Fitness effect of mutations between phases of the life cycle of the root-rot fungus *Heterobasidion parviporum*

Pierre-Henri Clergeot, Nicolas Rode, Sylvain Glémin, Mikael Brandström-Durling, Åke Olson

Collaborators

Fitness measurements
Genomic analyses

P-H. Clergeot

Ake Olson

Mikael Brandström-Durling

Collaborators

ECFG13
13th European Conference
on Fungal Genetics

Fitness measurements
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Theoretical modeling

Mikael Brandström-Durling

Collaborators

Fitness measurements
Genomic analyses

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Ake Olson

Theoretical modeling
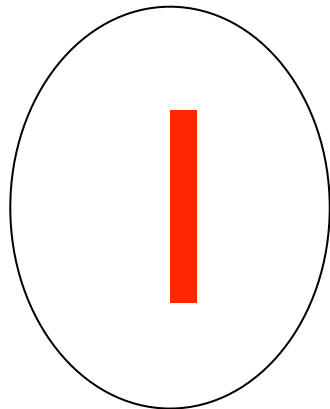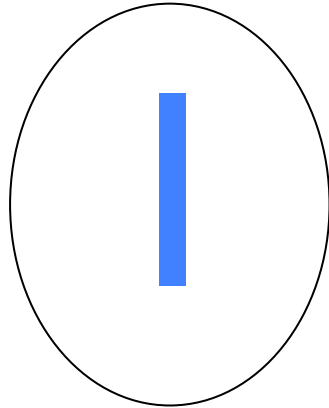
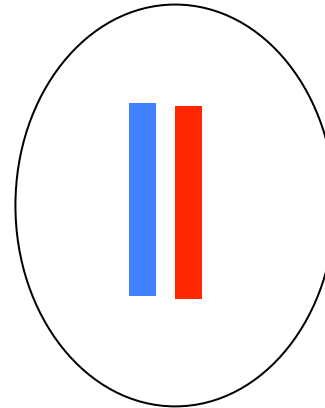Mikael Brandström-Durling

Sylvain Glémin

Alternation between ploidy levels:

Eukaryotic life cycle

Haploid cells

Diploid cell

Alternation between ploidy levels:
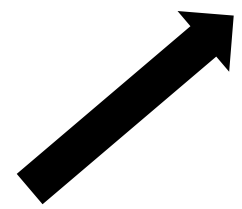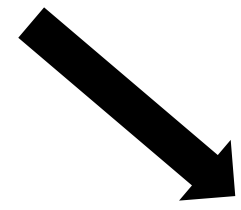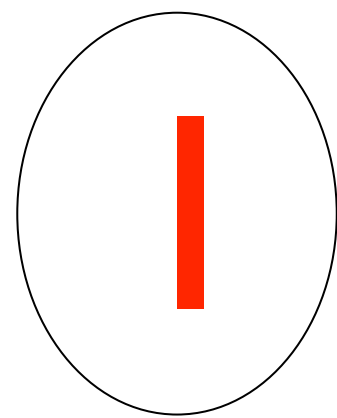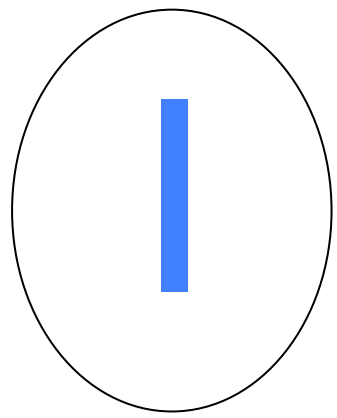➤ fertilization

Eukaryotic life cycle
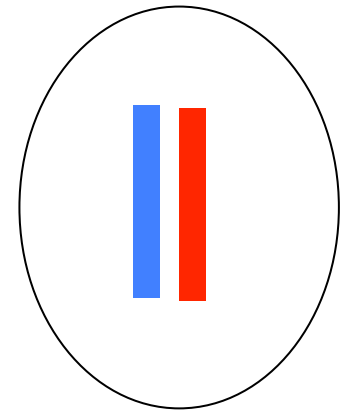
Haploid cells

Diploid cell

Alternation between ploidy levels:
➢ fertilization
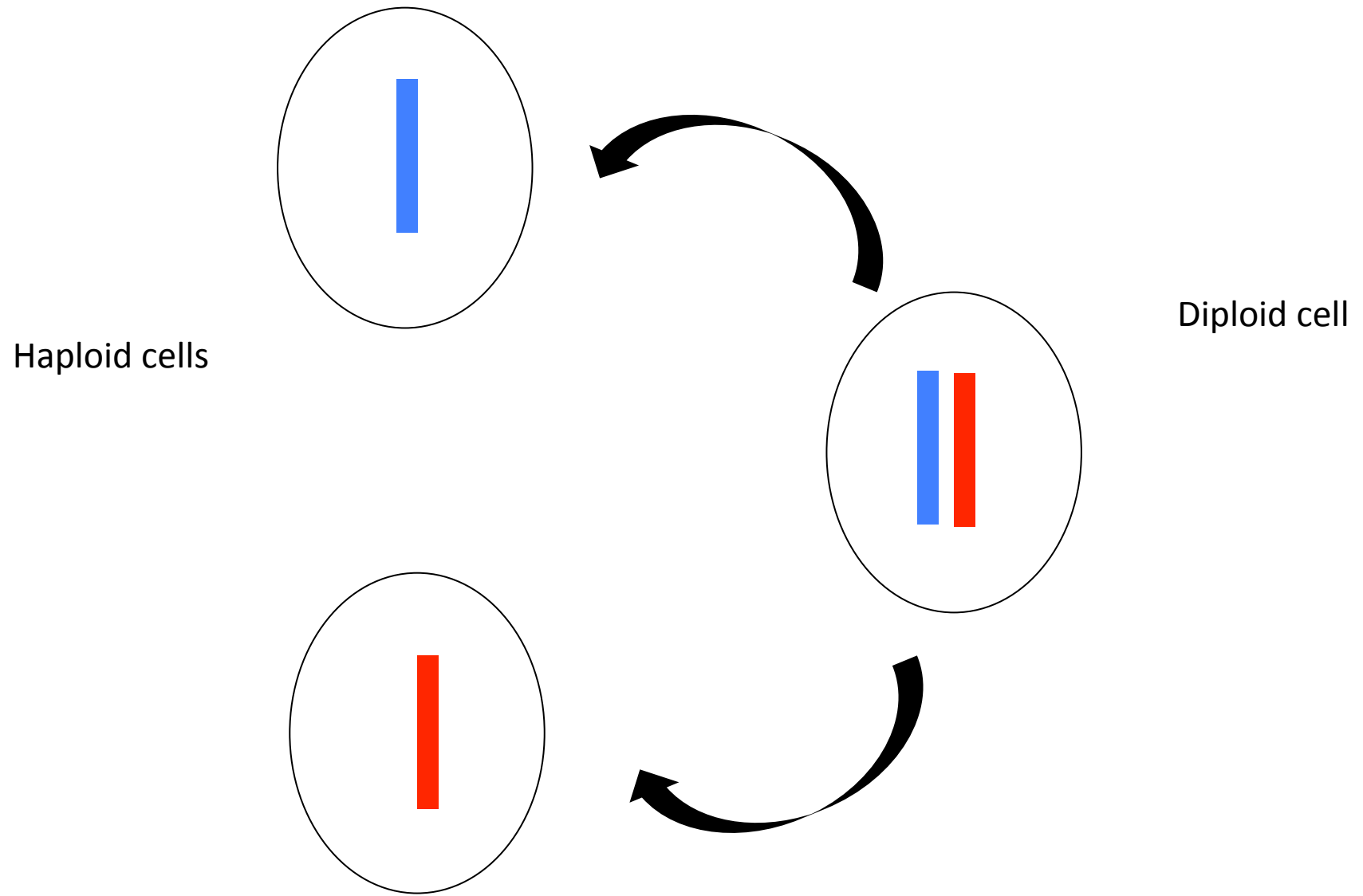➢ meiosis

Eukaryotic life cycle

Haploid cells
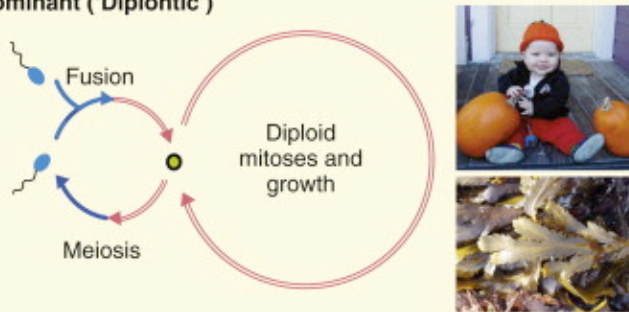
Diploid cell

Diversity of eukaryotic life cycles

A Haploidy dominant ('Haplontic')

Fusion

Haploid mitoses and growth

Meiosis

B Diploidy dominant ('Diplontic')

Fusion

Diploid mitoses and growth

Meiosis

(Otto & Gerstein 2008)

Diversity of eukaryotic life cycles

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Meiosis

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Diploid mitoses and growth

Meiosis
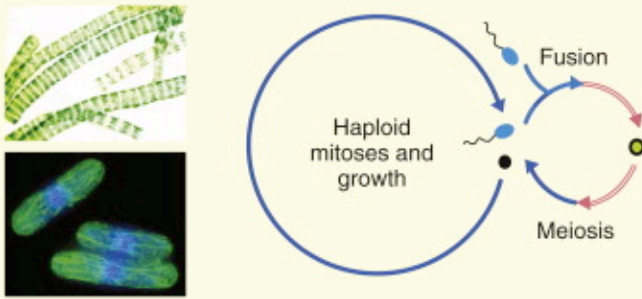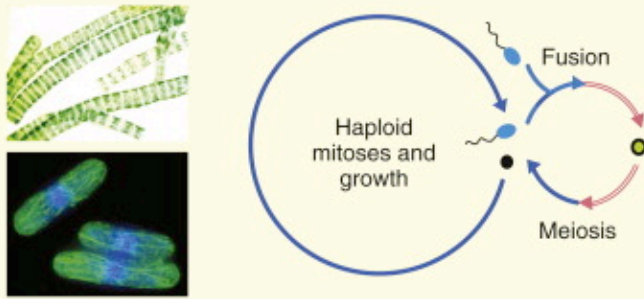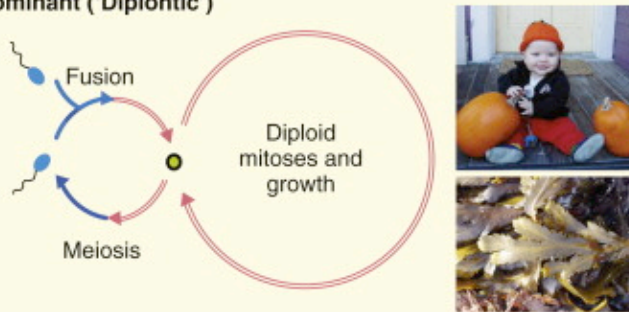
C Haploid-Diploid Life Cycle ('Diplohaplontic')

Fusion

Haploid mitoses and growth

Diploid mitoses and growth

Meiosis

Current Biology

(Otto & Gerstein 2008)

Diversity of eukaryotic life cycles

Development of the haploid phase

	No growth	Unicells, filamentous or small crustose	Parenchymatous thalli with extensive division of labour	Large, complex, highly integrated individuals
No growth		Apicomplexa Chytridiomycota Chrisophyta Zoomastigina Dinoflagellata	Gamophyta Dictyostelia Zygomycota Volvocales Ascomycota	Charophyta
Unicells, filamentous or small crustose	Bacyllariophyta Actinopoda: Ciliata Heliozoa Zoomastigina Opalinida	Primnesiophyta Foraminifera	Ulotrichales	Bangiophycae Scytosiphonales
Parenchymatous thalli with extensive division of labour	Oomycota Xantophyta	Myxomycota	Basidomycota Chaetophorales	Bryophyta
Large, complex, highly integrated individuals	Animalia Caulerpales Caulerpceae Fucales	Cycadophyta Gingkophyta Gnetophyta Coniferophyta Angiospermophyta Chordariales	Psilophyta Lycopodophyta Sphenophyta Pteridophyta	Florideophycidae Ulvales Dictyotales

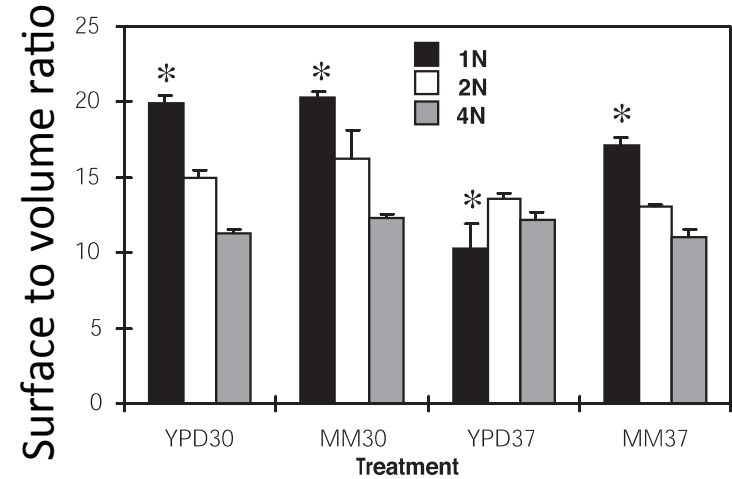**Development of the diploid phase**

(Rescan 2016)

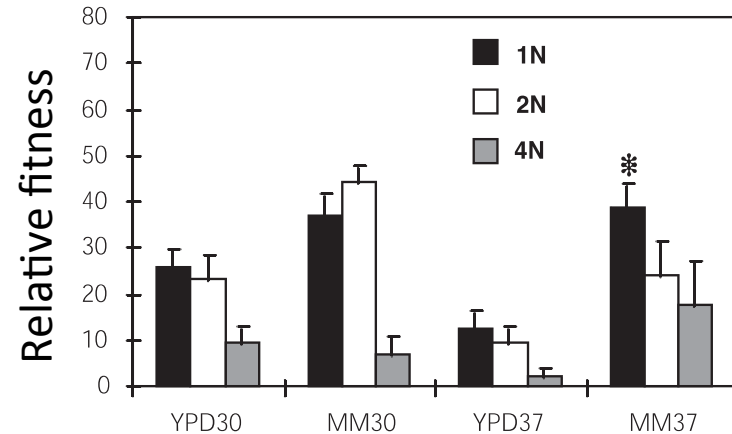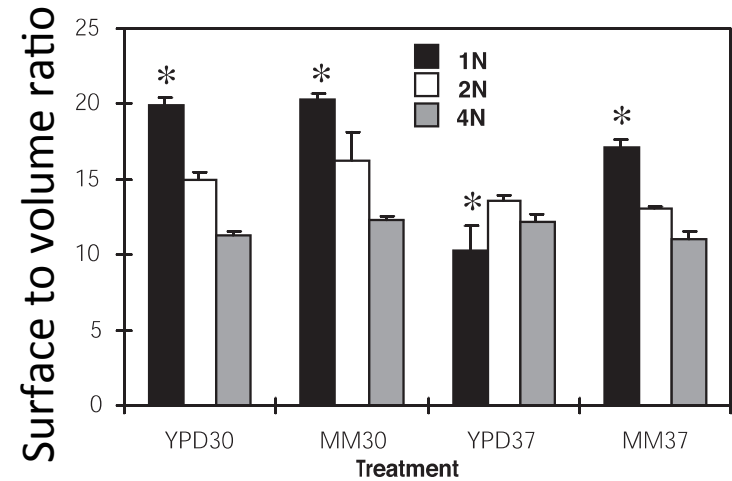➔ Physiological or genetic effects of ploidy levels

Physiological effects of ploidy

- Surface to volume ratio larger in haploid compared to diploid and polyploid cells

➢ Haploids favored in nutrient-limiting conditions

➢ Diploids favored in non nutrient-limiting conditions

(Mable 2001)

Physiological effects of ploidy

- Surface to volume ratio larger in haploid compared to diploid and polyploid cells

➤ Haploids favored in nutrient-limiting conditions

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- Fitness similar in haploids and diploids

(Mable 2001)

Physiological effects of ploidy

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- Fitness similar in haploids and diploids
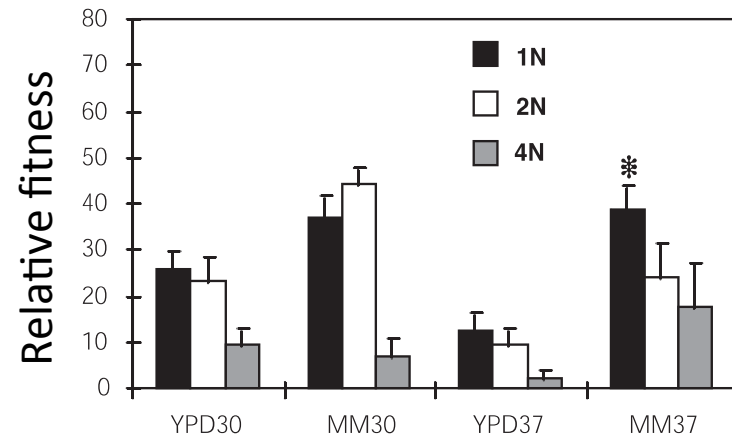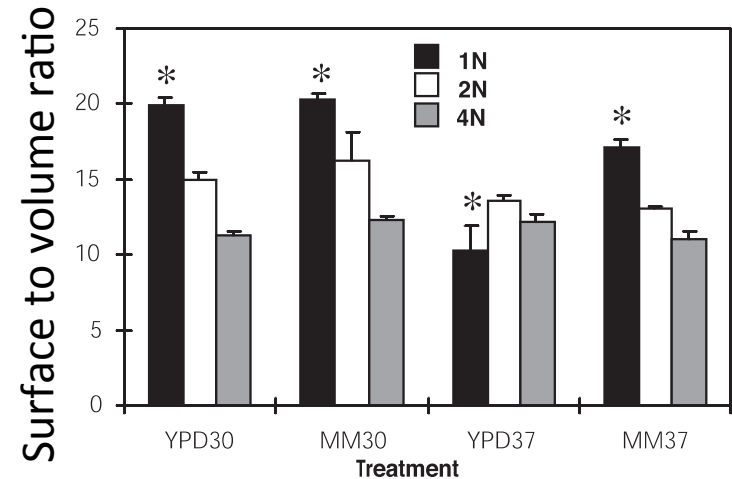
➔ No clear physiological effect of ploidy level
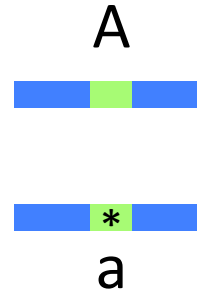➔ Genetic effects of ploidy?

(Mable 2001)

Fitness effect at locus k

➢ in haploids:

$$A_k \quad 1$$

$$a_k \quad 1 - \sigma_k$$
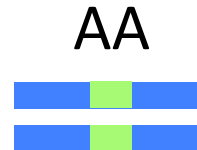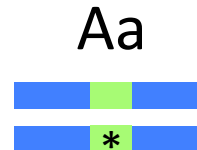
A

a

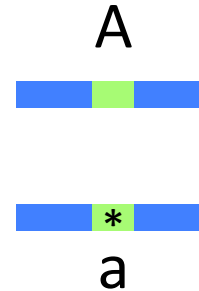Fitness effect at locus k

➤ in haploids:

A

A_k 1

a_k $1 - \sigma_k$

a

➤ in diploids:

Fitness effect at locus k

➢ in haploids:

A

A_k 1

a

a_k $1 - \sigma_k$

➢ in diploids:

AA

$A_k A_k$ 1
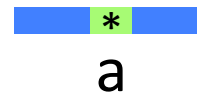
Aa

$A_k a_k$ $1 - h_k s_k$

aa

$a_k a_k$ $1 - s_k$

Fitness effect at a random locus
➢ in haploids:

$$1$$

$$1 - \bar{\sigma}$$

➢ in diploids:

A

a

AA

Aa

aa

Fitness effect at a random locus
➤ in haploids:

1

A

$1 - \bar{\sigma}$

a

➤ in diploids:

1

AA

$1 - \bar{h}\bar{s}$

Aa

$1 - \bar{s}$

aa

Fitness effect at a random locus
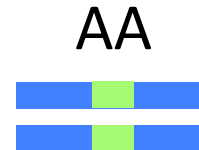
➤ in haploids:

$$\bar{s} = c_s \bar{\sigma}$$

1

A

$1 - \bar{\sigma}$

a

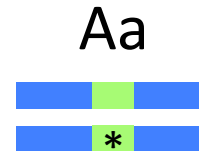➤ in diploids:

1

AA

$1 - \bar{h}\bar{s}$

Aa

$1 - \bar{s}$

aa

Fitness effect at a random locus
➤ in haploids:

1
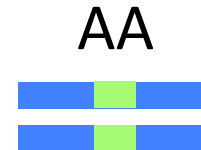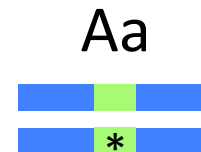
A

$1 - \bar{\sigma}$

a

➤ in diploids:

1

AA

$1 - \bar{h}c_s\bar{\sigma}$
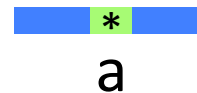
Aa

$1 - c_s\bar{\sigma}$

aa

Fitness effect at a random locus
➤ in haploids:

$$1$$
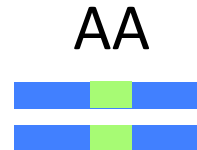
$$1 - \bar{\sigma}$$

➤ in diploids:

$$1$$

$$1 - \bar{h}c_s\bar{\sigma}$$

$$1 - c_s\bar{\sigma}$$

Fitness effect at a random locus
➢ in haploids:

$$1$$

$$1 - \bar{\sigma}$$

- Diploid phase favored when the effective dominance is lower than one: $\bar{h}c_s < 1$
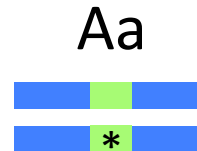
➢ in diploids:

$$1$$

$$1 - \bar{h}c_s\bar{\sigma}$$

$$1 - c_s\bar{\sigma}$$

Fitness effect at a random locus
➤ in haploids:

$$1$$

$$1 - \bar{\sigma}$$

➤ in diploids:

$$1$$

$$1 - \bar{h}c_s\bar{\sigma}$$

$$1 - c_s\bar{\sigma}$$

- Diploid phase favored when the effective dominance is lower than one: $\bar{h}c_s < 1$

➤ Partially recessive in heterozygous diploids:

$$\bar{h} < \frac{1}{2}$$

Fitness effect at a random locus
➢ in haploids:

$$1$$

$$1 - \bar{\sigma}$$

➢ in diploids:

$$1$$

$$1 - \bar{h}c_s\bar{\sigma}$$

$$1 - c_s\bar{\sigma}$$

- Diploid phase favored when the effective dominance is lower than one: $\bar{h}c_s < 1$

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➢ Stronger effect of deleterious mutations in haploids than in homozygous diploids: $c_s < 1$

Fitness effect at a random locus
- ➢ in haploids:

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$$1 - \bar{h}c_S\bar{\sigma}$$

➔ Estimation using mutation accumulation lines

$$1 - c_S\bar{\sigma}$$

Mutation accumulation lines in yeast

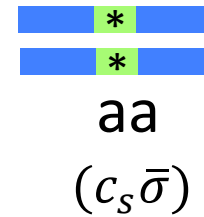Serial transfer of random single colonies
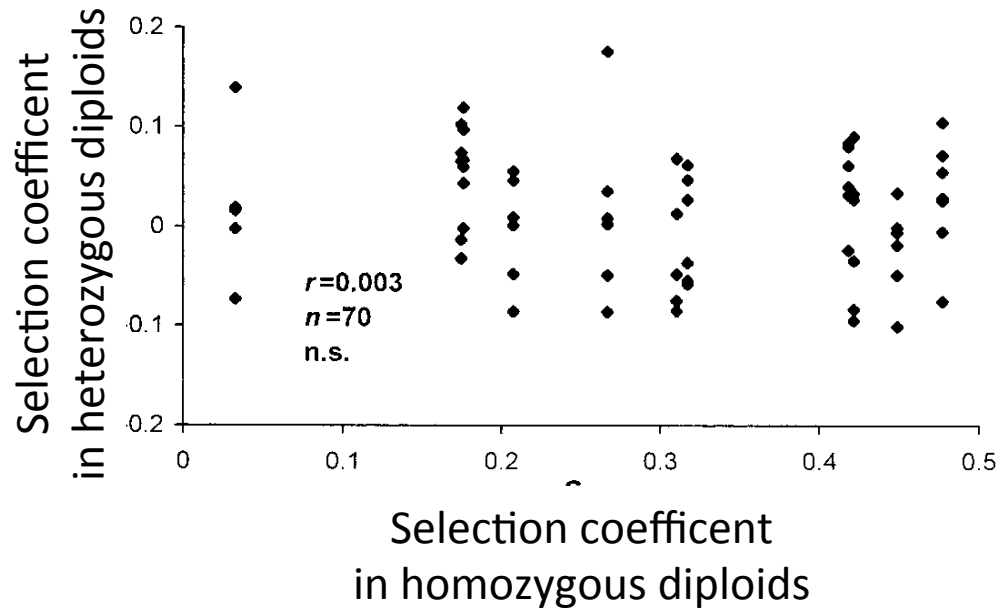mutation accumulation (MA)

ancestor

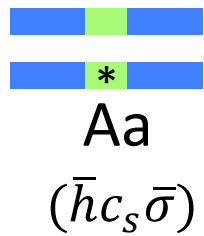replicate MA lines

(Zeyl 2004)
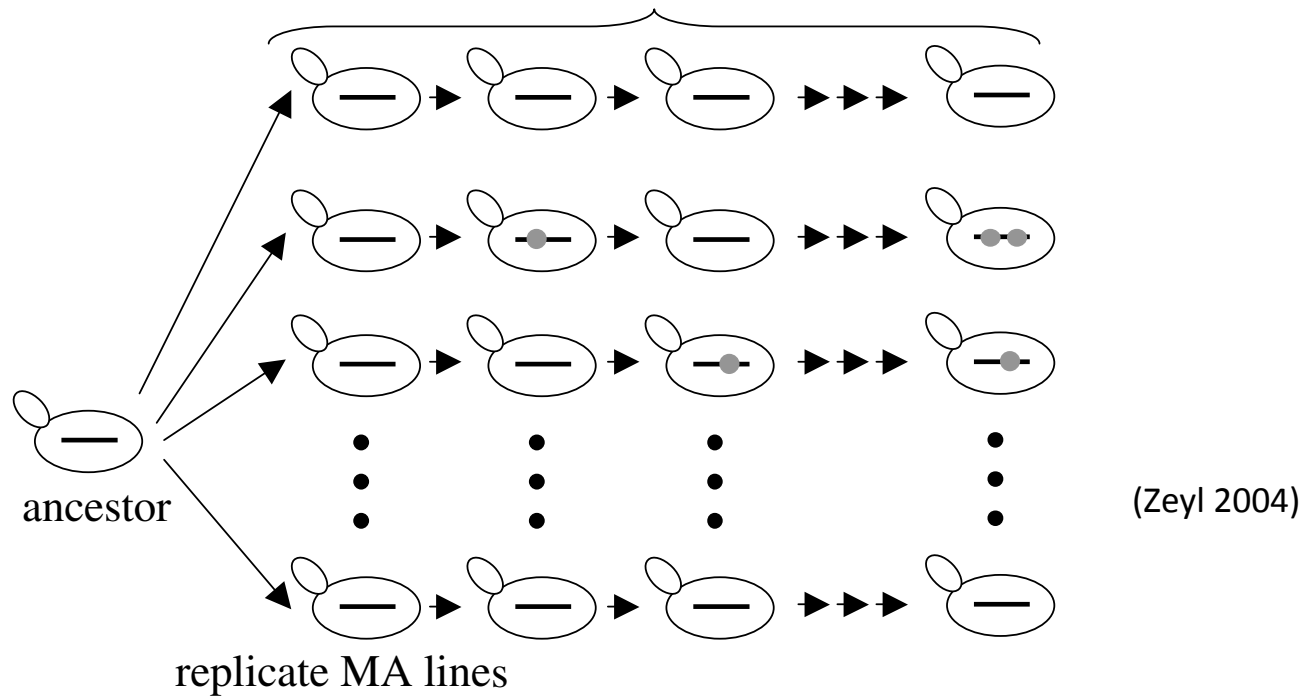
➔ Fixation of spontaneous mutations by drift

Mutation accumulation lines in yeast

(Korona 1999)

Mutation accumulation lines in yeast

Selection coefficent
in heterozygous diploids

0.2
0.1
0
-0.1
-0.2

0   0.1   0.2   0.3   0.4   0.5

$r = 0.003$
$n = 70$
n.s.

Selection coefficent
in homozygous diploids
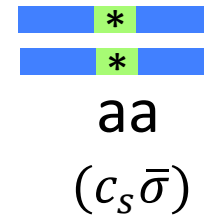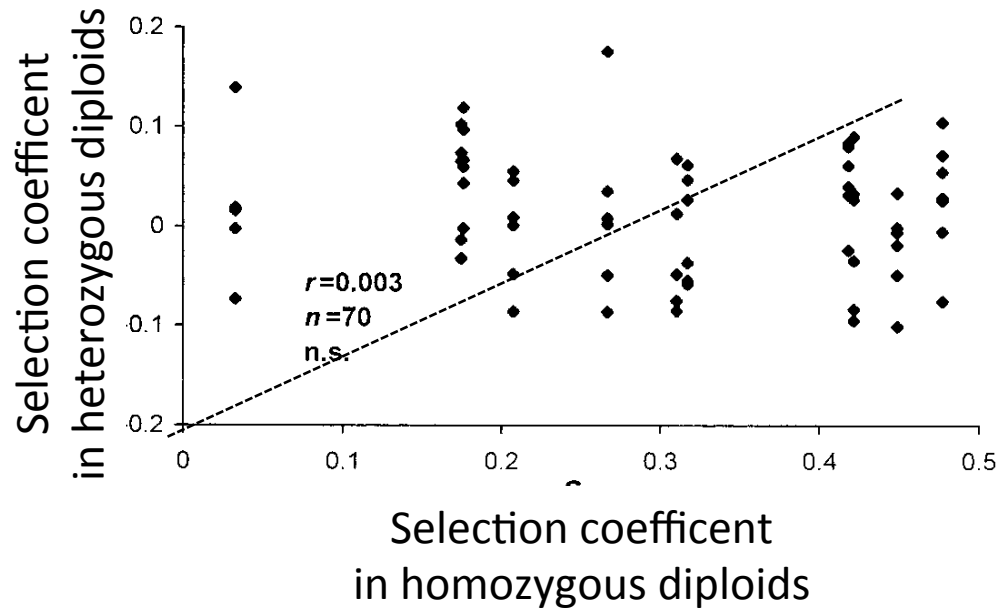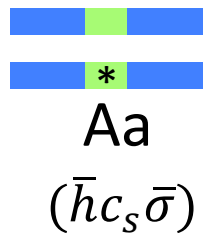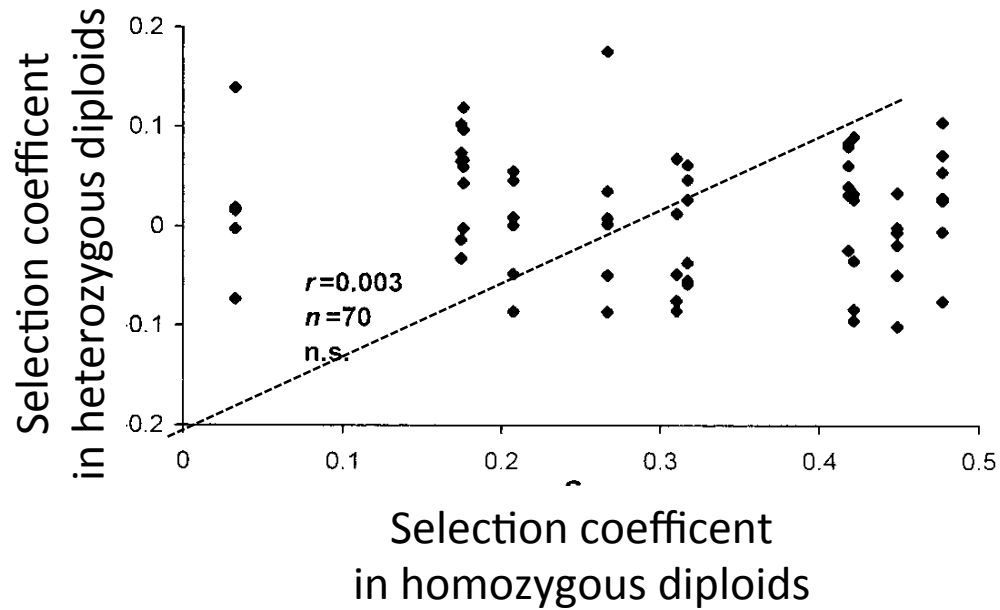
Aa
$(\bar{h} c_s \bar{\sigma})$

aa
$(c_s \bar{\sigma})$

*
*
*

(Korona 1999)

Mutation accumulation lines in yeast

Aa
$(\bar{h} c_s \bar{\sigma})$

aa
$(c_s \bar{\sigma})$

Selection coefficent in heterozygous diploids

Selection coefficent in homozygous diploids

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$n=70$
n.s.

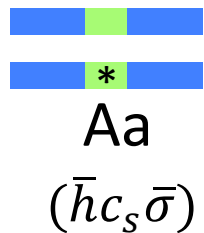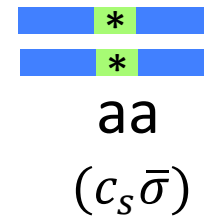(Korona 1999)

- Estimate of the average dominance: $\bar{h} = 0.08$

Mutation accumulation lines in yeast

(Korona 1999)

Aa
$(\bar{h}c_s\bar{\sigma})$

aa
$(c_s\bar{\sigma})$

- Estimate of the average dominance: $\bar{h} = 0.08$
- Estimate from other studies: $\bar{h} = 0.2$

(Agrawal and Whitlock 2011, Manna et al 2011)

Mutation accumulation lines in yeast

(Korona 1999)

Aa

$(\bar{h}c_s\bar{\sigma})$
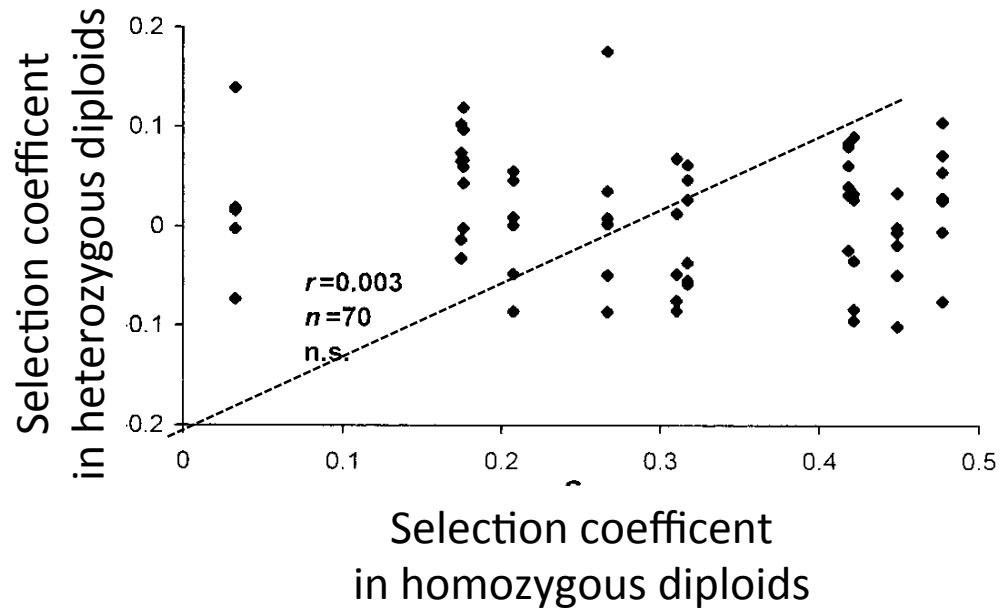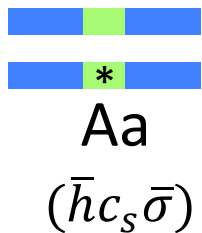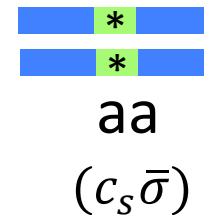
aa

$(c_s\bar{\sigma})$

- Estimate of the average dominance: $\bar{h} = 0.08$
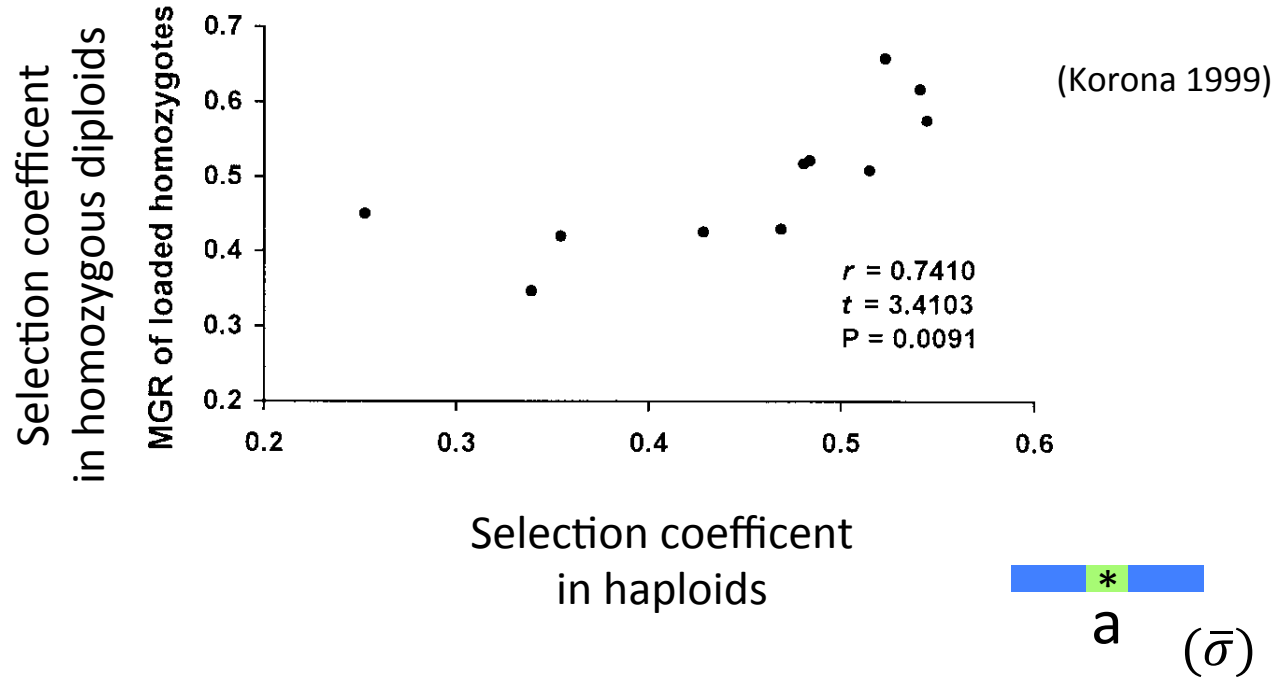- Estimate from other studies: $\bar{h} = 0.2$

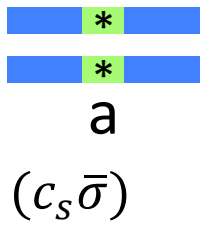(Agrawal and Whitlock 2011, Manna et al 2011)

➔ Mutations are recessive on average $\bar{h} < \dfrac{1}{2}$

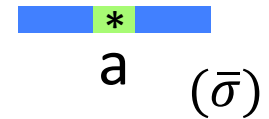# Mutation accumulation lines in yeast

(Korona 1999)

Mutation accumulation lines in yeast

(Korona 1999)

Selection coefficient in homozygous diploids — $(c_s\bar{\sigma})$

Selection coefficient in haploids — $(\bar{\sigma})$

MGR of loaded homozygotes (y-axis)

$r = 0.7410$
$t = 3.4103$
$P = 0.0091$

Mutation accumulation lines in yeast

(Korona 1999)

$r = 0.7410$
$t = 3.4103$
$P = 0.0091$

$(c_s \bar{\sigma})$

$(\bar{\sigma})$
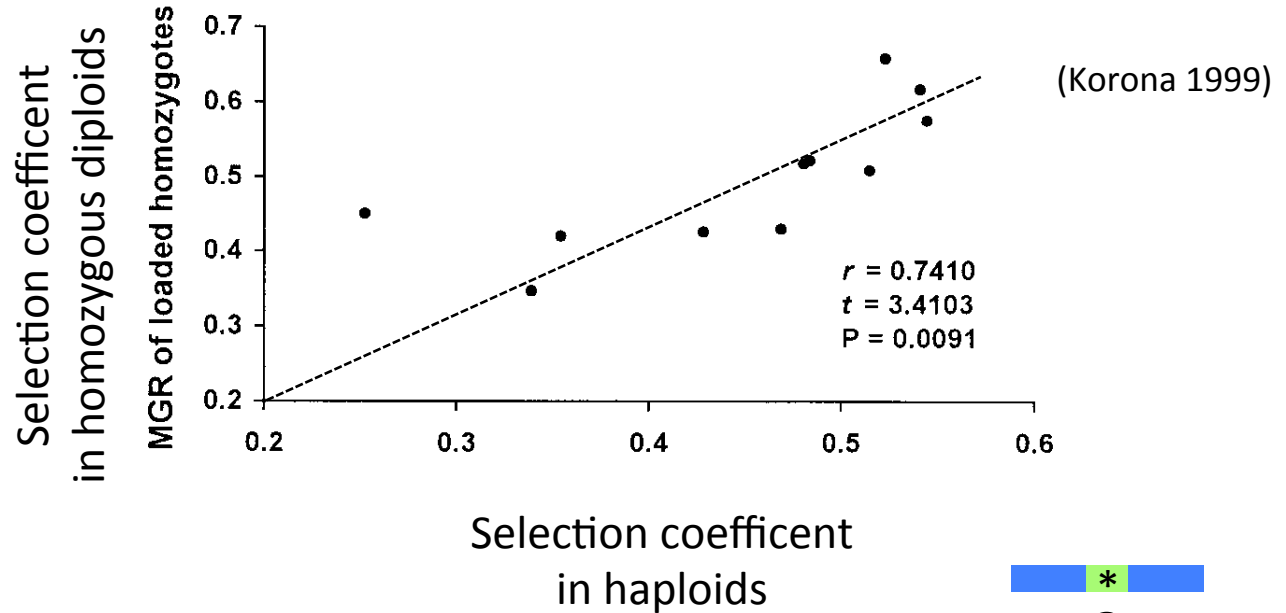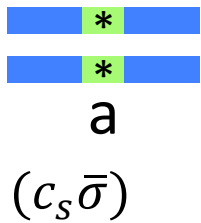
- Same selection coefficient in haploids and homozygous diploids: $c_s \approx 1$

Mutation accumulation lines in yeast
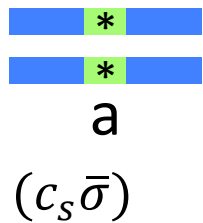
(Korona 1999)

$r = 0.7410$
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Selection coefficent in homozygous diploids

MGR of loaded homozygotes
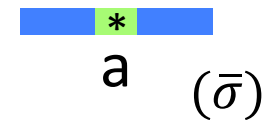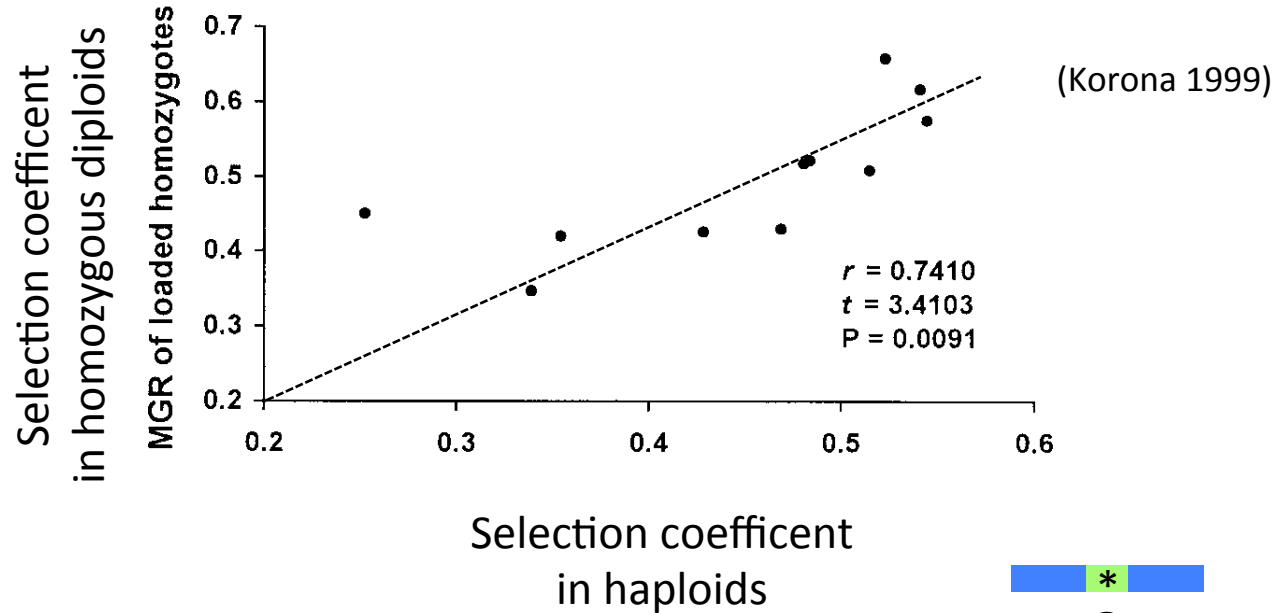
Selection coefficent in haploids

$(c_s \bar{\sigma})$

a

$(\bar{\sigma})$

- Same selection coefficient in haploids and homozygous diploids: $\quad c_s \approx 1$

➔ Effective dominance lower than one:
➔ Selection for an increased diploid phase

$$\bar{h}c_s < 1$$

Mutation accumulation lines in yeast

(Korona 1999)

$r = 0.7410$
$t = 3.4103$
$P = 0.0091$

Selection coefficent in homozygous diploids

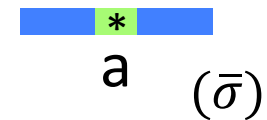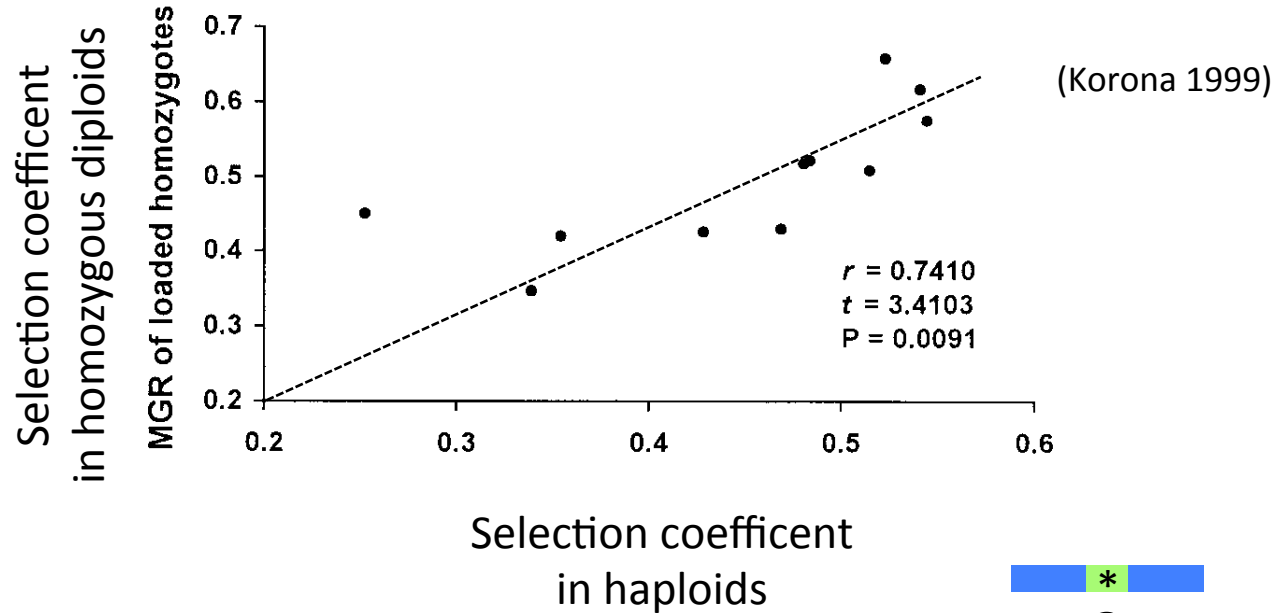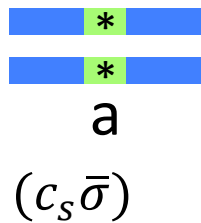MGR of loaded homozygotes

Selection coefficent in haploids

a

$(c_s \bar{\sigma})$

a

$(\bar{\sigma})$

- Same selection coefficient in haploids and homozygous diploids: $c_s \approx 1$

➜ Effective dominance lower than one: $\bar{h} c_s < 1$
➜ Selection for an increased diploid phase
➜ Diploid yeast in the wild (Landry et al 2006)

Alternative approaches?

- Mutation accumulation is tedious
- Auto-compatibility impedes the construction of homozygous diploids
- Crosses between haploid strains with increasing genetic distance?

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- Mutation accumulation is tedious
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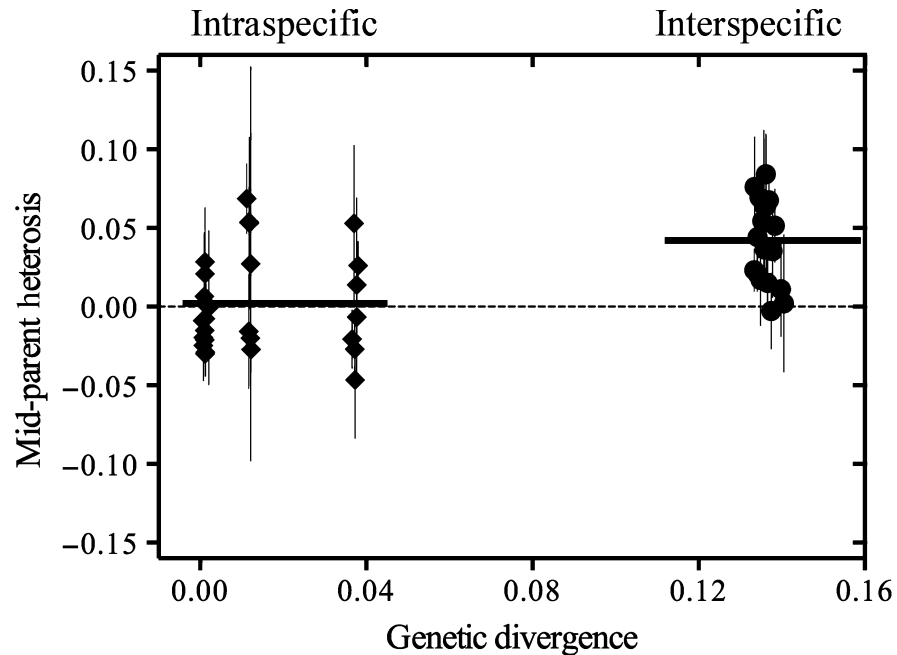

(Bernardes et al 20017)
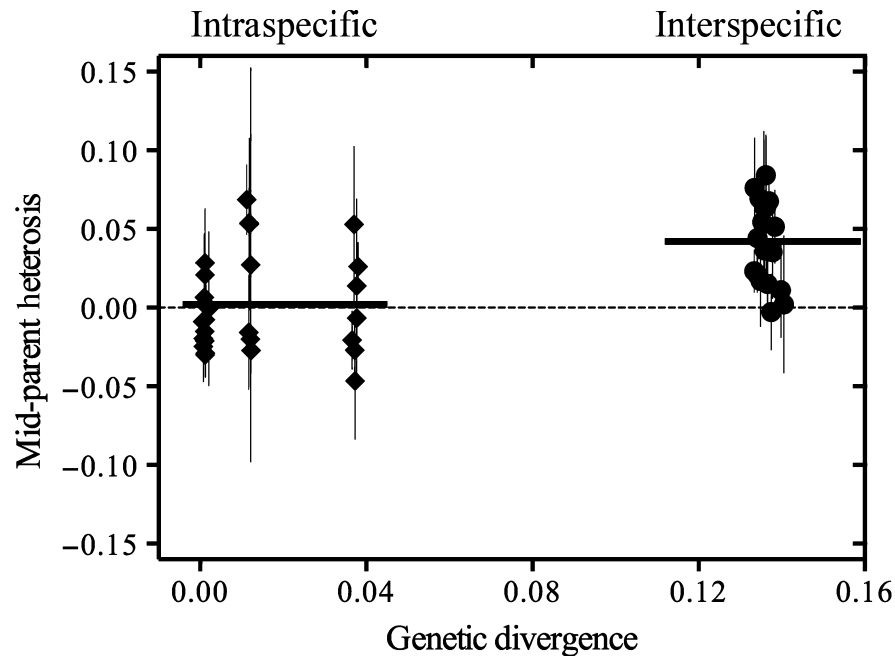
Alternative approaches?

- Mutation accumulation is tedious
- Auto-compatibility impedes the construction of homozygous diploids
- Crosses between haploid strains with increasing genetic distance?

(Bernardes et al 20017)

➔ No theoretical framework with effective dominance $(\bar{h}c_s)$

Fitness effect at a random locus
- ➤ in haploids:

$$1$$

$$1 - \bar{\sigma}$$

- ➤ in diploids:

$$1$$

$$1 - \bar{h}c_s\bar{\sigma}$$

$$1 - c_s\bar{\sigma}$$

Fitness effect at a random locus

➢ in haploids:
$$w_i = w_0 \exp\left(-\sum_{k=1}^{n} \sigma_k X_k^i\right)$$

$$1$$

$$1 - \bar{\sigma}$$

➢ in diploids:
$$W_{ij} = W_0 \exp\left(-\sum_{k=1}^{n} s_k \left(\frac{X_k^i + X_k^j}{2}\right) + d_{ij} \sum_{k=1}^{n} s_k \left(\frac{1 - 2h_k}{2}\right)\right)$$

$$1$$

$$1 - \bar{h} c_S \bar{\sigma}$$

$$1 - c_S \bar{\sigma}$$

Fitness effect at a random locus

➢ in haploids:

$$w_i = w_0 \exp\left(-\sum_{k=1}^{n} \sigma_k X_k^i\right)$$

$$1$$

$$1 - \bar{\sigma}$$

➢ in diploids:

$$W_{ij} = W_0 \exp\left(-\sum_{k=1}^{n} s_k \left(\frac{X_k^i + X_k^j}{2}\right) + d_{ij} \sum_{k=1}^{n} s_k \left(\frac{1 - 2h_k}{2}\right)\right)$$

Statistical model:
Haploids:

$$1$$

$$\ln(w_i) = \ln(w_0) - A_i$$

$$1 - \bar{h} c_s \bar{\sigma}$$

$$1 - c_s \bar{\sigma}$$

Fitness effect at a random locus

➢ in haploids: $\quad\quad w_i = w_0 \exp\left(-\sum_{k=1}^{n} \sigma_k X_k^i\right)$

$$1$$

$$1 - \bar{\sigma}$$

➢ in diploids: $\quad W_{ij} = W_0 \exp\left(-\sum_{k=1}^{n} s_k \left(\frac{X_k^i + X_k^j}{2}\right) + d_{ij} \sum_{k=1}^{n} s_k \left(\frac{1 - 2h_k}{2}\right)\right)$

$$1$$

Statistical model:

Haploids:

$$1 - \bar{h} c_S \bar{\sigma}$$

$$\ln(w_i) = \ln(w_0) - A_i$$

Diploid (cross between strain *i* and *j*):

$$\ln(W_{ij}) = \ln(W_0) - c_S \frac{A_i + A_j}{2} + d_{ij} H$$

$$1 - c_S \bar{\sigma}$$

Fitness effect at a random locus

➢ in haploids:

$$w_i = w_0 \exp\left(-\sum_{k=1}^{n} \sigma_k X_k^i\right)$$

$$1$$

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➢ in diploids:

$$W_{ij} = W_0 \exp\left(-\sum_{k=1}^{n} s_k \left(\frac{X_k^i + X_k^j}{2}\right) + d_{ij} \sum_{k=1}^{n} s_k \left(\frac{1 - 2h_k}{2}\right)\right)$$

Statistical model:
Haploids:

$$1$$

$$\ln(w_i) = \ln(w_0) - A_i$$

$$1 - \bar{h} c_s \bar{\sigma}$$

Diploid (cross between strain *i* and *j*):

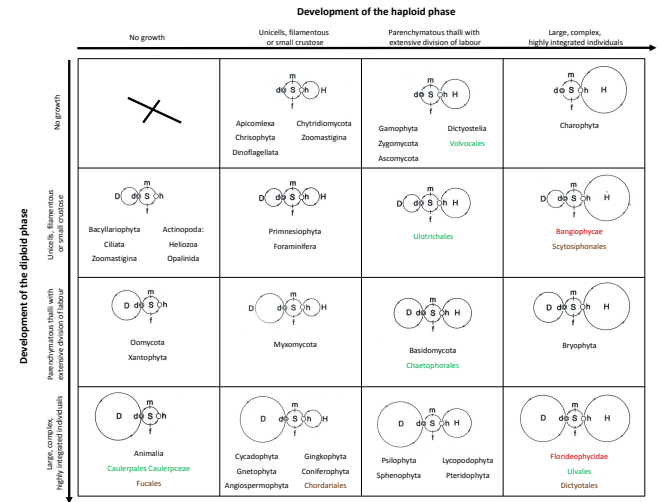$$\ln(W_{ij}) = \ln(W_0) - \boxed{c_S}\frac{A_i + A_j}{2} + d_{ij}\boxed{H}$$

$$1 - c_s \bar{\sigma}$$

Fitness effect at a random locus
➤ in haploids:

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$$1$$

$$1 - \bar{\sigma}$$

➤ in diploids:

$$W_{ij} = W_0 \exp\left(-\sum_{k=1}^{n} s_k \left(\frac{X_k^i + X_k^j}{2}\right) + d_{ij} \sum_{k=1}^{n} s_k \left(\frac{1 - 2h_k}{2}\right)\right)$$

Statistical model:
Haploids:

$$1$$

$$\ln(w_i) = \ln(w_0) - A_i$$

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Diploid (cross between strain *i* and *j*):

$$\ln(W_{ij}) = \ln(W_0) - \boxed{c_S}\frac{A_i + A_j}{2} + d_{ij}\boxed{H}$$

$$1 - c_s \bar{\sigma}$$

➜ c$_s$< 1 or H > 0 $(\bar{h} < \frac{1}{2})$

Heterobasidion parviporum

Application to an auto-incompatible fungus
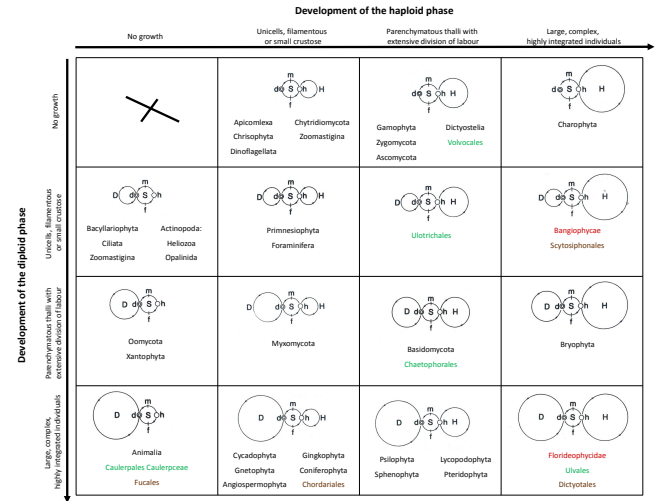

Heterobasidion parviporum
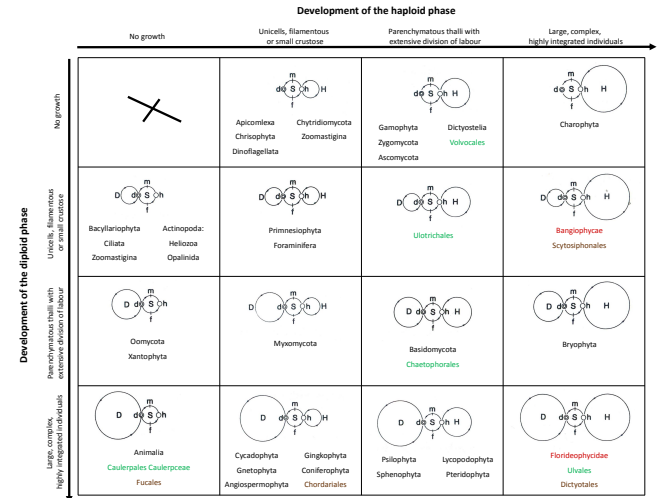
Homokaryons ~ haploids
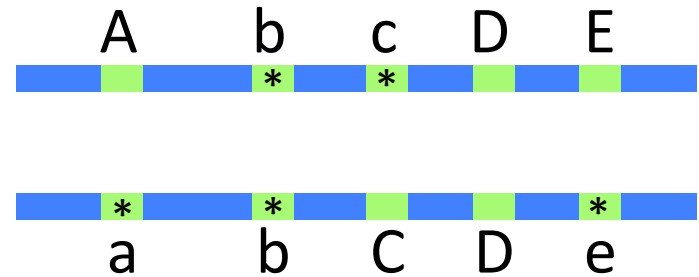
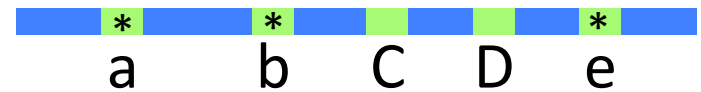# Application to an auto-incompatible fungus

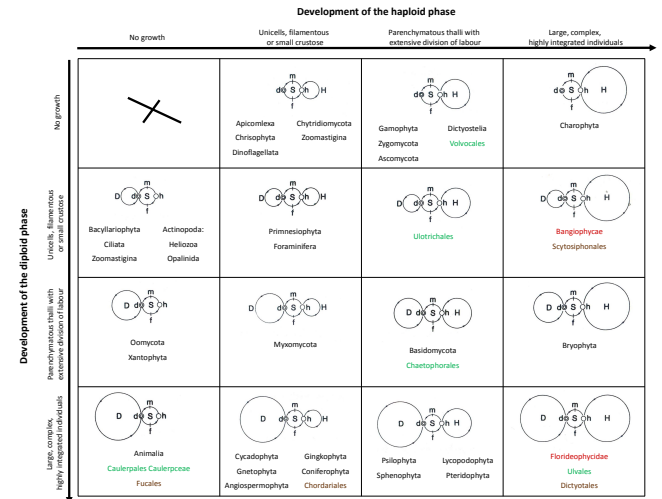*Heterobasidion parviporum*

Homokaryons ~ haploids

Heterokaryons ~ diploids
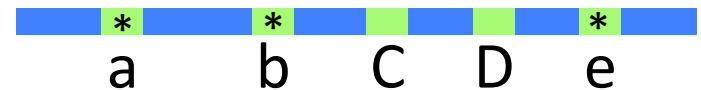
Application to an auto-incompatible fungus

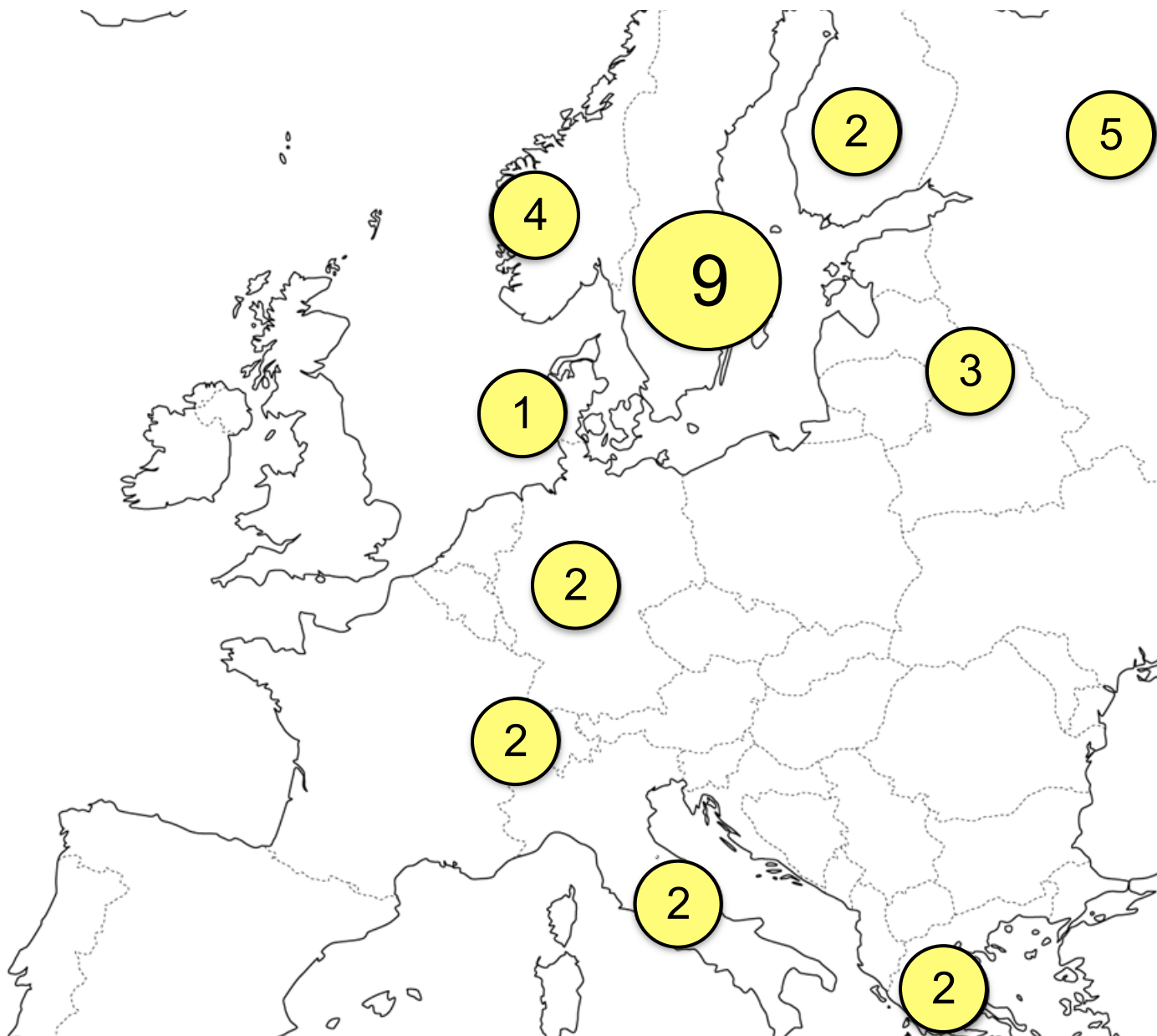*Heterobasidion parviporum*

Homokaryons ~ haploids

Heterokaryons ~ diploids

➔ Heterokaryons often observed
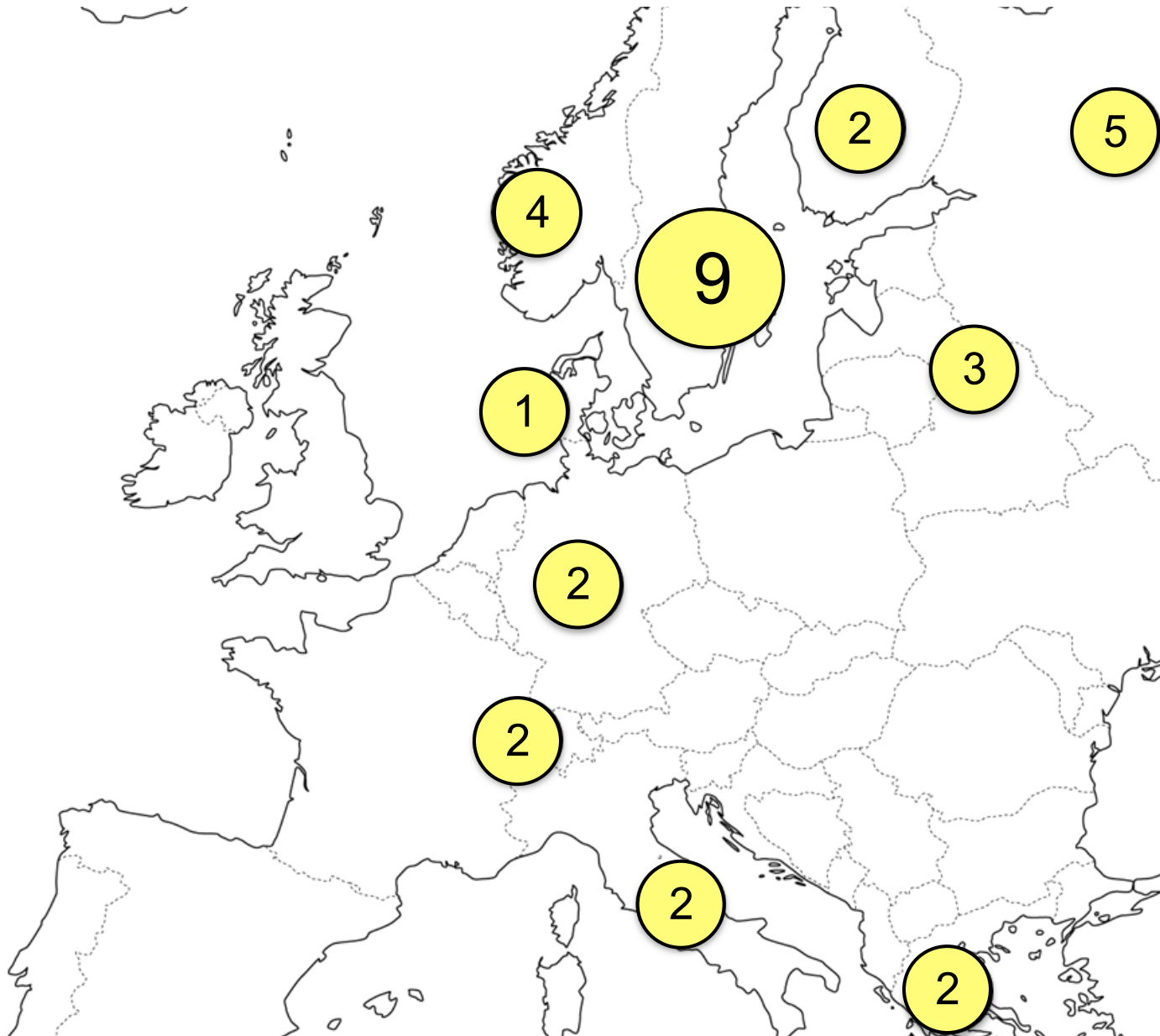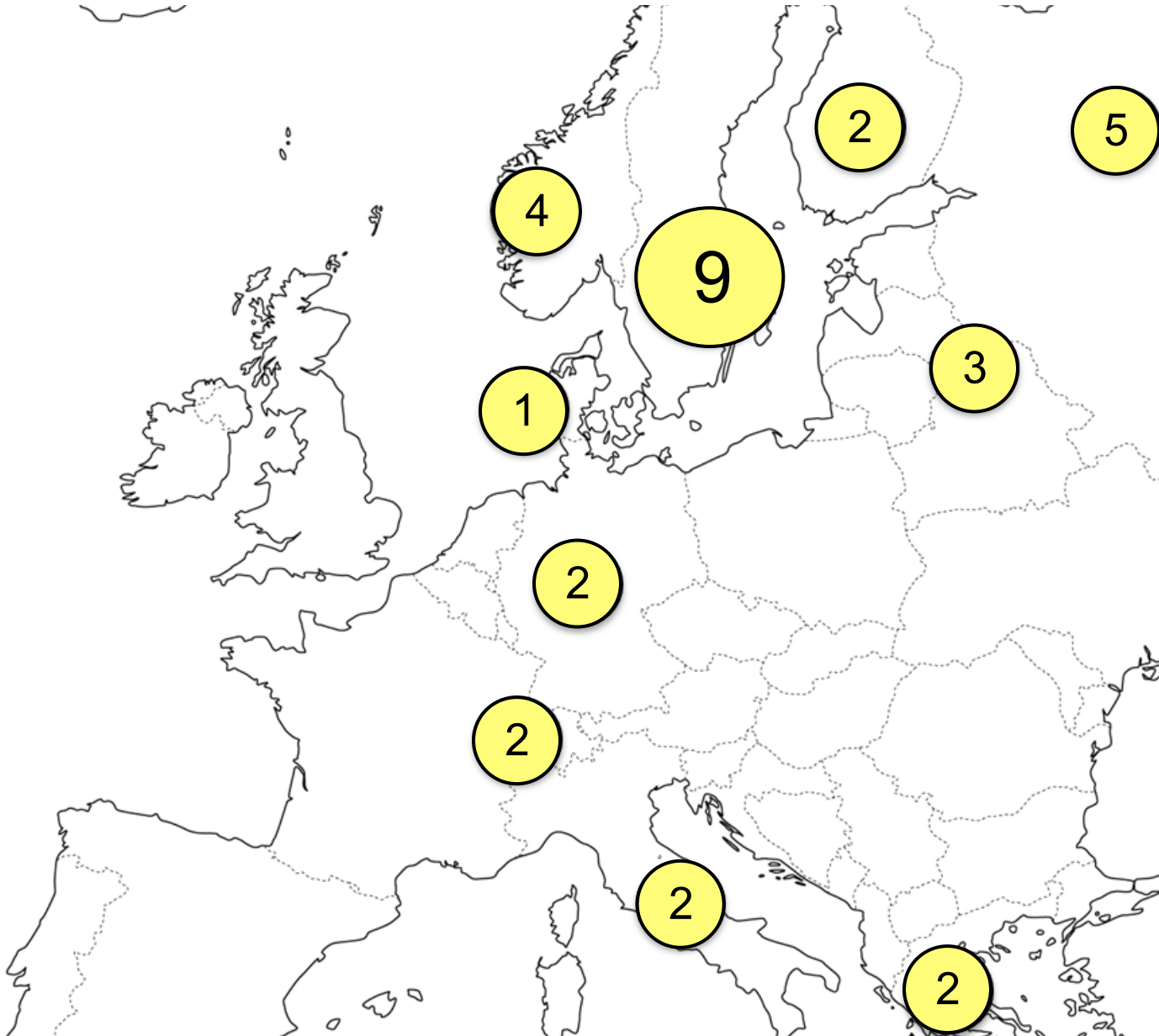in nature (Joahnneson & Stenlid 2004)

32 samples

32 x 31 crosses

32 samples

32 x 31 crosses

18 homokaryons
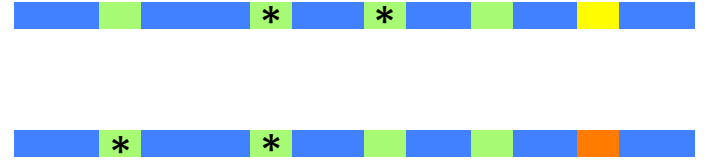
32 samples

32 x 31 crosses

18 homokaryons

277 heterokaryons:
18 acceptors
 (nucleus+cytosplasm)
x 32 donors
 (nucleus only)

Genetic distance between parental strains

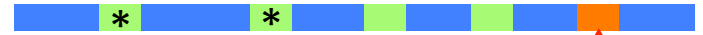Homokaryons ~ haploids

Heterokaryons ~ diploids
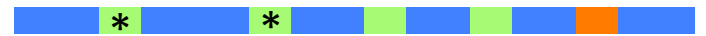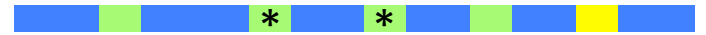
Genetic distance between parental strains

Homokaryons ~ haploids

Heterokaryons ~ diploids

incompatibility locus

Genetic distance between parental strains

Homokaryons ~ haploids

incompatibility locus

Heterokaryons ~ diploids

Genetic distance between parental strains
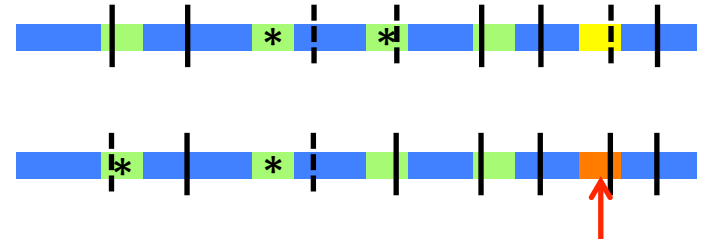
Homokaryons ~ haploids
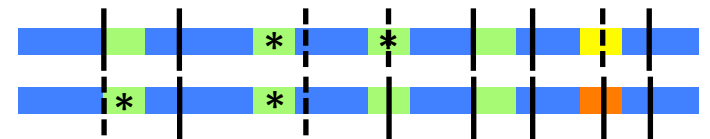
Heterokaryons ~ diploids

incompatibility locus

➔ Genetic distance between parental homokaryons

Genetic distance between parental strains

Homokaryons ~ haploids

incompatibility locus

Heterokaryons ~ diploids

➔ Genetic distance between parental homokaryons
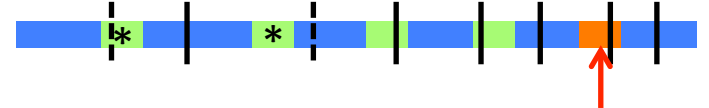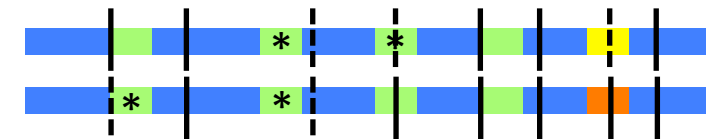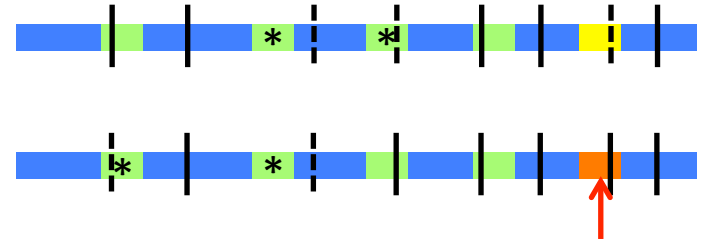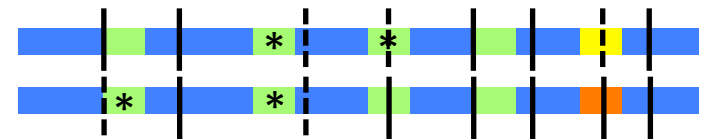
Genetic distance between parental strains

Homokaryons ~ haploids

Heterokaryons ~ diploids

incompatibility locus

➔ Genetic distance between parental homokaryons

➔ Effective dominance lower than one? $(\bar{h}c_s < 1)$
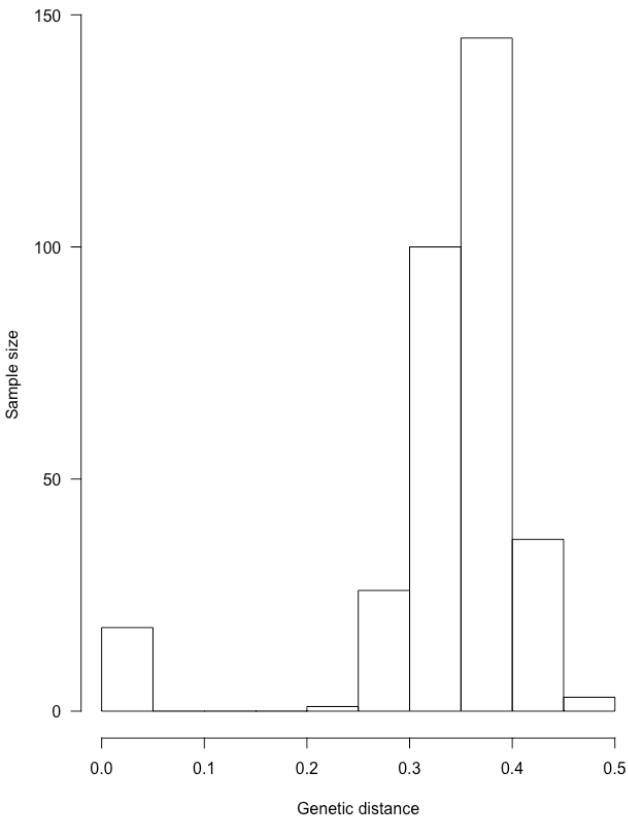
Linear mixed model:

$$\log(growth\ rate_{ijkl}) = average\ grow\ rate + growth\ rate\ H *$$
$$genetic\ distance_{ij} + c_s^{Type} \frac{growth\ rate\ acceptor_i + groth\ rate\ donor_j}{2} +$$
$$growth\ rate\ assay_{ijk} + growth\ rate\ plate_{ijkl} + error$$

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$$growth\ rate\ assay_{ijk} + growth\ rate\ plate_{ijkl} + error$$

➔ AICc model selection

Results

	ΔAICc
Genetic distance, $c_s \neq 1$	0.00
Genetic distance, $c_s = 1$	5.47
No genetic distance, $c_s \neq 1$	12.32
No genetic distance, $c_s = 1$	21.54

Linear mixed model:

$$\log(growth\ rate_{ijkl}) = average\ grow\ rate + growth\ rate\ H * genetic\ distance_{ij} + c_s^{Type} \frac{growth\ rate\ acceptor_i + groth\ rate\ donor_j}{2} + growth\ rate\ assay_{ijk} + growth\ rate\ plate_{ijkl} + error$$

Average growth rate	0.2999	0.0071
growth rate H	0.0071	0.0021
Cs	1.8	0.16

Conclusions

Fitness in haploids:

A 1

a $1 - \bar{\sigma}$

Fitness in diploids:

AA 1

Aa $1 - \bar{h}c_s\bar{\sigma}$

aa $1 - c_s\bar{\sigma}$

- Diploid phase favored when:

$$\bar{h}c_s < 1$$

$$\bar{h} < \frac{1}{2} \text{ or } c_s < 1$$

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➢ Partially recessive in heterozygous diploids (H<0)

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➤ But stronger effect of deleterious mutations in haploids than in homozygous diploids $c_s > 1$

Conclusions

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a $1 - \bar{\sigma}$

Fitness in diploids:

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  ➢ But stronger effect of deleterious mutations in haploids than in homozygous diploids $c_s > 1$

  $$\bar{h} < \frac{1}{2}$$

  $$\bar{h}c_s < \frac{1.8}{2} < 1$$

Conclusions

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$$\bar{h}c_s < \frac{1.8}{2} < 1$$

➜ Effective dominance lower than one

Conclusions

Fitness in haploids:

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a $1 - \bar{\sigma}$

Fitness in diploids:

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- Diploid phase favored when:

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➤ Partially recessive in heterozygous diploids (H<0)
➤ But stronger effect of deleterious mutations in haploids than in homozygous diploids $c_s > 1$

$$\bar{h} < \frac{1}{2}$$

$$\bar{h}c_s < \frac{1.8}{2} < 1$$

➔ Effective dominance lower than one
➔ Diploid phase is actually observed more often in nature (Joahnneson & Stenlid 2004)

Fitness in homokaryons:

$A_k A_l$ 1
$A_k a_l$ $1 - \sigma_k$
$a_k A_l$ $1 - \sigma_l$
$a_k a_l$ $(1 - \sigma_k)(1 - \sigma_l) + \varepsilon_{kl}$

Fitness in heterokaryons:

$A_k A_k\ A_l A_l$ 1
$A_k a_k\ A_l A_l$ $1 - h_k s_k$
$a_k a_k\ A_l A_l$ $1 - s_k$
$A_k A_k\ A_l a_l$ $1 - h_l s_l$
$A_k a_k\ A_l a_l$ $(1 - h_k s_k)(1 - h_l s_l) + e_{kl}$
$a_k a_k\ A_l a_l$ $(1 - s_k)(1 - h_l s_l) + 2e_{kl}$
$A_k A_k\ a_l a_l$ $1 - s_l$
$A_k a_k\ a_l a_l$ $(1 - h_k s_k)(1 - s_l) + 2e_{kl}$
$a_k a_k\ a_l a_l$ $(1 - s_k)(1 - s_l) + 4e_{kl}$

$$\ln(w_i) = \ln(w_0) - A_i - E_i$$

$$\ln(W_{ij}) \approx \ln(W_0) - c_S \frac{A_i + A_j}{2} + d_{ij}\left(H - n\frac{c_E \varepsilon}{2}\right) - c_E\left(E_i + E_j + 2\sqrt{E_i E_j}\right)$$

Fitness in homokaryons:

$A_k A_l$ 1

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$a_k a_l$ $(1 - \sigma_k)(1 - \sigma_l) + \varepsilon_{kl}$

Fitness in heterokaryons:

$A_k A_k \, A_l A_l$ 1

$A_k a_k \, A_l A_l$ $1 - h_k s_k$

$a_k a_k \, A_l A_l$ $1 - s_k$

$A_k A_k \, A_l a_l$ $1 - h_l s_l$

$A_k a_k \, A_l a_l$ $(1 - h_k s_k)\,(1 - h_l s_l) + e_{kl}$

$a_k a_k \, A_l a_l$ $(1 - s_k)\,(1 - h_l s_l) + 2e_{kl}$

$A_k A_k \, a_l a_l$ $1 - s_l$

$A_k a_k \, a_l a_l$ $(1 - h_k s_k)(1 - s_l) + 2e_{kl}$

$a_k a_k \, a_l a_l$ $(1 - s_k)\,(1 - s_l) + 4e_{kl}$

$$\ln(w_i) = \ln(w_0) - A_i - E_i$$

$$\ln(W_{ij}) \approx \ln(W_0) - c_S \frac{A_i + A_j}{2} + d_{ij}\left(H - n\frac{c_E \varepsilon}{2}\right) - c_E\left(E_i + E_j + 2\sqrt{E_i E_j}\right)$$

➔ Other fitness traits (wood degradation data)

➔ New experimental tool to study the life cycle of haploid-diploid organisms

Acknowledgements

P-H. Clergeot

Ake Olson
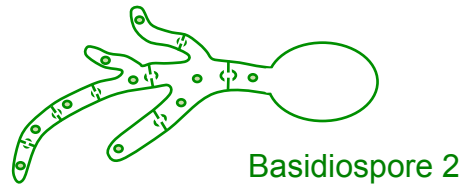

Mikael Brandström-Durling

Sylvain Glémin

Merci!

Fungal life cycle

Basidiospore 1

Basidiospore 2
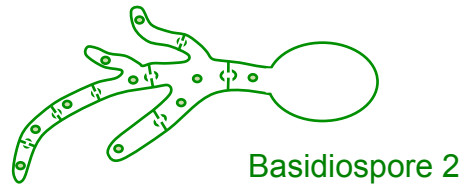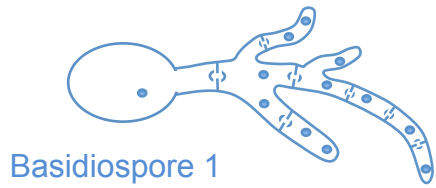
1. Homokaryotic growth (n)
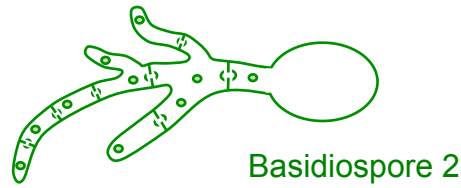
Fungal life cycle

Basidiospore 1

Basidiospore 2
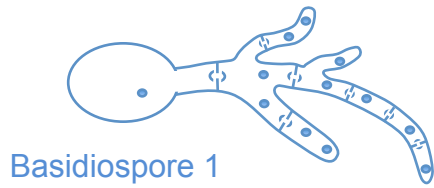
1. Homokaryotic growth (n)
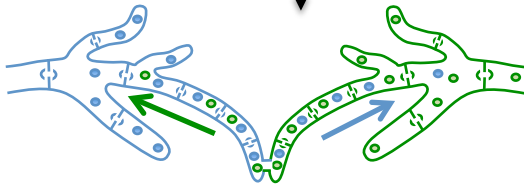
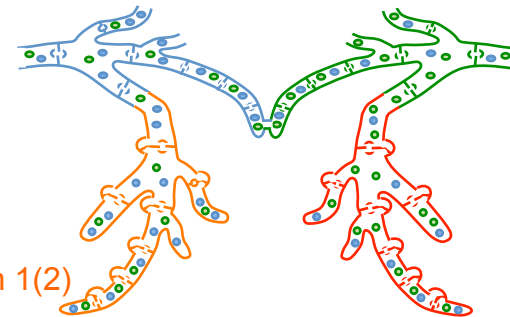2. Plasmogamy and nuclear exchange

Fungal life cycle
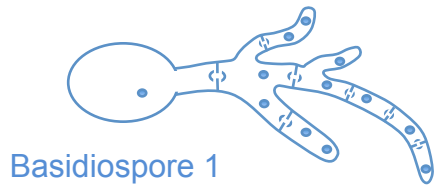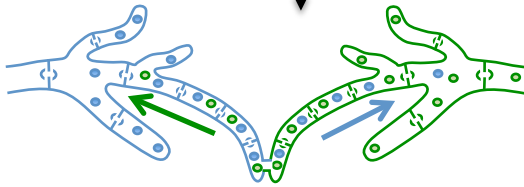
Basidiospore 1

Basidiospore 2

1. Homokaryotic growth (n)
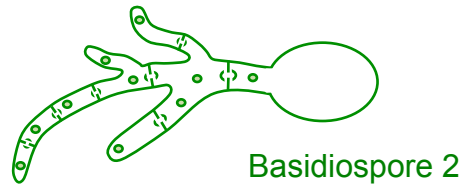
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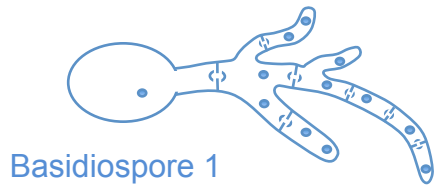
Heterokaryon 1(2)
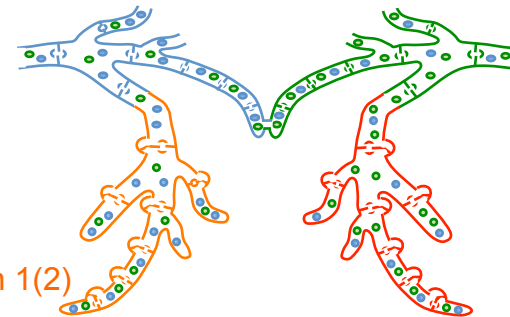
Heterokaryon 2(1)
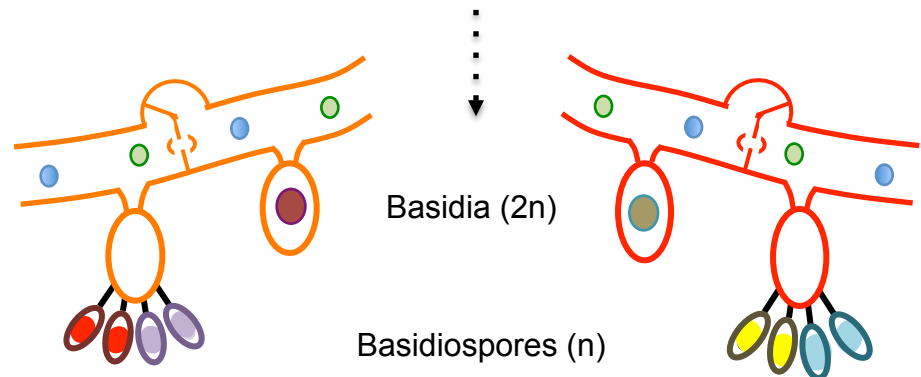
3. Heterokaryotic growth (n + n)

Fungal life cycle

Basidiospore 1

Basidiospore 2

1. Homokaryotic growth (n)

2. Plasmogamy and nuclear exchange

Heterokaryon 1(2)

Heterokaryon 2(1)

3. Heterokaryotic growth (n + n)

➔ Homokaryon: haploid
➔ Heterokaryon: diploid

Basidia (2n)
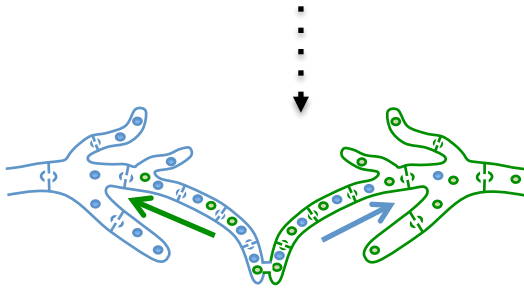
Basidiospores (n)

4. Karyogamy and meiosis in the fruiting body

Liu et al 2017

H. parviporum mating

Crossings

Nuclei acceptor

279 Heterokaryons (178 in 89 pairs)

Results