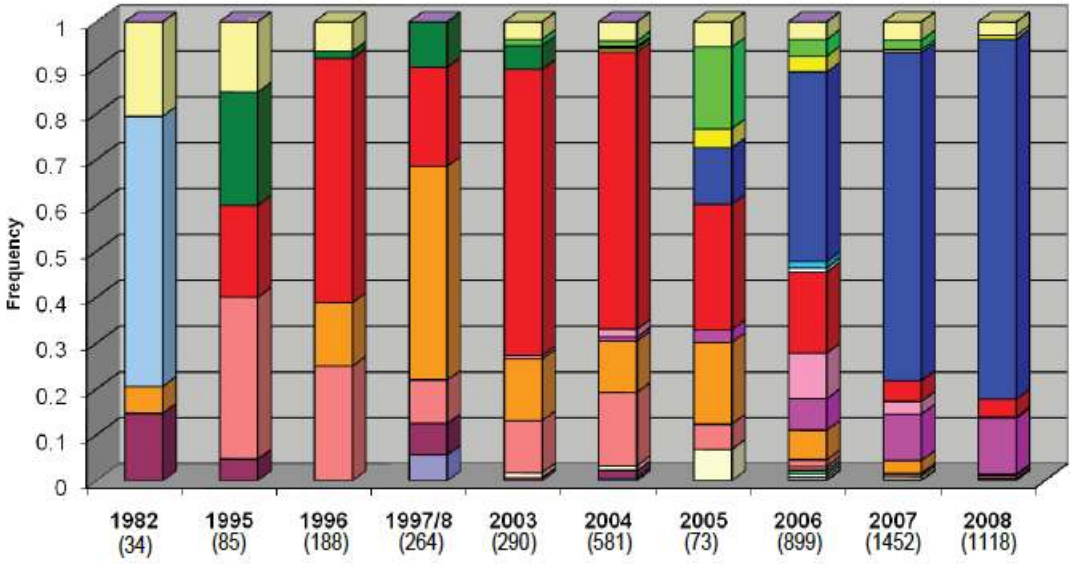
The new strain first showed up near Ipswich in 2005 and has rocketed in prevalence from 38% that year to almost 80% now.

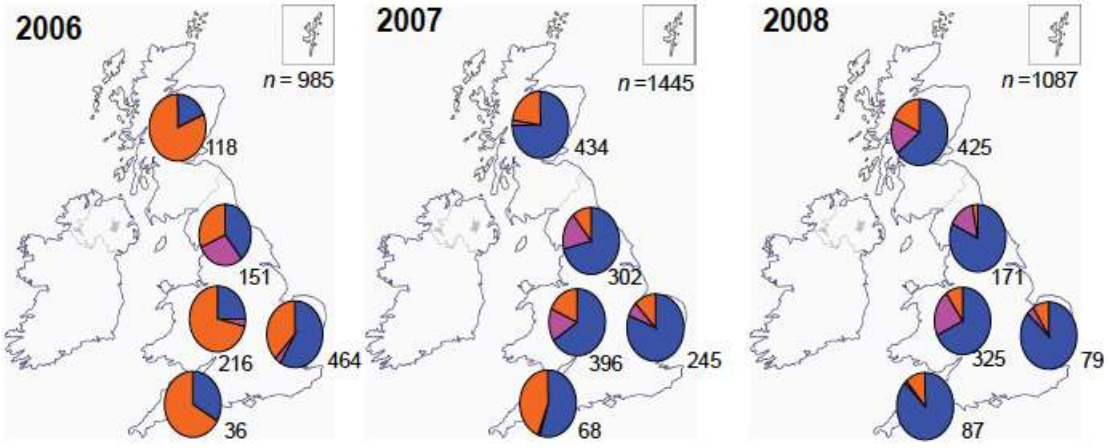
When combined with blight-conducive weather and poor spraying conditions, as in 2007, it can put pressure on blight control programmes, leading to some of the worst potato blight on record.

"Growers need to be aware that we are dealing with a different type of blight these days," advises Potato Council blight specialist Gary Collins. "It is more aggressive, it is fitter and it will come into crops earlier. So consult an agronomist to ensure you correctly interpret the risk of blight, indicated by Smith Periods, and choose the right control strategy."

blight has
ato growing
April to
t just
mercial
expert on
versity of
xtension

Genome sequencing of *P. infestans* epidemic strains: "blue 13" asexual lineage in the UK



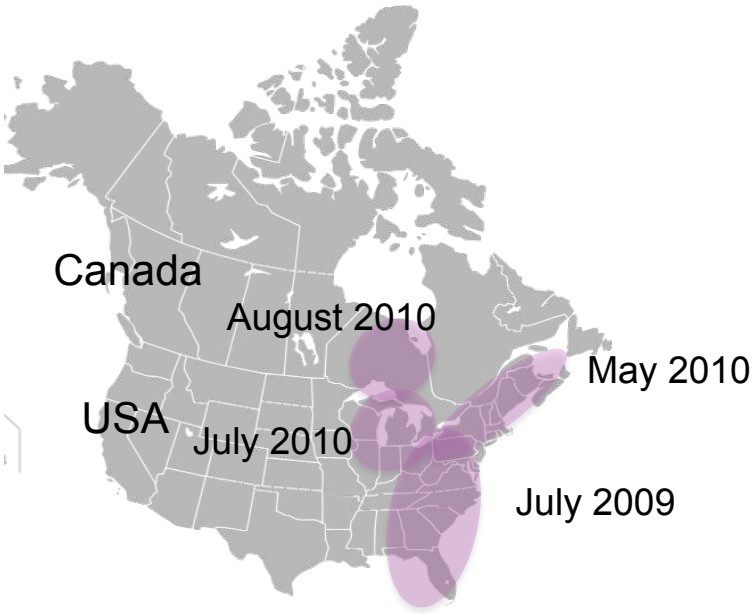


T30-4 **"blue 13"**

Associated with **severe epidemics**, **metalaxyl resistant**, **more aggressive**

Liliana Cano; with David Cooke @ JHI

Tomato (and potato) epidemics caused by US22 clonal lineage in North America



- Emerged in Northeast US in summer 2009
- Moved to Canada in 2010

US22
P17777 strain

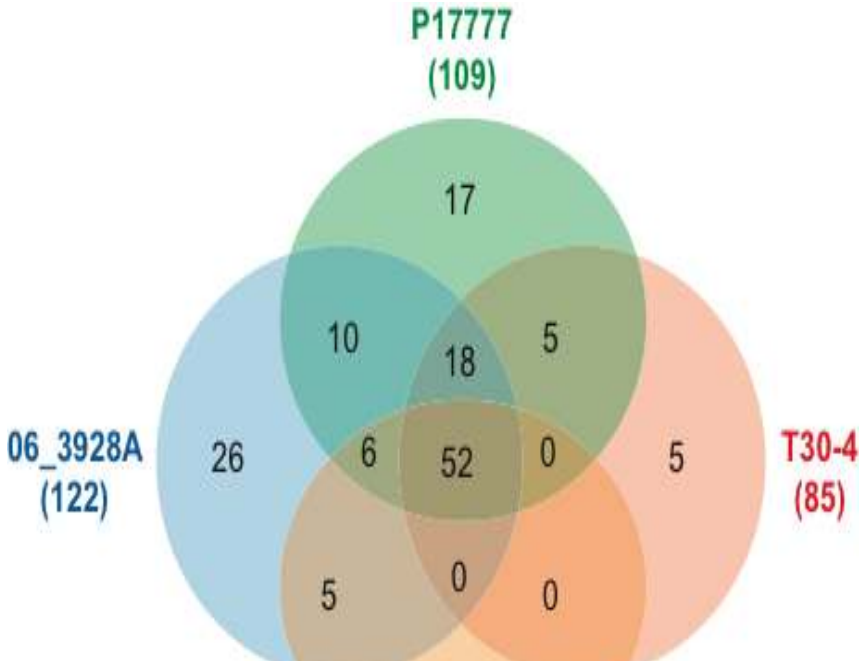
Aggressive on tomato

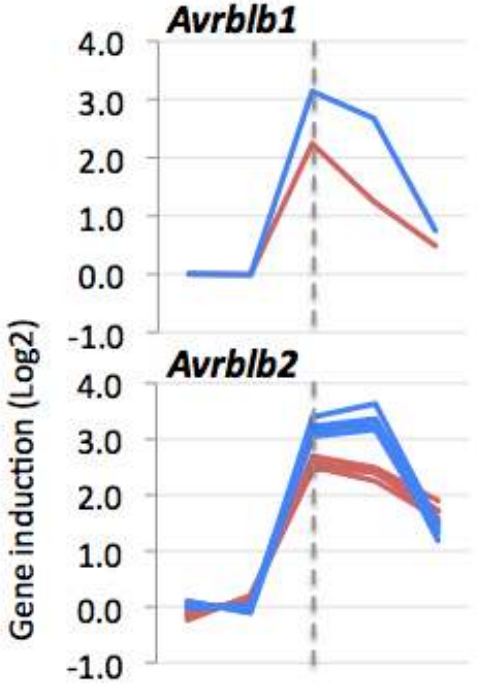
- A2 mating type
- Susceptible to mefenoxam and metalaxyl

W. E. Fry
M. D. Coffey
UC RIVERSIDE

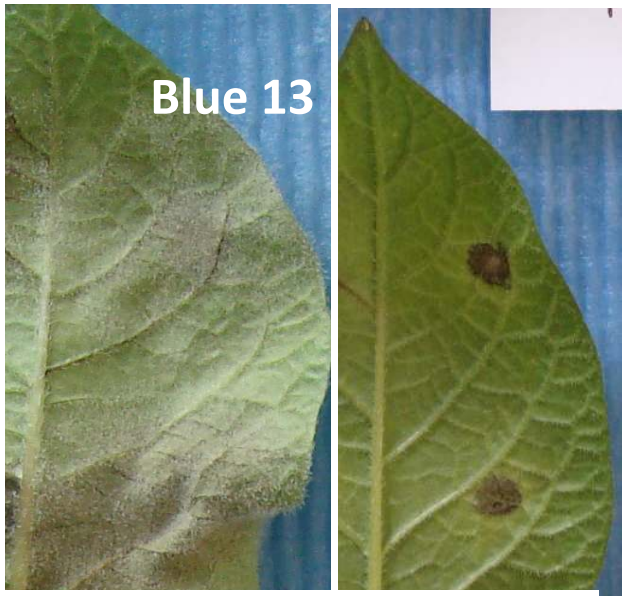
Core effectors as targets for resistance

>550 RXLR effector genes in *P. infestans*





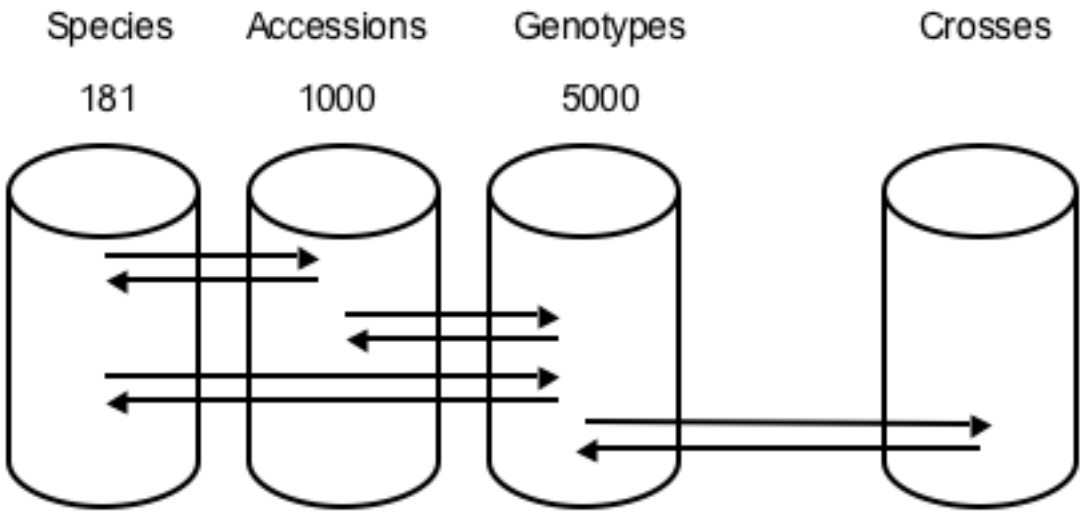
blight assay on potato



- By focusing on *R* genes that recognize “core” *P. infestans* effectors, we maximize the potential for resistance durability in the field

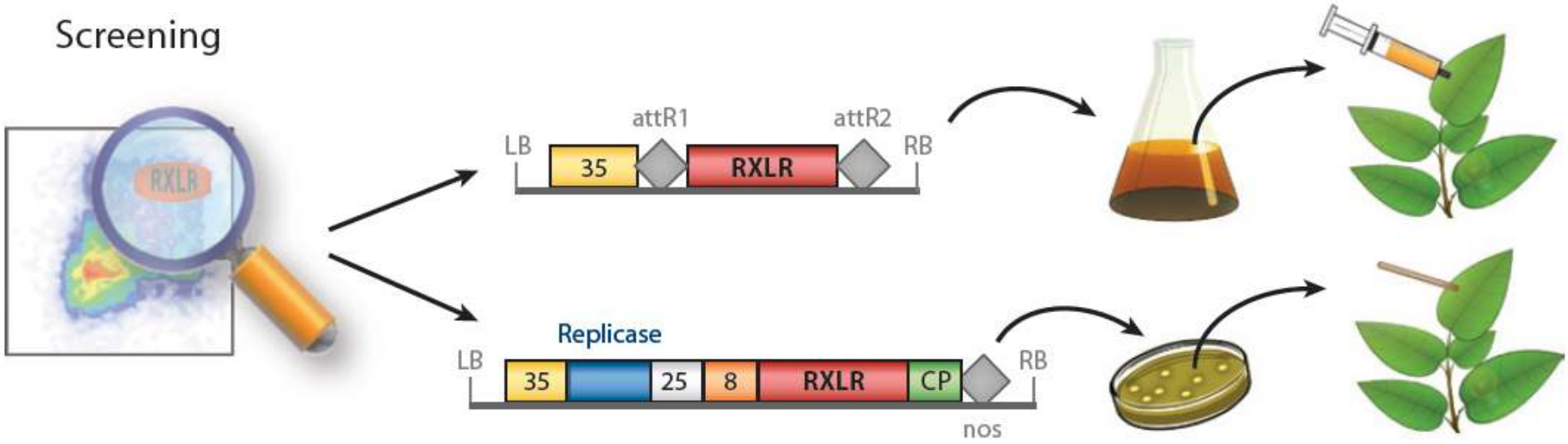
Late blight resistance in *Solanum* germplasm

V. Vleeshouwers, E. van der Vossen *et al*. Wageningen



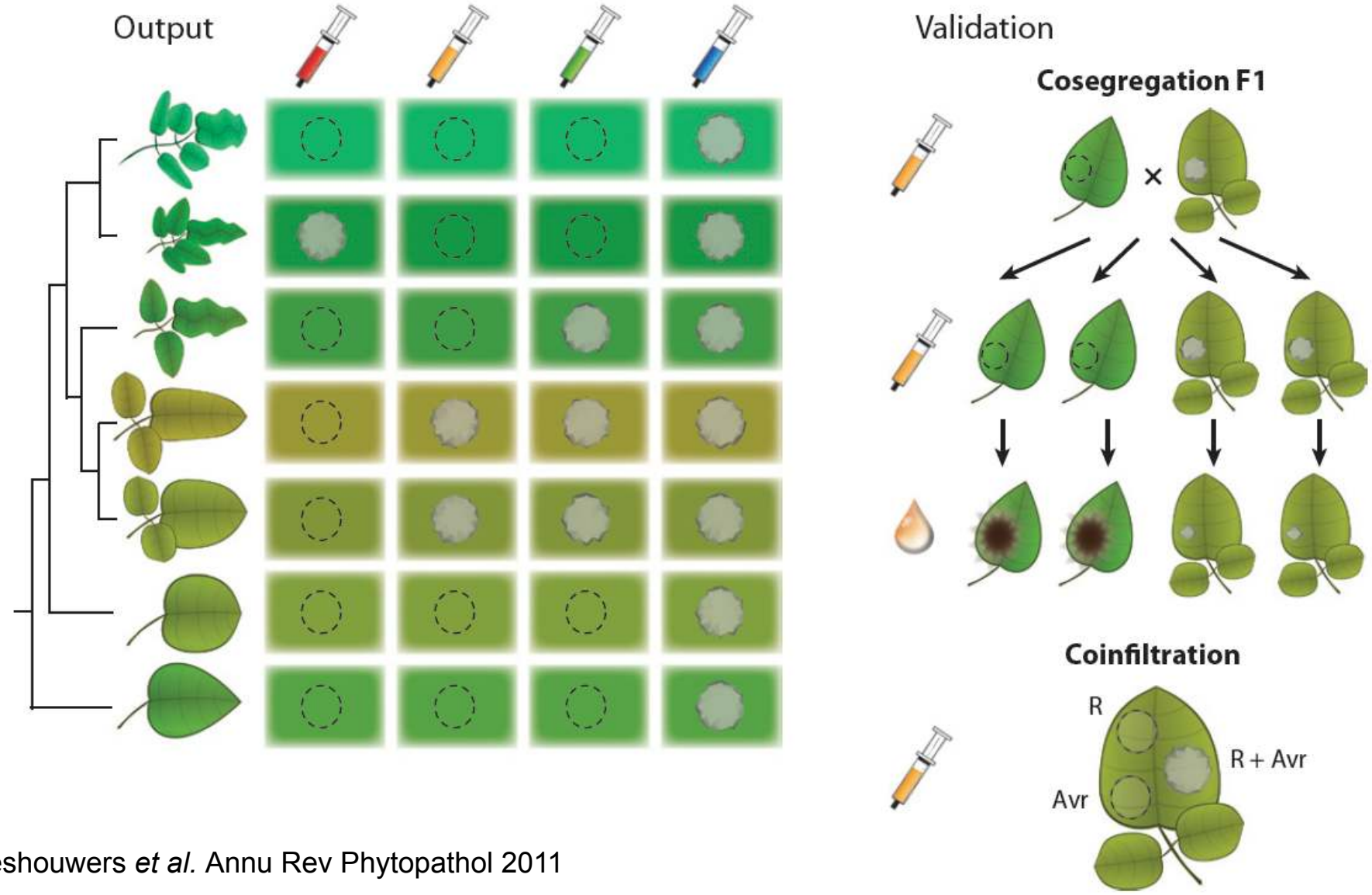
- ✓ Resistant accessions
- ✓ Segregation for resistance
- ✓ Positional cloning

Effectoromics for late blight resistance



Vleeshouwers *et al.* Annu Rev Phytopathol 2011

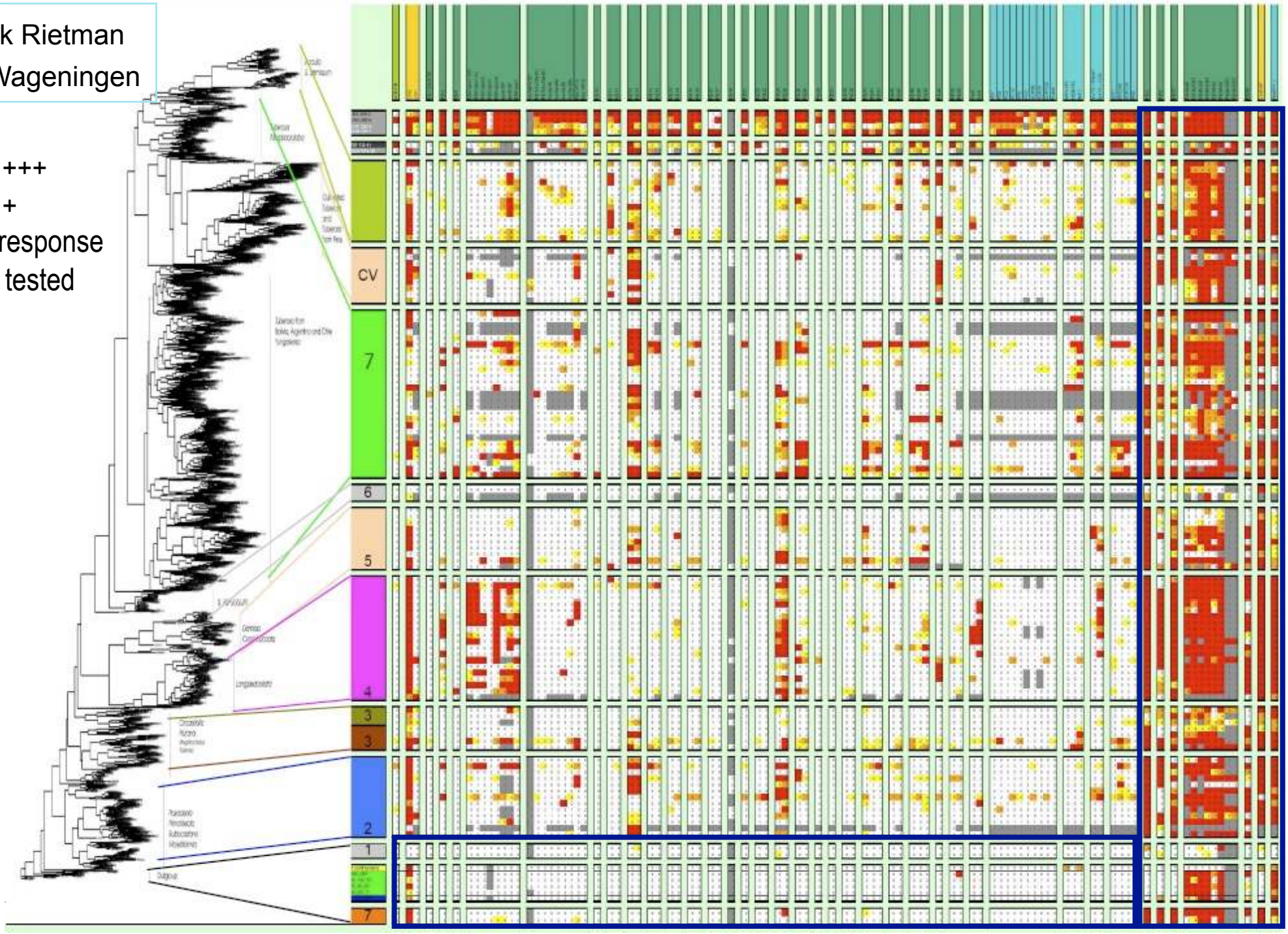
Effectoromics for late blight resistance



Vleeshouwers *et al.* Annu Rev Phytopathol 2011

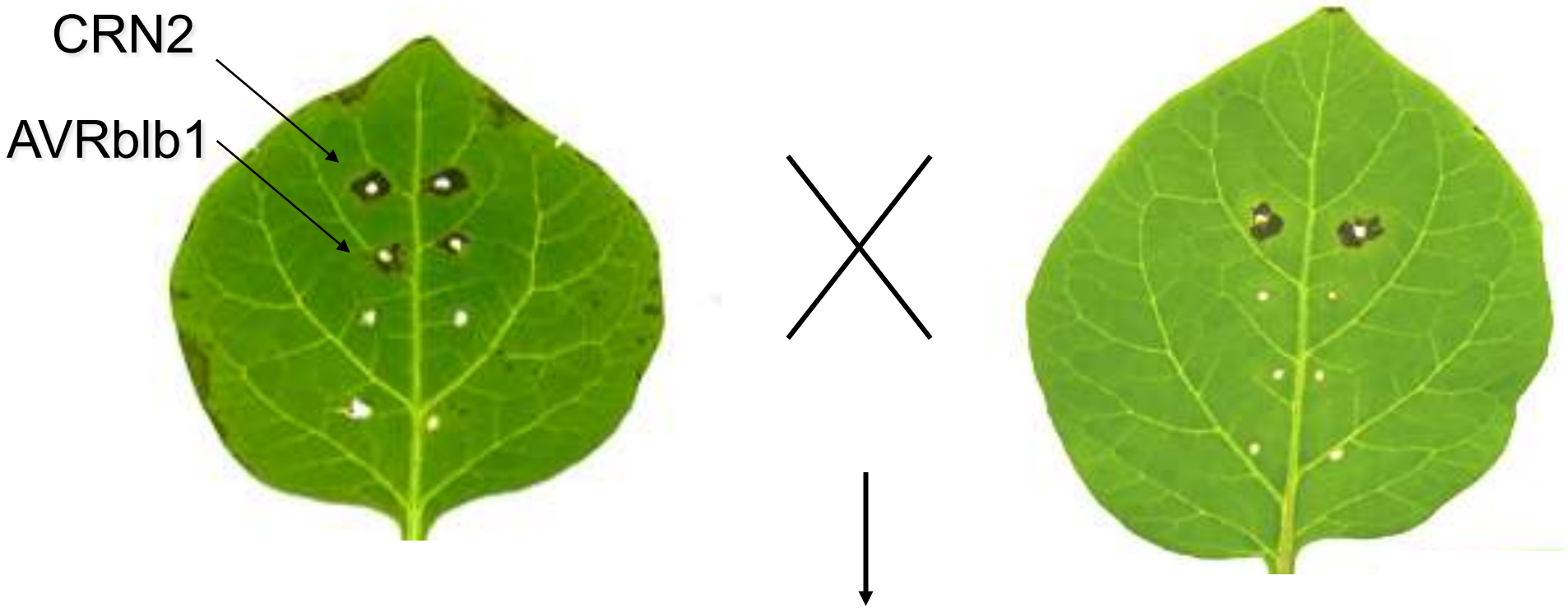
Hendrik Rietman
et al. Wageningen

- HR +++
- HR +
- No response
- Not tested



Accelerates cloning and profiling of *R* genes

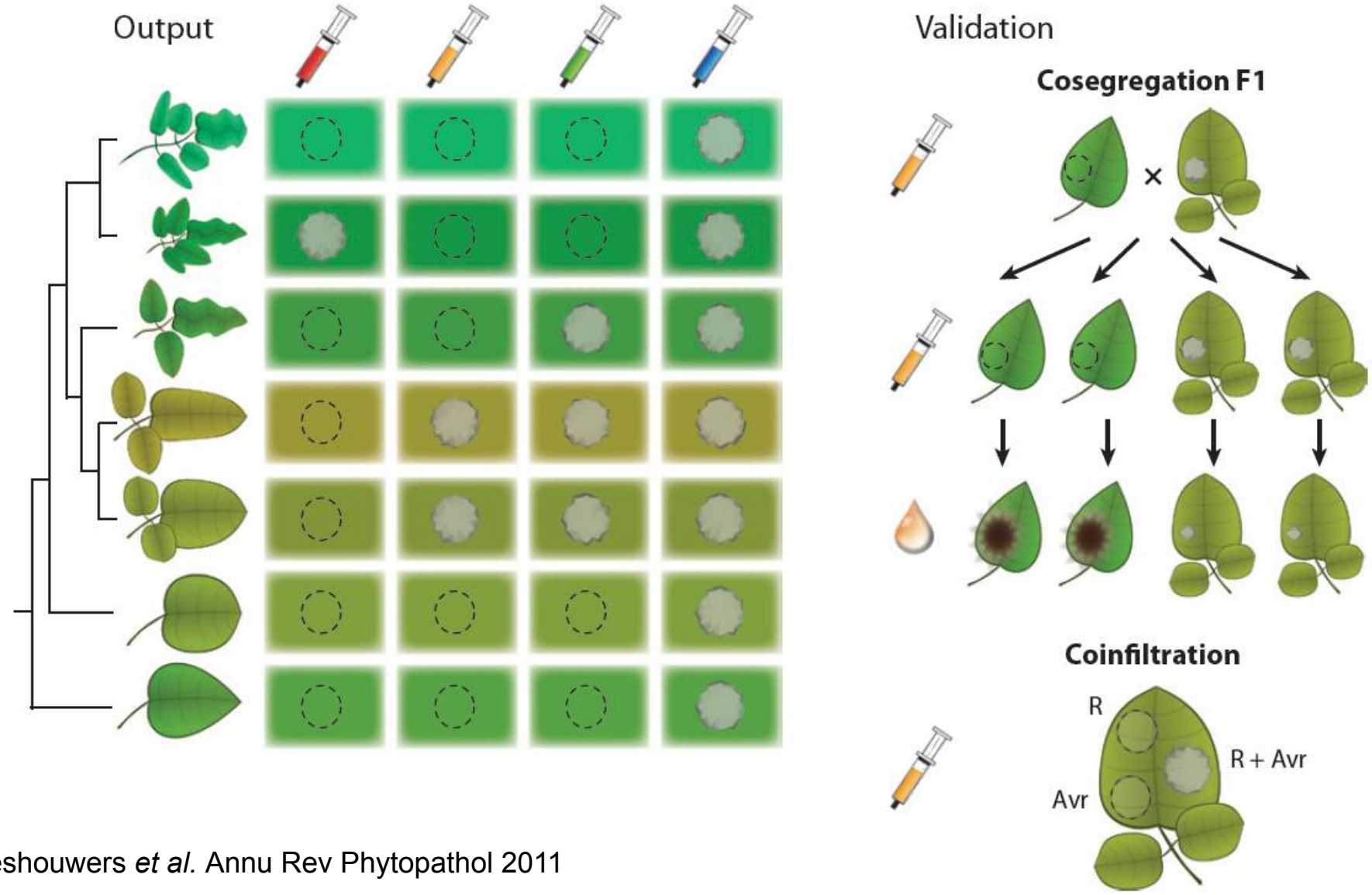
V. Vleeshouwers *et al*. (2008) PLoS One



Co-segeregation of late blight resistance and effector response

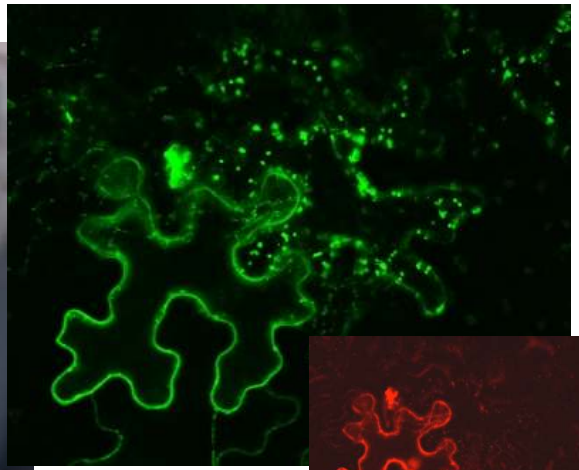
Cloning of *Rpi-blb1* (=*RB*) homologs from *S. stoloniferum* and *S. papita*

Effectoromics for late blight resistance



Vleeshouwers *et al.* Annu Rev Phytopathol 2011

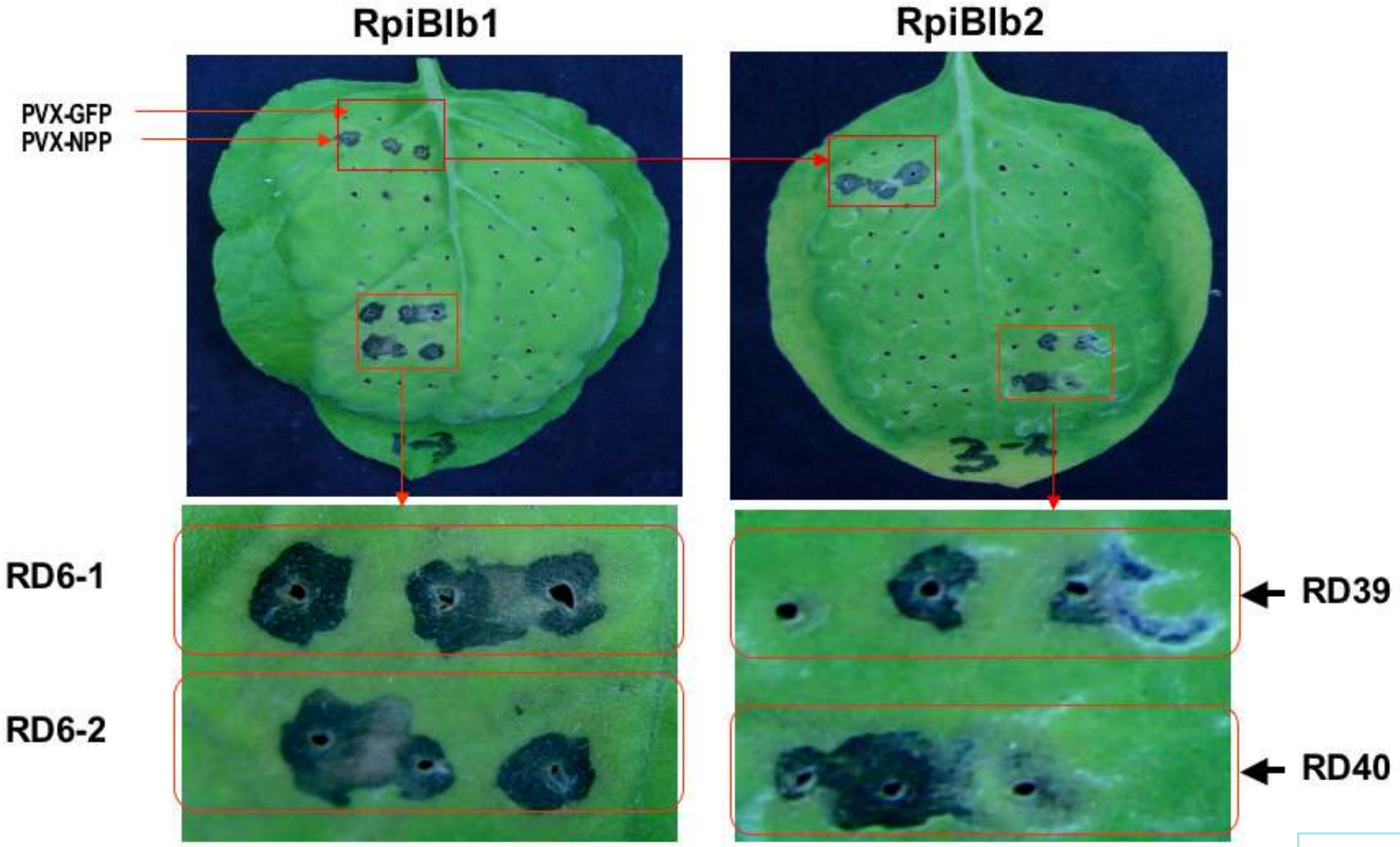
Nicotiana benthamiana: The ‘HeLa cells’ system of plant biology



Agroinfiltration

- Virus vectors
- Gene co-expression
- Gene silencing
- Cell biology
- Protein biochemistry
- Protein complexes
- High-throughput screens

Functional cloning of AVRblb1and AVRblb2



Exploiting effectors in breeding and deployment of resistance

breeding, biotech

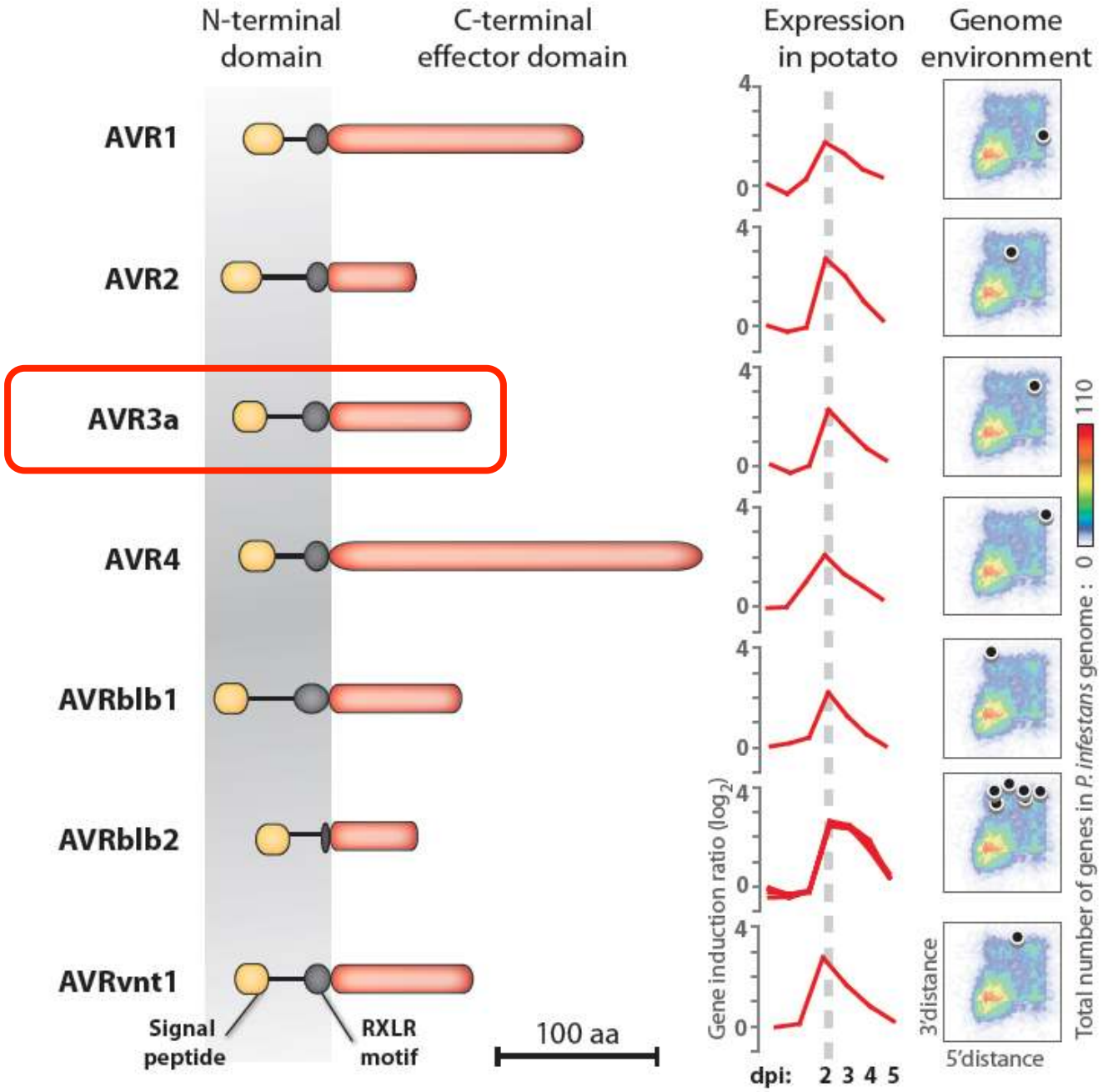
- **Accelerate cloning of disease resistance (R) genes** – *effectoromics*: R gene activity screens, R gene allele mining
- **Profiling R gene specificities** – classify germplasm/R genes, avoid redundant breeding/cloning
- **Synthetic R genes** – Expand effector recognition

- **Monitoring pathogen populations** – population status in different geographic regions, effector allelic diversity

deployment

AVR effectors of *P. infestans*

- AVR1 and AVR4 are dispensable
- AVR2, AVR3a, and AVRblb2 are always present and expressed; polymorphic families



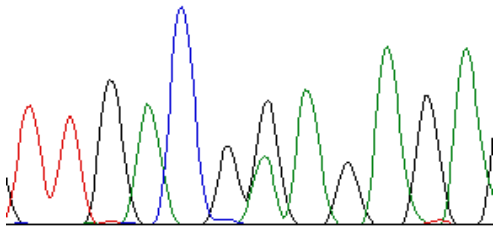
Vleeshouwers *et al.* Annu Rev Phytopathol 2011

The RXLR effector AVR3a is recognized by the NB-LRR protein R3a

Avirulent on R3a

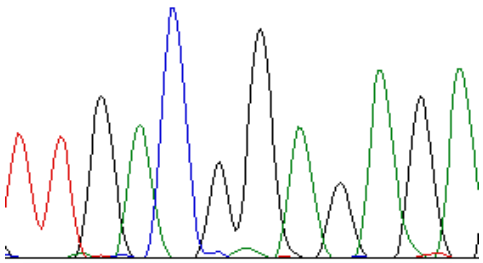
Leu Thr E/K Arg

T T G A C G G A G A G A

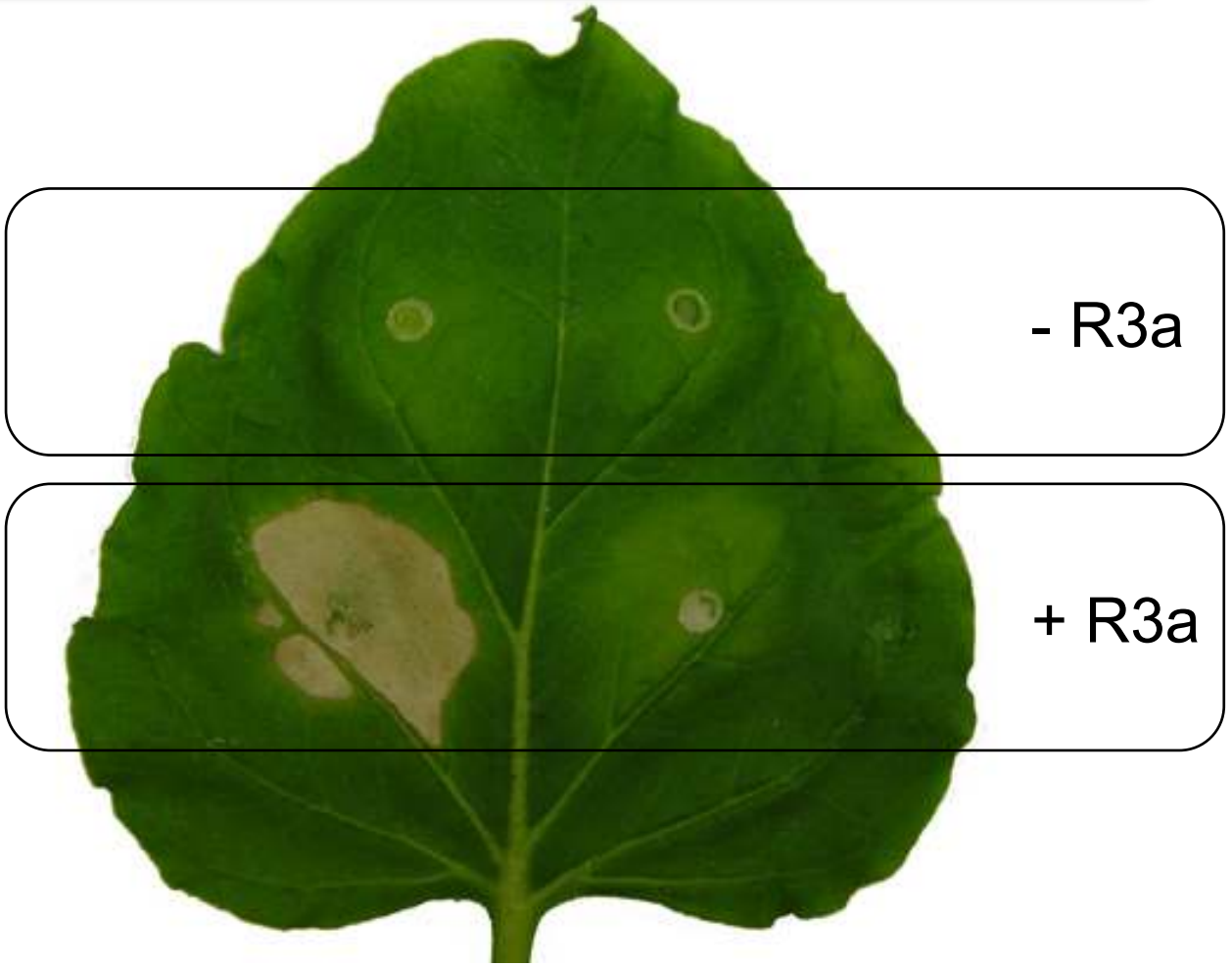


Leu Thr E Arg

T T G A C G G A G A G A



virulent on R3a



$AVR3a^{KI}$ $AVR3a^{EM}$

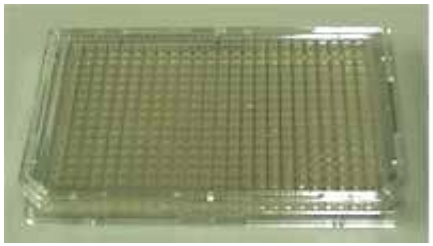
Balancing selection results in maintenance of both AVR3a alleles in *P. infestans* populations

- *P. infestans* strains always carry an intact AVR3a gene ($AVR3a^{KI}$ and/or $AVR3a^{EM}$)
- AVR3a knock-down mutants have markedly reduced virulence
- $AVR3a^{EM}$ also recognized by an (uncloned) *Solanum R* gene
- Both $AVR3a^{KI}$ & $AVR3a^{EM}$ are predicted to have virulence activities

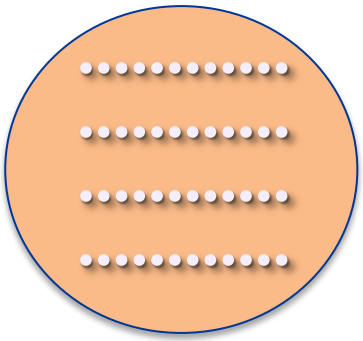
An R3a mutant that recognizes both $AVR3a^{KI}$ and $AVR3a^{EM}$ is expected to be effective against all *P. infestans* isolates

• Armstrong *et al.*, *PNAS,* 2005; Bos *et al.*, Plant J., 2006; Bos *et al.*, PNAS 2010

Artificial evolution to extend R3a recognition: Experimental design (Maria Eugenia Segretin)



Random mutagenesis on R3a
1,37 > num. mut/1000bp > 1,92
75-80% positive clones
Library (19x384w plates)



Re-inoculate in L-agar plates
(4x96colonies/plate)

Inoculate 96 deep wells plates
(4x96colonies/plate)

Growth @28°C 2 days

Measure OD of 1 column

Centrifuge 5min @3400rpm

Resuspend in Infiltration buffer to have a final OD of 0.3 when mixed

Growth @28°C (O.N.):
pGR106-AVR3aEM (23-147, N-FLAG)
pCB302-3/AVR3aKI

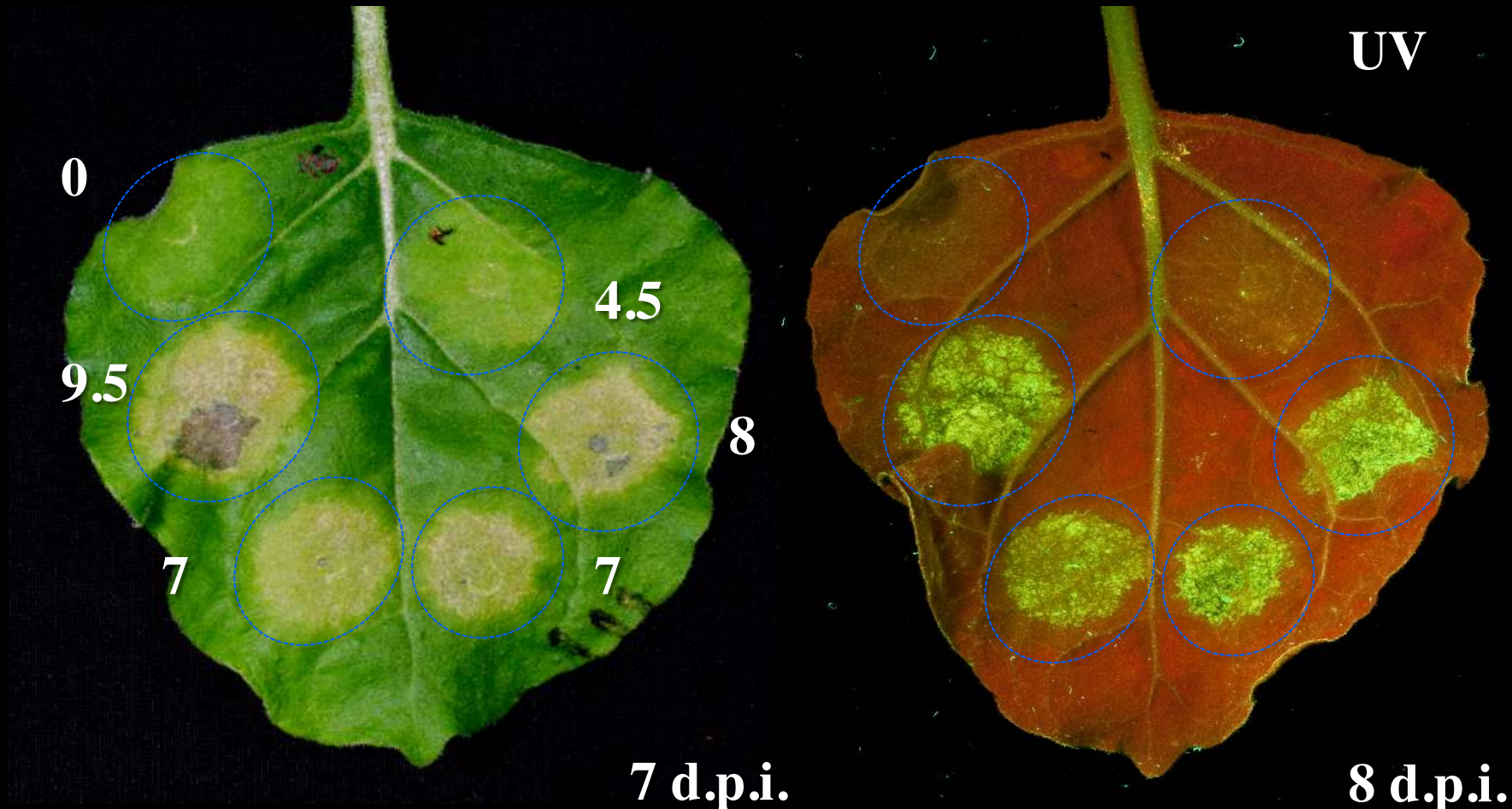
Centrifuge 5min @3400rpm

Resuspend in Infiltration buffer to have a final OD of 0.15 when mixed

Mix
pGR106-AVR3aEM 1:2 R3A mutant clones
Evaluate phenotypes at 5 d.p.i.

Confirm positive clones co-infiltrating again with pGR106-AVR3aEM and pGR106-DGFP (to exclude autoactivation). Also with pCB302-3/AVR3aEM

R3a mutants that recognize AVR3a^{EM} recovered



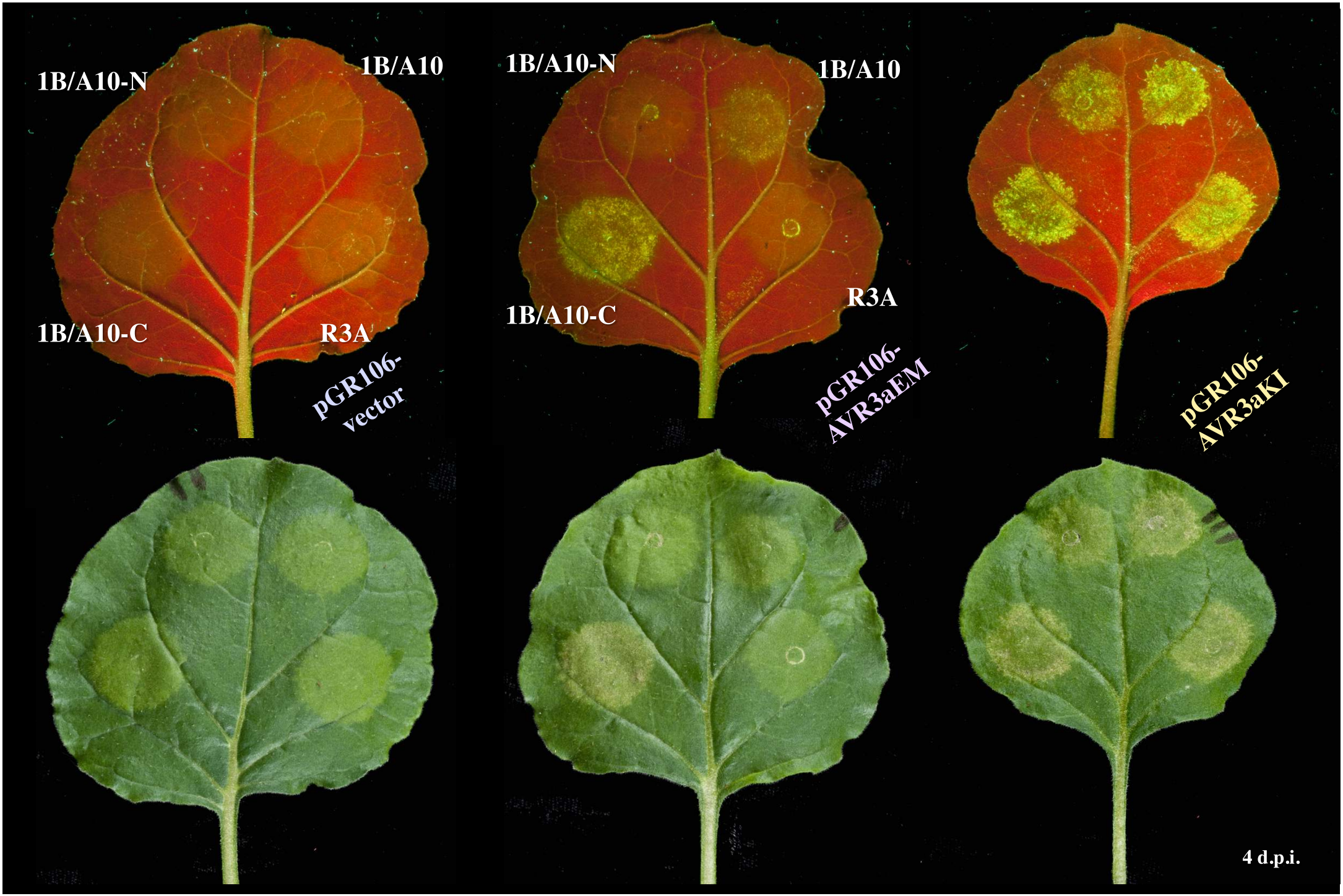
Co-infiltrate the candidate clones with pGR106-AVR3aEM, pGR106-DGFP or pGR106-AVR3aKI.
Analyze the phenotype day by day (starting at 2 d.p.i.). 12 spots per clone.
Establish and "HR index" from 0 (nothing visible) to 10 (confluent necrosis)

1B/A10

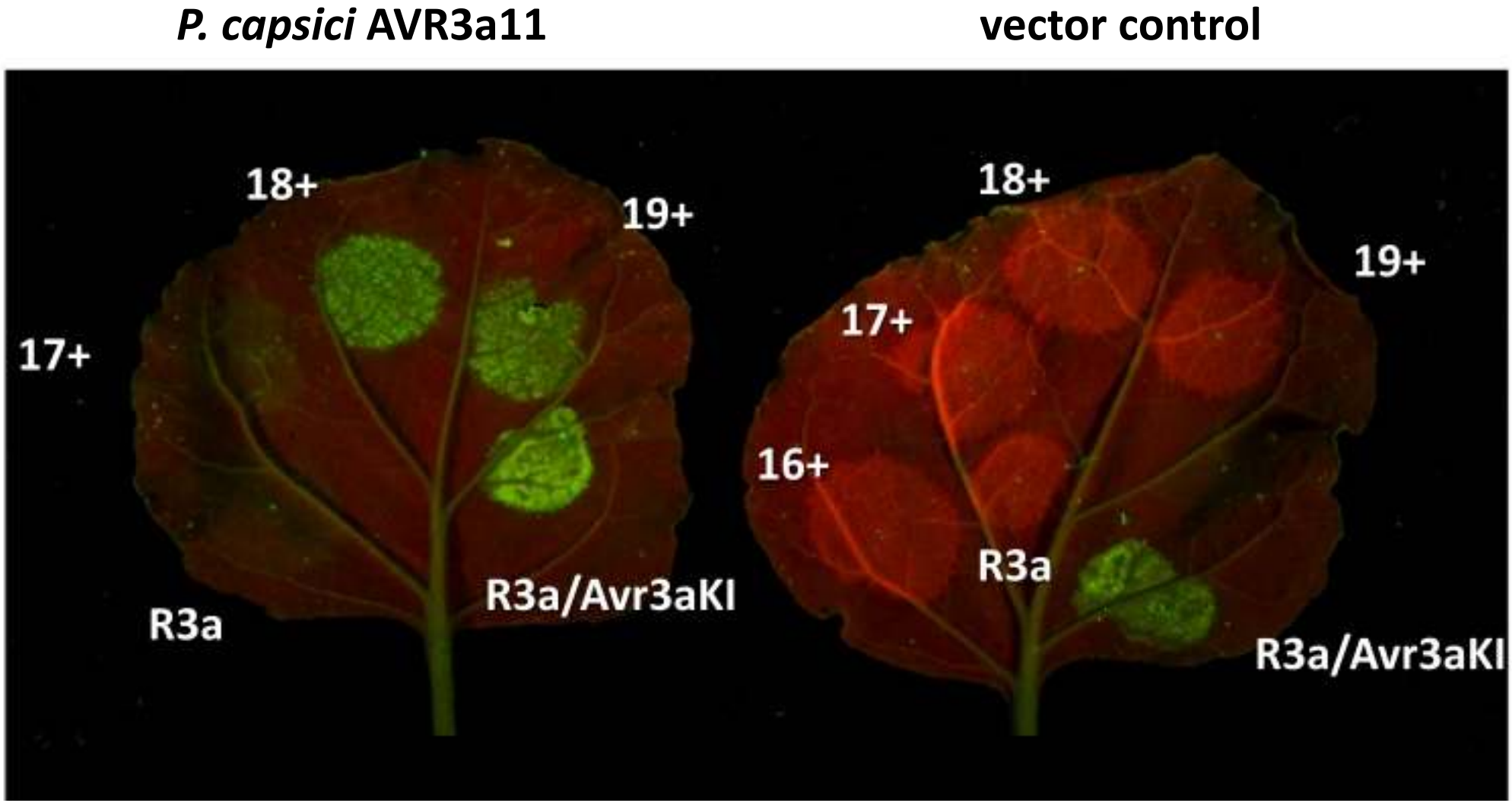
6.33

1B/A10-N

1B/A10-C


1B/A10-N
1B/A10
1B/A10-C
R3A
pGR106-vector
1B/A10-N
1B/A10
1B/A10-C
R3A
pGR106-AVR3aEM
pGR106-AVR3aKI
4 d.p.i.

R3a+ mutants that sense AVR3a homologs from other *Phytophthora* species

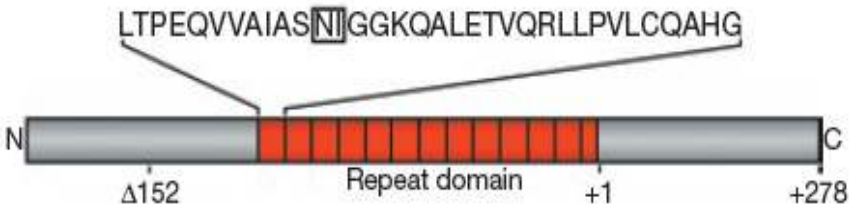


Next generation resistance breeding

- R3a+ predicted to confer resistance to all strains of *Phytophthora infestans* and some other *Phytophthora* spp.
- Single amino acid mutations expand effector recognition
- Recognition of effectors from diverse species
- Basic knowledge of pathogen effectors essential
- Non-GM solutions?

Targeted genome mutagenesis and editing

TAL effectors – Designer DNA binding proteins

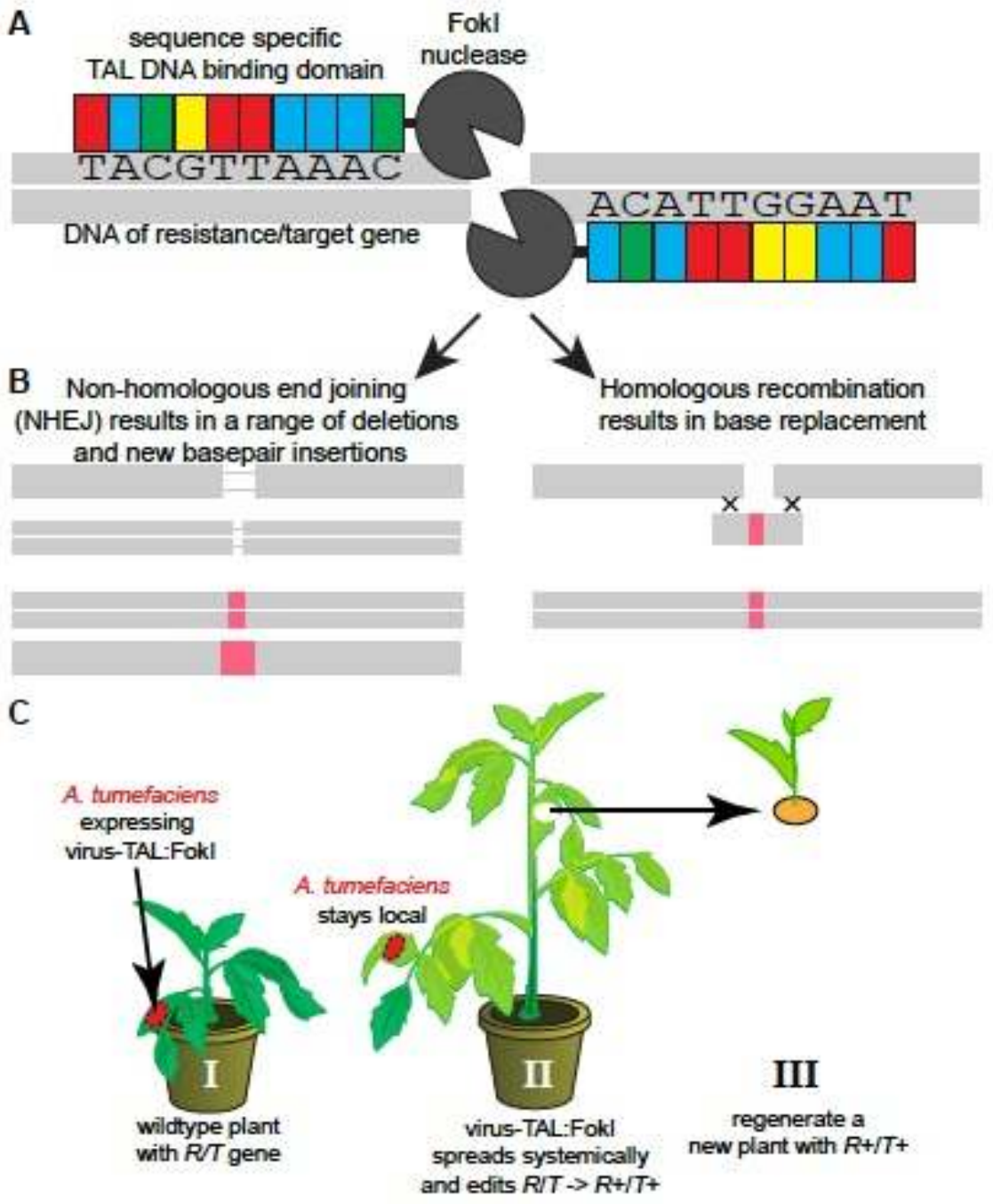


TAL hypervariable amino acids: **NI** **HD** **HG** **NG**

Target base: **A** **C** **G** **T**

Moscou *et al*.; Boch *et al*. Science 2009

Marton *et al*. Plant Physiol 2010



Targeted genome mutagenesis to engineer disease resistant crops

- TALN (TAL-nuclease) technology greatly facilitates genome engineering
- Mutant plants are recombinant DNA-free (no transgenic sequences, indistinguishable from naturally occurring mutations)
- Opportunity to further integrate biotechnology with plant breeding

An arms race between the biotechnologist and the pathogen?

- Ability of the pathogen to adapt is astounding
- "*Never bet against the pathogen*" – silver bullet solutions unlikely to be durable
- *Our vision*: Framework to rapidly generate new resistance specificities and introduce these traits into crop genomes
- Can we generate and deploy new resistance traits faster than the pathogen can evolve?