# Presentation of ”Which recurrent selection scheme to improve mixtures of crop species? Theoretical expectations” by Sampoux et al. (2020)

Jean-Paul Sampoux

# Which recurrent selection scheme to improve mixtures of crop species? Theoretical expectations

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https://www.g3journal.org/content/ggg/10/1/89.full.pdf

# Objectives of the paper

Wright, 1985 proposed a recurrent selection scheme to improve reciprocal mixture ability of plant species

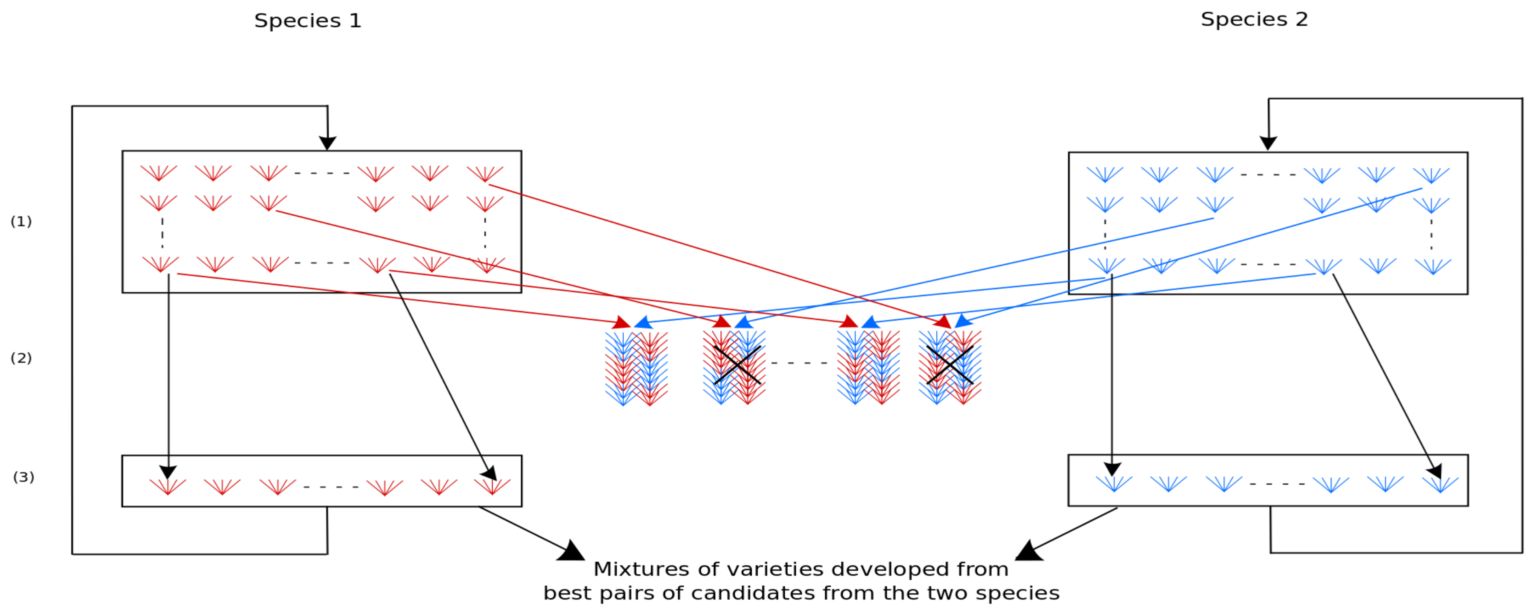
In the case of mixtures of two species:

- We aimed to compare the efficiency of the recurrent scheme of Wright, 1985 to:
    - an alternative recurrent scheme aiming to improve General Mixture Ability
    - selection in pure stands in each species

- We proposed a index selection to control the responses to selection of species contributions to the mixture

We extended our results to the case of any number of species included in the mixture

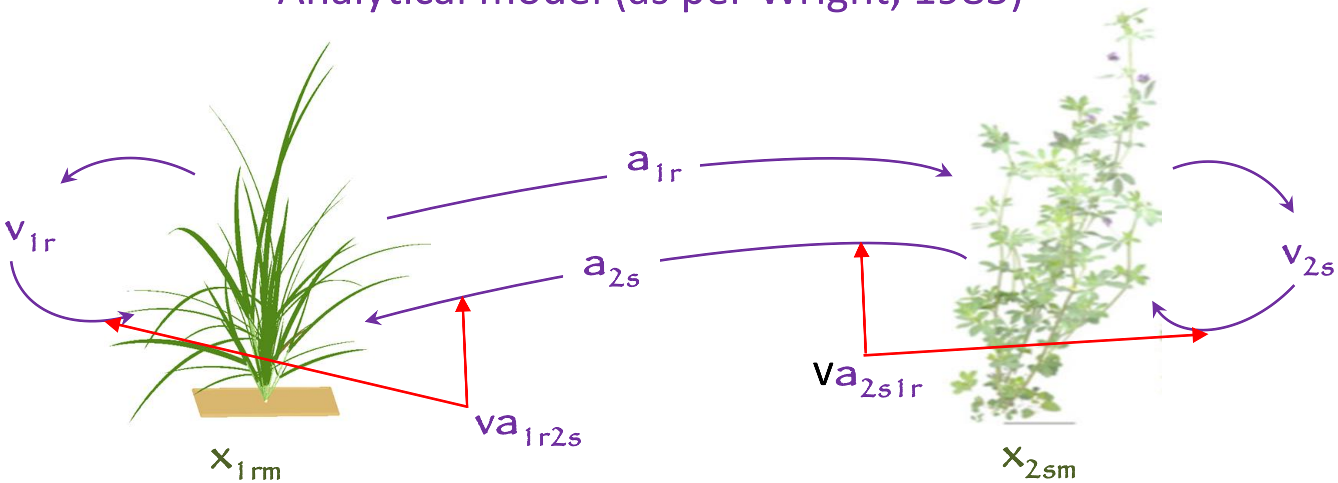
# Recurrent Selection for Reciprocal Mixture Ability (SRMA) in two species
## (as per Wright, 1985)




→ Each progeny family from a species is tested in mixture with a progeny family from the other species
→ Best pairs (mixtures) of progeny families are selected
→ Candidates from best pairs are recombined in each species

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

## Analytical model (as per Wright, 1985)




$$y_{1r2sm} = x_{1rm} + x_{2sm}$$

$y_{1r2sm}$ = observed performance of the mixture of progeny families *r* from species *1* and *s* from species *2* (replicate *m*)
$x_{1rm}$ = observed contribution of progeny family *r* from species *1* (replicate *m*)
$x_{2sm}$ = observed contribution of progeny family *s* from species *2* (replicate *m*)

**Anova models:**

$x_{1rm} = u_1 + v_{1r} + a_{2s} + va_{1r2s} + e_{1rm}$ and $x_{2sm} = u_2 + v_{2s} + a_{1r} + va_{2s1r} + e_{2sm}$

$u_1$ (alt. $u_2$) expectancy of contribution of progeny families from species *1* (alt. *2*) in mixture with progeny families from species *2* (alt. *1*)

$v_{1r}$ et $v_{2s}$ direct genetic effects ⟵ **Genetic effect of a progeny family on its own phenotype**

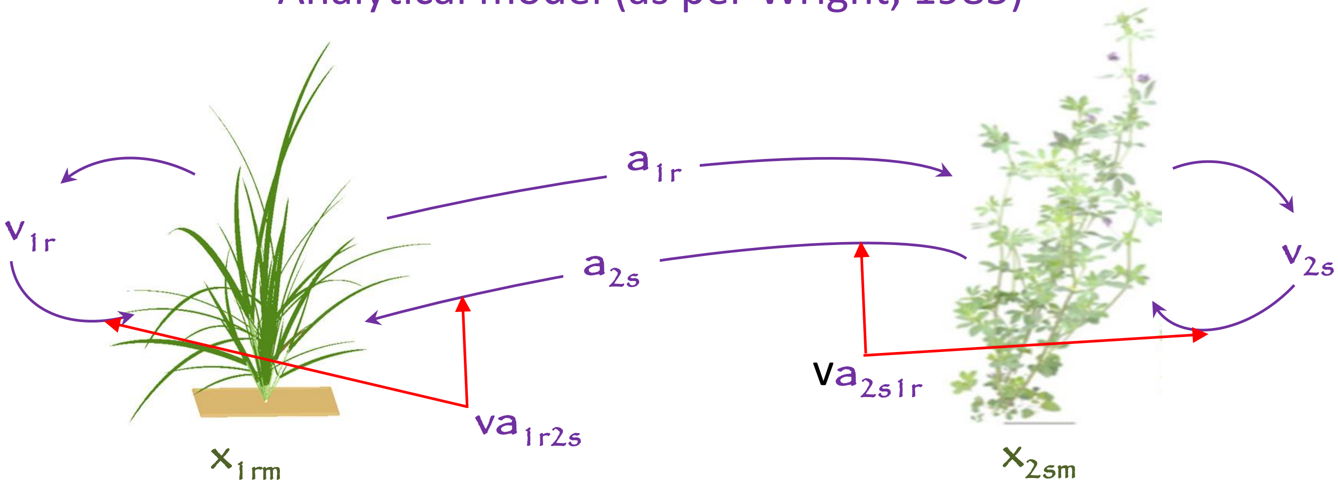
$a_{1r}$ et $a_{2s}$ associate genetic effects ⟵ **Mean genetic effect of a progeny family on the phenotype of any progeny family from the other species**

$va_{1r2s}$ et $va_{2s1r}$ interaction effects specific of progeny families *1r* and *2s*

$e_{1rm}$ et $e_{2sm}$ experimental errors on progeny famlilies *r* from species *1* and *s* from species *2*, respectively (replicate *m*)

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

## Analytical model (as per Wright, 1985)




$$y_{1r2sm} = x_{1rm} + x_{2sm}$$

**Anova model:**

$x_{1rm} = u_1 + v_{1r} + a_{2s} + va_{1r2s} + e_{1rm}$ and $x_{2sm} = u_2 + v_{2s} + a_{1r} + va_{2s1r} + e_{2sm}$

$v_{1r}$ et $v_{2s}$ direct genetic effects ⟵ **Genetic effect of a progeny family on its own phenotype**

$a_{1r}$ et $a_{2s}$ associate genetic effects ⟵ **Mean genetic effect of a progeny family on the phenotype of any progeny family from the other species**

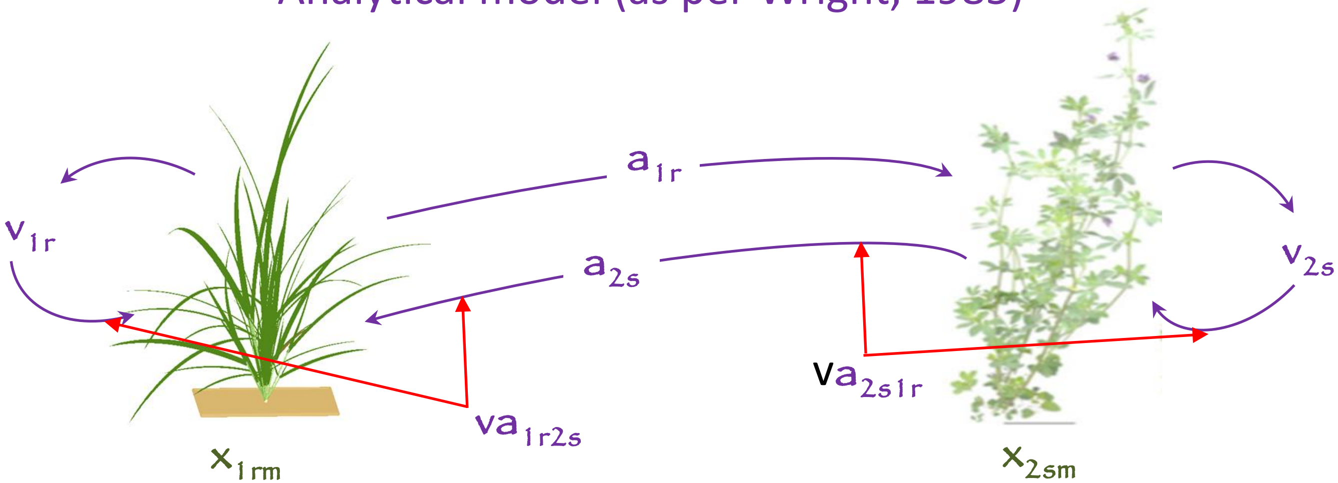
$va_{1r2s}$ et $va_{2s1r}$ interaction effects specific of progeny families *1r* and *2s*

**Remarks:**

- ***Correlations between direct and associate effects, cor($v_{1r}$, $a_{1r}$) and cor($v_{2s}$, $a_{2s}$), are expected to be negative in case of compensation effects, but experimental data are still missing to confirm this***
- ***Similarly, we can expect that cor($va_{1r2s}$, $va_{2s1r}$) < 0 in case of compensation***
- ***The ANOVA model (Wright, Griffing) models the genetic variability of 'ecophysiological' effects (competition, facilitation, niche differentiation) ⇨ But there is no straightforward link between the ANOVA model effects (v, a , va) and the ecophysiological effects***

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

## Analytical model (as per Wright, 1985)




$$y_{1r2sm} = x_{1rm} + x_{2sm}$$

**Anova model:**

$x_{1rm} = u_1 + v_{1r} + a_{2s} + va_{1r2s} + e_{1rm}$ and $x_{2sm} = u_2 + v_{2s} + a_{1r} + va_{2s1r} + e_{2sm}$

$v_{1r}$ et $v_{2s}$ direct genetic effects ⟵ **Genetic effect of a progeny family on its own phenotype**

$a_{1r}$ et $a_{2s}$ associate genetic effects ⟵ **Mean genetic effect of a progeny family on the phenotype of any progeny family from the other species**

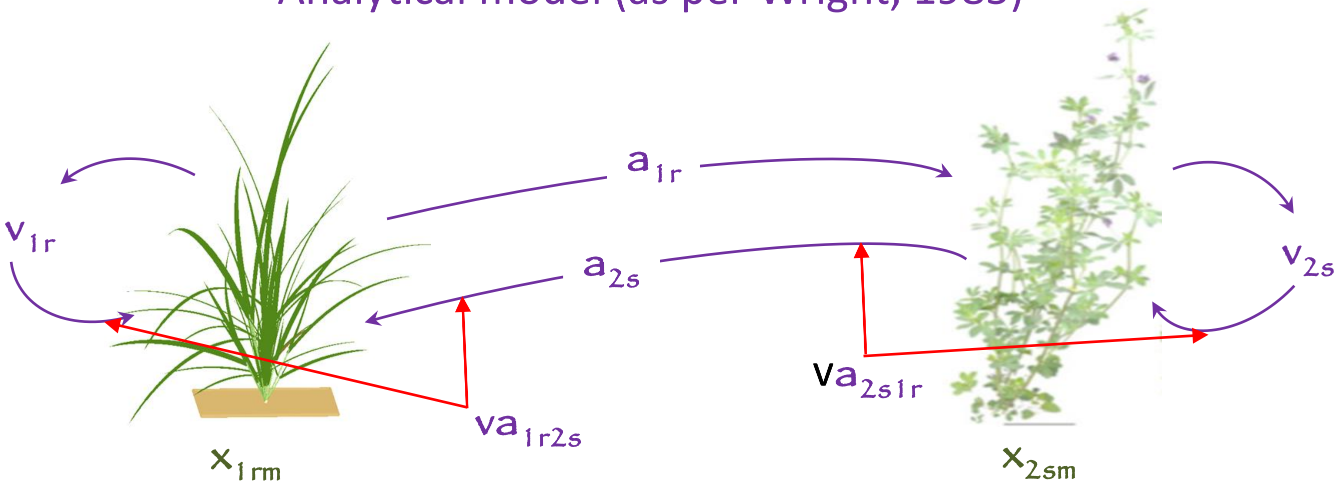
$va_{1r2s}$ et $va_{2s1r}$ interaction effects specific of progeny families *1r* and *2s*

**Important remarks:**

- ***Direct and associate effects are not assessable if progeny families from each species are tested in mixture with a single progeny family from the other species (or not assessable with sufficient accuracy if tested with a small number of progeny families from the other species)***
- ***Only the genetically additive components of direct and associate effects are inherited by offsprings of selected candidates at the next selection cycle***

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

Analytical model (as per Wright, 1985)



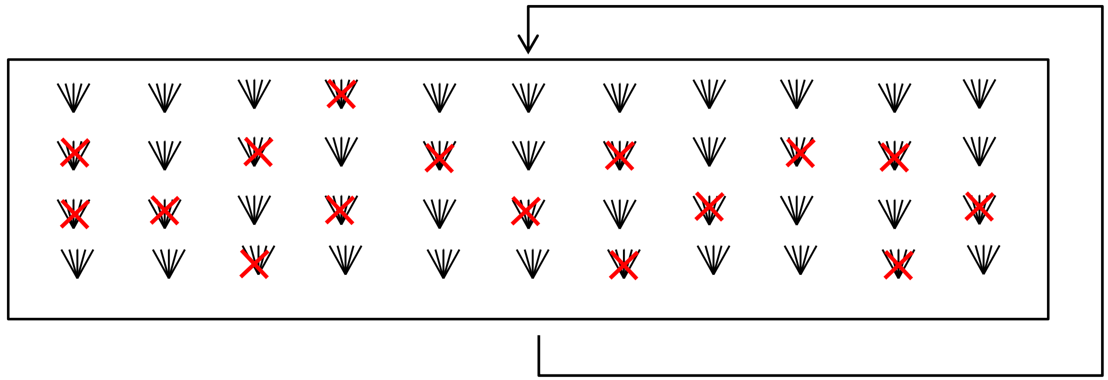

$$y_{1r2sm} = x_{1rm} + x_{2sm}$$

**Anova model:**

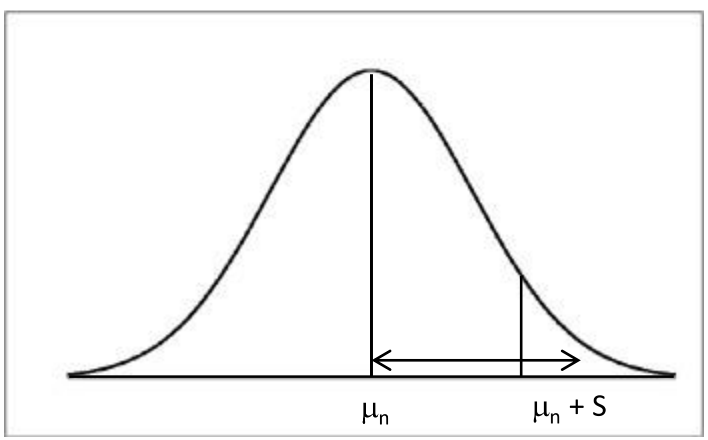
$x_{1rm} = u_1 + v_{1r} + a_{2s} + va_{1r2s} + e_{1rm}$ and $x_{2sm} = u_2 + v_{2s} + a_{1r} + va_{2s1r} + e_{2sm}$

| | |
|---|---|
| $g_{1r} = v_{1r} + a_{1r}$ | → General Mixture Ability (GMA) of progeny family *r* of species *1* (in mixture with species *2*) |
| $g_{2s} = v_{2s} + a_{2s}$ | → General Mixture Ability (GMA) of progeny family *s* of species *2* (in mixture with species *1*) |
| $d_{1r2s} = va_{1r2s} + va_{2s1r}$ | → Specific Mixture Ability between progeny families *1r* et *2s* |

# Natural selection or massal selection



## → Expected response to selection (difference between mean value of population at cycles *n+1* and *n*):




Selection differential: $S = i\, \sigma_P$

Expected value of offsprings at cycle *n+1* of candidate *i* from cycle *n*:

$M_i - \mu_n = \beta_{PO} (P_i - \mu_n)$ → (parents – offsprings regression of F. Galton, 1887)

$\beta_{PO} = \text{cov}(P, O) / \sigma_P^2$

$\sigma_P^2$ = phenotypic variance = $\sigma_g^2 + \sigma_e^2$ ($\sigma_e^2$ = environmental variance)

Expected response to selection:

$\Delta_G = \theta\, \beta_{PO}\, S = \theta\, \beta_{PO}\, i\, \sigma_P = \theta\, i / \sigma_P\, \text{cov}(P,O)$

$\theta$ = 1 si sélection sur un seul sexe ou 2 si sélection sur les deux sexes

*i* = intensité de sélection

Quantitative genetics model (R.A. Fisher, 1918):

$\sigma_g^2 = \sigma_A^2 + \sigma_D^2$ (without epistasis) and $\beta_{PO} = ½\sigma_A^2 / \sigma_P^2$

$\Delta_G = i\, \theta\, (½\sigma_A^2/\sigma_P^2)\, \sigma_P = i\, \theta\, ½\, h_n^2\, \sigma_P$

$h_n^2$ = héritabilité = $\sigma_A^2/\sigma_P^2$

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

## Expected genetic gains from one cycle of recurrent selection

Selection criterion → $I_{1r2s.} = \alpha_1 x_{1r.} + \alpha_2 x_{2s.}$

(Selection index weighting the contributions to the mixture of the two species )

**Genetic gains expected after recombination of selected candidates (general case):**

$\Delta G_{x1} = i_1 \theta_1 / \sigma_I \, cov(I_{1r2s.}, Av_{1r}) + i_2 \theta_2 / \sigma_I \, cov(I_{1r2s.}, Aa_{2s})$

$= i_1 \theta_1 / \sigma_I (\alpha_1 \, cov(v_{1r}, Av_{1r}) + \alpha_2 \, cov(a_{1r}, Av_{1r})) + i_2 \theta_2 / \sigma_I (\alpha_1 \, cov(a_{2s}, Aa_{2s}) + \alpha_2 \, cov(v_{2s}, Aa_{2s}))$

$\Delta G_{x2} = i_1 \theta_1 / \sigma_I \, cov(I_{1r2s.}, Aa_{1r}) + i_2 \theta_2 / \sigma_I \, cov(I_{1rs2s.}, Av_{2s})$

$= i_1 \theta_1 / \sigma_I (\alpha_1 \, cov(v_{1r}, Aa_{1r}) + \alpha_2 \, cov(a_{1r}, Aa_{1r})) + i_2 \theta_2 / \sigma_I (\alpha_1 \, cov(a_{2s}, Av_{2s}) + \alpha_2 \, cov(v_{2s}, Av_{2s}))$

and $\Delta G_y = \Delta G_{x1} + \Delta G_{x2}$

$Av_{1r}$, $Aa_{2s}$, $Aa_{1r}$ et $Av_{2s}$ additive genetic values inherited for $v_{1r}$ and $a_{1r}$ by offsprings of candidate 1r and for $v_{2s}$ and $a_{2s}$ by offsprings of candidate 2s at next selection cycle

→ *Covariances between candidates at cycle n and their offsprings at cycle n+1 can be approximated as variance-covariances of genetic effects at cycle n in some situations (half-sibs and topcross progenies if additive x additive epistasis effects are negligible, full-sibs and S1 progenies if non additive genetic effects can be assumed as negligible)*

**Genetic gains expected after recombination of selected candidates (half-sib progenies):**

$\Delta G_{x1} = i_1 \theta_1 / \sigma_I (\alpha_1 \sigma^2_{v1} + \alpha_2 \, cov(a_1, v_1)) + i_2 \theta_2 / \sigma_I (\alpha_1 \sigma^2_{a2} + \alpha_2 \, cov(v_2, a_2))$

$\Delta G_{x2} = i_1 \theta_1 / \sigma_I (\alpha_1 \, cov(v_1, a_1) + \alpha_2 \sigma^2_{a1}) + i_2 \theta_2 / \sigma_I (\alpha_1 \, cov(a_2, v_2) + \alpha_2 \sigma^2_{v2})$

and $\Delta G_y = \Delta G_{x1} + \Delta G_{x2}$

→ *However, genetic gains after recombination are not assessable if direct and associate effects are not assessable (see preceding slide)*

# Recurrent Selection for Reciprocal Mixture Ability (SRMA)

## Expected genetic gains from one cycle of recurrent selection

Selection criterion → $\mathbf{I_{1r2s.} = \alpha_1 x_{1r.} + \alpha_2 x_{2s.}}$
(Selection index weighting the contributions to the mixture of the two species )

**Genetic gains expected before recombination of selected candidates:**

$G_1 = v_{1r} + a_{2s} + va_{1r2s}$ (genetic component of $x_{1r.}$)
$G_2 = v_{2s} + a_{1r} + va_{2s1r}$ (genetic component of $x_{2s.}$)

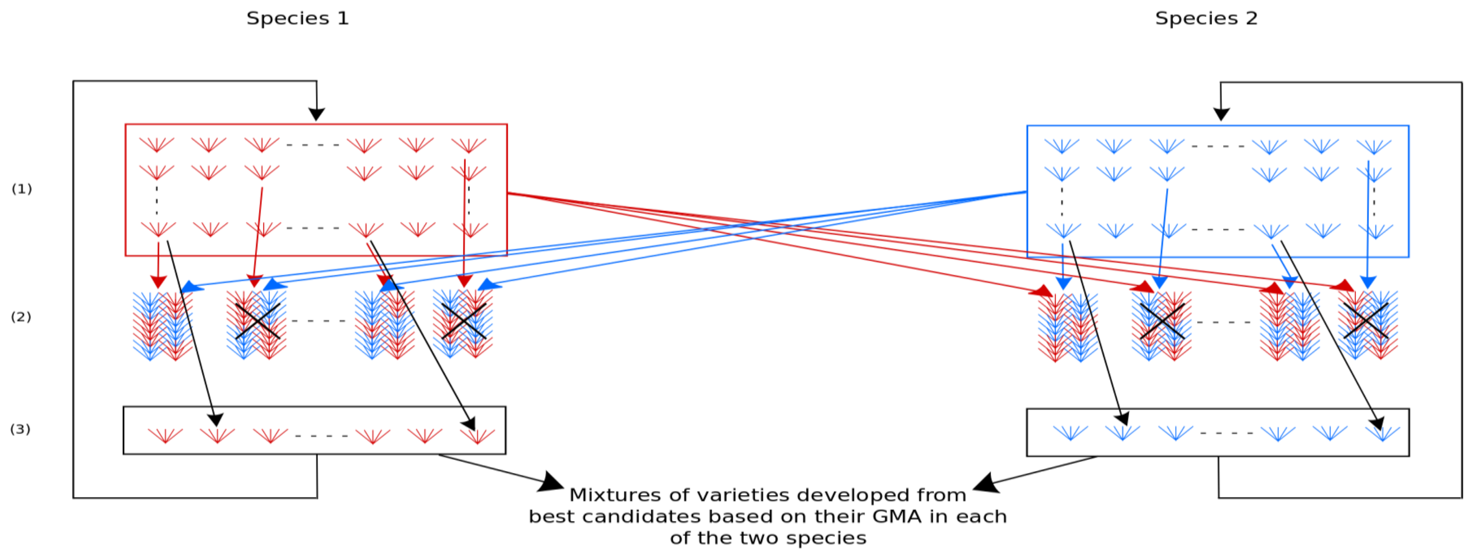
Only if same selection intensity i and same number $\theta$ of sexes under selection in the two species:
$\delta G_{x1} = i\,\theta / \sigma_I\,(cov(I_{1r2s.}, G_1) = i\,\theta / \sigma_I\,(\alpha_1\,\sigma^2_{G1} + \alpha_2\,cov(G_1, G_2))$
$\delta G_{x2} = i\,\theta / \sigma_I\,(cov(I_{1r2s.}, G_2) = i\,\theta / \sigma_I\,(\alpha_1\,cov(G_1, G_2) + \alpha_2\,\sigma^2_{G2})$
and $\delta G_y = \delta G_{x1} + \delta G_{x2}$

$\sigma^2_{G1}$, $\sigma^2_{G2}$ and $cov(G_1, G_2)$ are always assessable from the analysis of variance of tested mixtures (provided that the contributions of the two species are recorded separately)

→ *Genetic gains before recombination are always assessable (whatever the kind of progeny families tested)*

→ *Possible to choose $\alpha_1$ and $\alpha_2$ in order to control the ratio $\delta G_{x1} / \delta G_{x2}$ , **but only feasible if contributions of the two species are recorded separately***

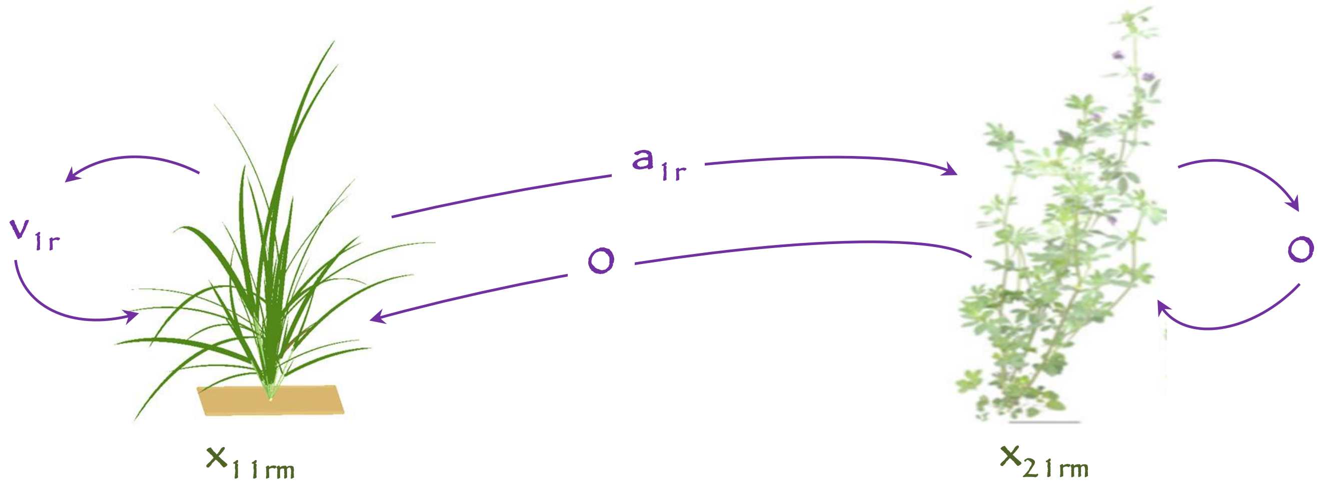
# Parallel Recurrent Selections for General Mixture Ability (SGMA) in two species




→ Each progeny family from a species is tested in mixture with a bulk of all progeny families from the other species
→ Best progeny families are selected in each species
→ In each species, candidates selected at cycle n are recombined to generate cycle n + 1 population

## Parallel Recurrent Selections for General Mixture Ability (SGMA)

### Analytical model for the test in mixture of progeny families from species 1




$$y_{1rm} = x_{11rm} + x_{21rm}$$

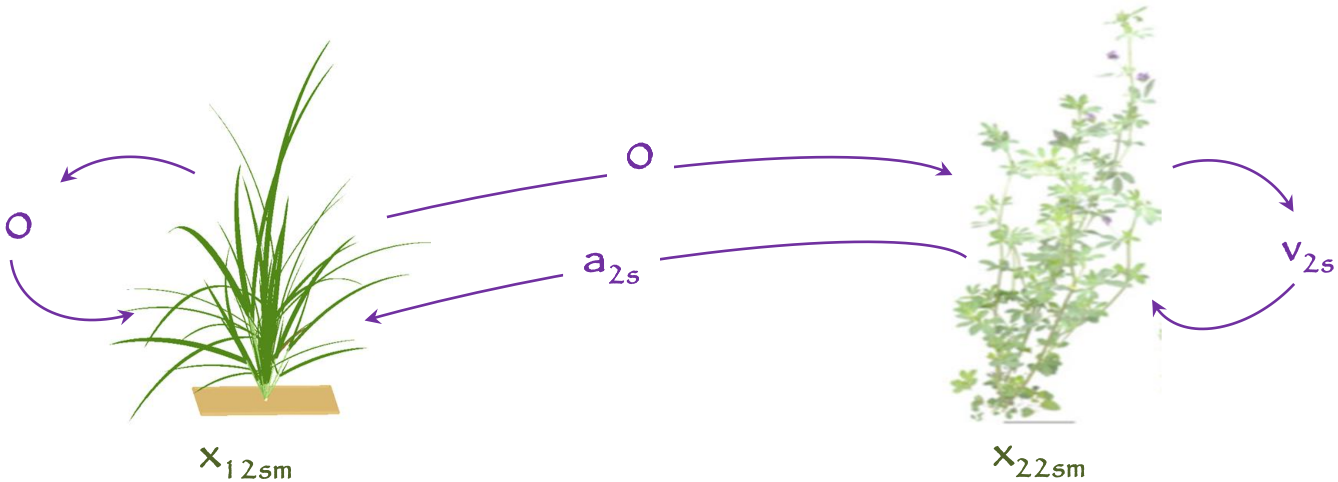
$y_{1rm}$ = observed performance of the mixture of progeny family *r* from species *1* with a bulk of all progeny families from species *2* (replicate *m*)
$x_{11rm}$ = observed contribution of progeny family *r* from species *1* (replicate *m*)
$x_{21rm}$ = observed contribution of the bulk of all progeny families of species *2* (replicate *m*)

**ANOVA models:** $x_{11rm} = u_1 + v_{1r} + e_{11rm}$ and $x_{21rm} = u_2 + a_{1r} + e_{21rm}$

→ ***Effects $v_{1r}$ and $a_{1r}$ are always directly assessables from the analysis of variance of tested mixtures*** *(provided that the contributions of the two species are recorded separately)*

# Parallel Recurrent Selections for General Mixture Ability (SGMA)

## Analytical model for the test in mixture of progeny families from species 2




$$y_{2sm} = x_{12sm} + x_{22sm}$$

$y_{2sm}$ = observed performance of the mixture of progeny family *s* from species *2* with a bulk of all progeny families from species *1* (replicate *m*)
$x_{12sm}$ = observed contribution of progeny family *s* from species *2* (replicate *m*)
$x_{22sm}$ = observed contribution of the bulk of all progeny families of species *1* (replicate *m*)

$x_{12sm} = u_1 + a_{2s} + e_{12sm}$ and $x_{22sm} = u_2 + v_{2s} + e_{22sm}$

→ ***Effects $v_{2s}$ and $a_{2s}$ are always directly assessables from the analysis of variance of tested mixtures*** *(provided that the contributions of the two species are recorded separately)*

# Parallel Recurrent Selections for General Mixture Ability (SGMA)

## Expected genetic gains from one cycle of recurrent selection

**Genetic gains expected after recombination with selection in species 1 (general case):**

Selection index applied to species 1 → $\mathbf{I_{1r.} = \alpha_{11}\, x_{11r.} + \alpha_{21}\, x_{21r.}}$

$\Delta G_{x11} = i_1\, \theta_1 / \sigma_{I1}\, (cov(I_{1r.}, Av_{1r}) = i_1\, \theta_1 / \sigma_{I1}\, (\alpha_{11}\, cov(v_{1r}, Av_{1r}) + \alpha_{21}\, cov(a_{1r}, Av_{1r}))$

$\Delta G_{x21} = i_1\, \theta_1 / \sigma_{I1}\, (cov(I_{1r.}, Aa_{1r}) = i_1\, \theta_1 / \sigma_{I1}\, (\alpha_{11}\, cov(v_{1r}, Aa_{1r}) + \alpha_{21}\, cov(a_{1r}, Aa_{1r}))$

et $\Delta G_{y1} = \Delta G_{x11} + \Delta G_{x21}$

**Genetic gains expected after recombination with selection in species 2 (general case):**

Selection index applied to species 2 → $\mathbf{I_{2s.} = \alpha_{12}\, x_{12s.} + \alpha_{22}\, x_{22s.}}$

$\Delta G_{x12} = i_2\, \theta_2 / \sigma_{I2}\, (cov(I_{2s.}, Aa_{2s}) = i_2\, \theta_2 / \sigma_{I2}\, (\alpha_{12}\, cov(a_{2s}, Aa_{2s}) + \alpha_{22}\, cov(v_{2s}, Aa_{2s}))$

$\Delta G_{x22} = i_2\, \theta_2 / \sigma_{I2}\, (cov(I_{2s.}, Av_{2s}) = i_2\, \theta_2 / \sigma_{I2}\, (\alpha_{12}\, cov(a_{2s}, Av_{2s}) + \alpha_{22}\, cov(v_{2s}, Av_{2s})\, )$

et $\Delta G_{y2} = \Delta G_{x12} + \Delta G_{x22}$

**→ Genetic gains expected from selection on species 1 and on species 2 can be cumulated:**

$\Delta G_{x1} = \Delta G_{x11} + \Delta G_{x12}$

$\Delta G_{x2} = \Delta G_{x21} + \Delta G_{x22}$

et $\Delta G_y = \Delta G_{y1} + \Delta G_{y2}$

# Parallel Recurrent Selections for General Mixture Ability (SGMA)

## Expected genetic gains from one cycle of recurrent selection

→ *Covariances between candidates at cycle n and their offsprings at cycle n+1 can be approximated as variance-covariances of genetic effects at cycle n in some situations (half-sibs and topcross progenies if additive x additive epistasis effects are negligible, full-sibs and S1 progenies if non additive genetic effects can be assumed as negligible)*

**Genetic gains expected after recombination with selection in species 1 (half-sib progenies):**

Selection index applied to species 1 → $\mathbf{I_{1r.} = \alpha_{11}\, x_{11r.} + \alpha_{21}\, x_{21r.}}$

$\Delta G_{x11} = i_1\, \theta_1 / \sigma_{I1}\, (cov(I_{1r.}, Av_{1r}) = i_1\, \theta_1 / \sigma_{I1}\, (\alpha_{11}\, \sigma^2_{v1r} + \alpha_{21}\, cov(v_{1r}, a_{1r}))$

$\Delta G_{x21} = i_1\, \theta_1 / \sigma_{I1}\, (cov(I_{1r.}, Aa_{1r}) = i_1\, \theta_1 / \sigma_{I1}\, (\alpha_{11}\, cov(v_{1r}, a_{1r}) + \alpha_{21}\, \sigma^2_{a1r})$

et $\Delta G_{y1} = \Delta G_{x11} + \Delta G_{x21}$

**Genetic gains expected after recombination with selection in species 2 (half-sib progenies):**

Selection index applied to species 2 → $\mathbf{I_{2s.} = \alpha_{12}\, x_{12s.} + \alpha_{22}\, x_{22s.}}$

$\Delta G_{x12} = i_2\, \theta_2 / \sigma_{I2}\, (cov(I_{2s.}, Av_{2s}) = i_2\, \theta_2 / \sigma_{I2}\, (\alpha_{12}\, \sigma^2_{a2s} + \alpha_{22}\, cov(v_{2s}, a_{2s}))$

$\Delta G_{x22} = i_2\, \theta_2 / \sigma_{I2}\, (cov(I_{2s.}, Aa_{2s}) = i_2\, \theta_2 / \sigma_{I2}\, (\alpha_{12}\, cov(v_{2s}, a_{2s}) + \alpha_{22}\, \sigma^2_{v2s})$

et $\Delta G_{y2} = \Delta G_{x12} + \Delta G_{x22}$

**→ Genetic gains expected from selection on species 1 and on species 2 can be cumulated:**

$\Delta G_{x1} = \Delta G_{x11} + \Delta G_{x12}$

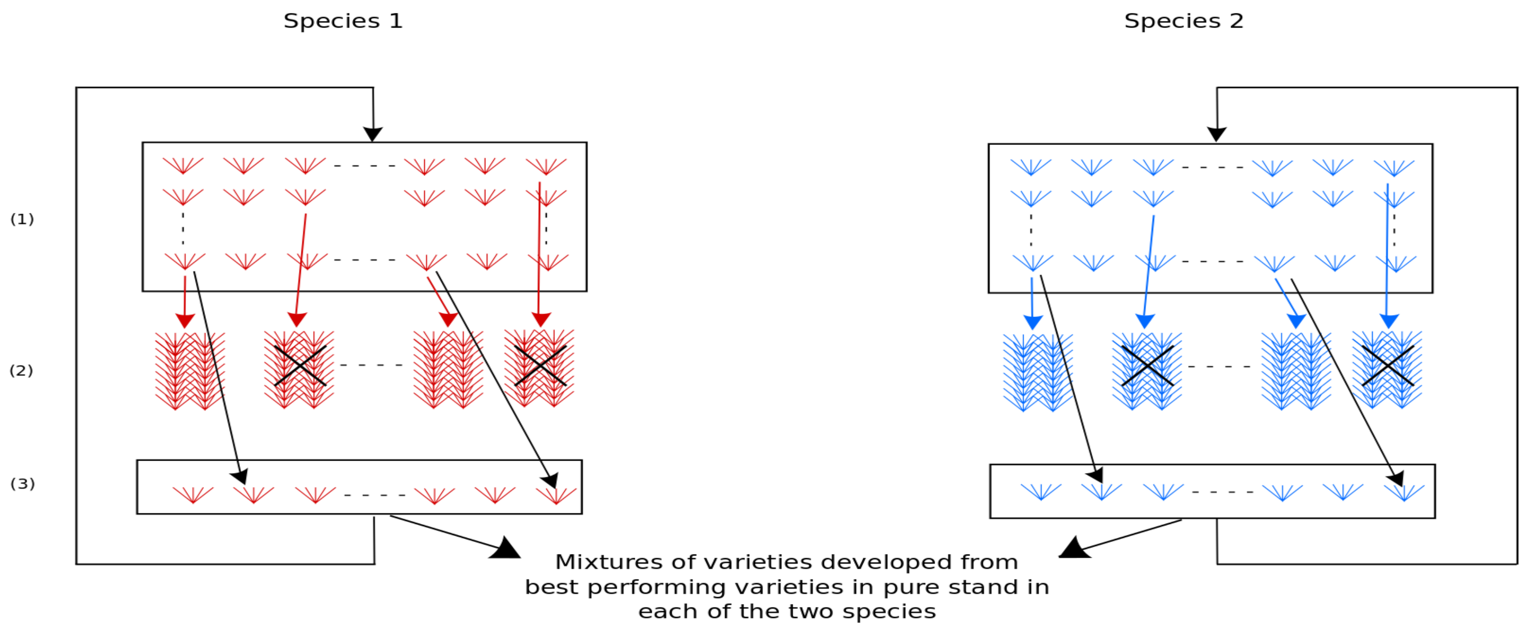
$\Delta G_{x2} = \Delta G_{x21} + \Delta G_{x22}$

et $\Delta G_y = \Delta G_{y1} + \Delta G_{y2}$

**→ *Possible to choose* $\alpha_{11}, \alpha_{21}, \alpha_{12}$ and $\alpha_{22}$ :**

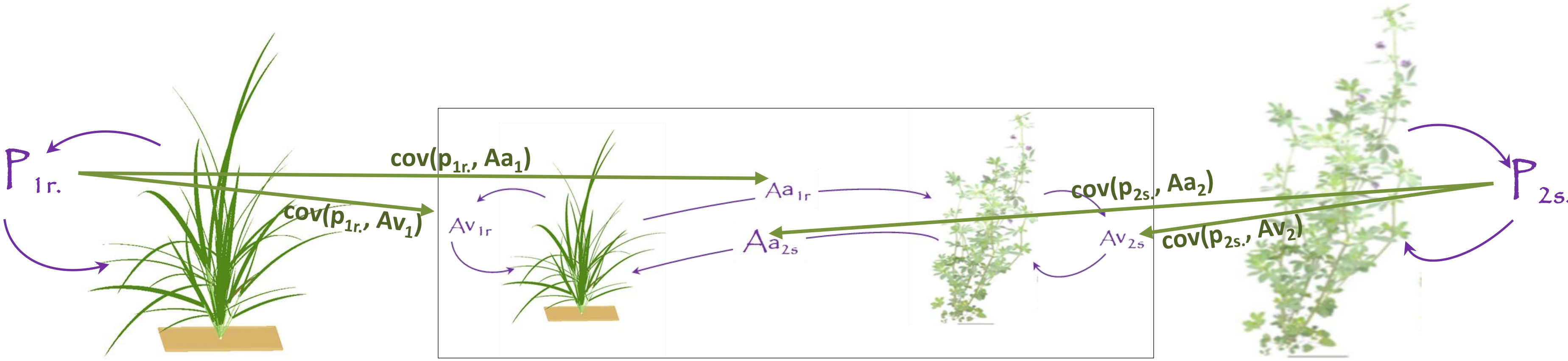
$\Delta G_y$ maximum under the constraint that the ratio $\Delta G_{x1} / \Delta G_{x2} = k_1 / k_2$ (non linear constrained optimisation)

# Parallel recurrent selections in pure stands



# Parallel recurrent selections in pure stands

## Analytical model




*Progeny families of species 1 in pure stands at cycle n*

*Mixtures of progeny families of species 1 and 2 at cycle n+1*

*Progeny families of species 2 in pure stands at cycle n*

**Expected correlative responses to selection in pure stands of performances in mixture at the next selection cycle:**

Selection in species 1

$\Delta G^P_{x11} = i_1\ \theta_1 / \sigma_{P1}\ cov(p_{1r.}, Av_1)$

$\Delta G^P_{x21} = i_1\ \theta_1 / \sigma_{P1}\ cov(p_{1r.}, Aa_1)$

and $\Delta G^P_{y1} = \Delta G_{x11} + \Delta G_{x21}$

Selection in species 2

$\Delta G^P_{x12} = i_2\ \theta_2 / \sigma_{P2}\ cov(p_{2s.}, Aa_2)$

$\Delta G^P_{x22} = i_2\ \theta_2 / \sigma_{P2}\ cov(p_{2s.}, Av_2)$

and $\Delta G^P_{y2} = \Delta G_{x12} + \Delta G_{x22}$

Expected gains from two parallel selections can be cumulated:

$\Delta G^P_{x1} = \Delta G^P_{x11}\ \Delta G^P_{x12}$

$\Delta G^P_{x2} = \Delta G^P_{x21}\ \Delta G^P_{x22}$

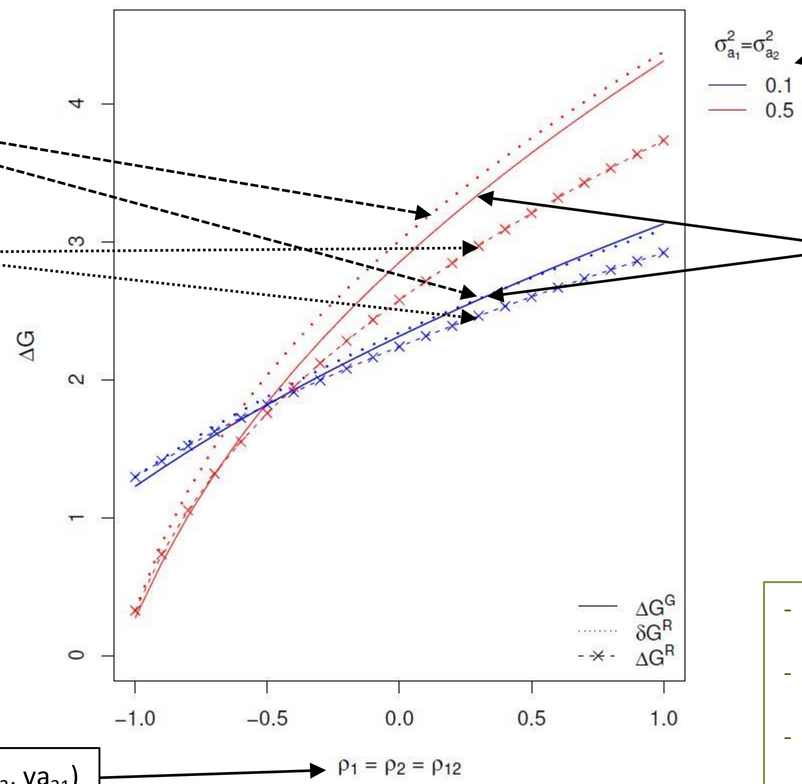
and $\Delta G^P_{y} = \Delta G^P_{y1} + \Delta G^P_{y2}$

# Comparison of genetic gains on mixture performance expected from SRMA and SGMA

SRMA: selection on $y_{1r2s.}$, SGMA: selection on $y_{1r.}$ and $y_{2s.}$

Selection differential for SRMA (expected gain before recombination)

Expected gain from SRMA after recombination




Ratio (var assoc effects) / (var direct effects)

$\sigma^2 va_{12} = \sigma^2 va_{21} = ½\ \sigma^2 a_1 = ½\ \sigma^2 a_2$

Expected gain from SGMA

Cor $(v_1, a_1)$ = cor $(v_2, a_2)$ = cor$(va_{12}, va_{21})$

- Half-sib family selection in both species ($\phi$ = 1 and $\Theta$ = 1, see paper)
- Equal number of experimental plot for SRMA and SGMA
- SRMA: families of a species tested in mixture with a single familiy from the other species
- Selection rate 10% SRMA, 20% SGMA
- 3 replicates (m= 3)

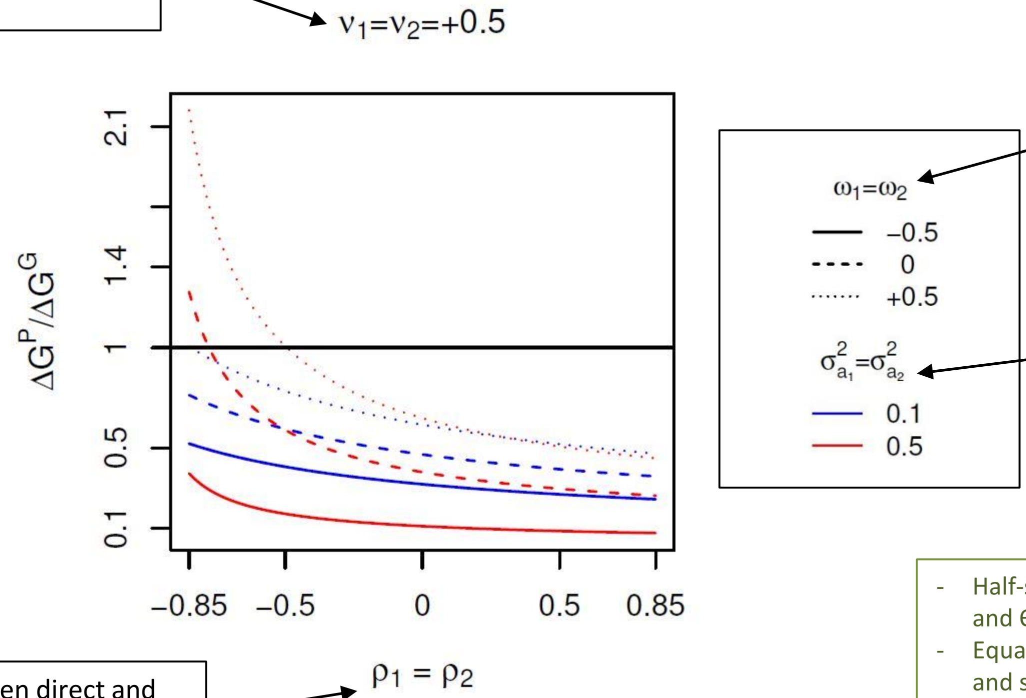
***⇨SRMA: expected gains before recombination overestimate selection effciency especially if cor (direct, associate) > 0***

***⇨With equal experimental resources, SRMA is less efficient than SGMA especially if cor (direct, associate) > 0***

# Correlative response of mixture performance expected from selection in pure stands ($\Delta G^P$) vs direct response expected from SGMA ($\Delta G^G$)

Correlations between performance in pure stands and direct effects

Correlations between performance in pure stands and associate effects




Ratio (var assoc effects) / (var direct effects)

Correlations between direct and associate effects

- Half-sib family selection in both species (ϕ = 1 and Θ = 1, see paper)
- Equal number of experimental plot for SGMA and selection in pure stands
- Selection rate 20% SGMA and pure stands
- 3 replicates (m= 3)

***⇨Selection in pure stands is efficient only if:***

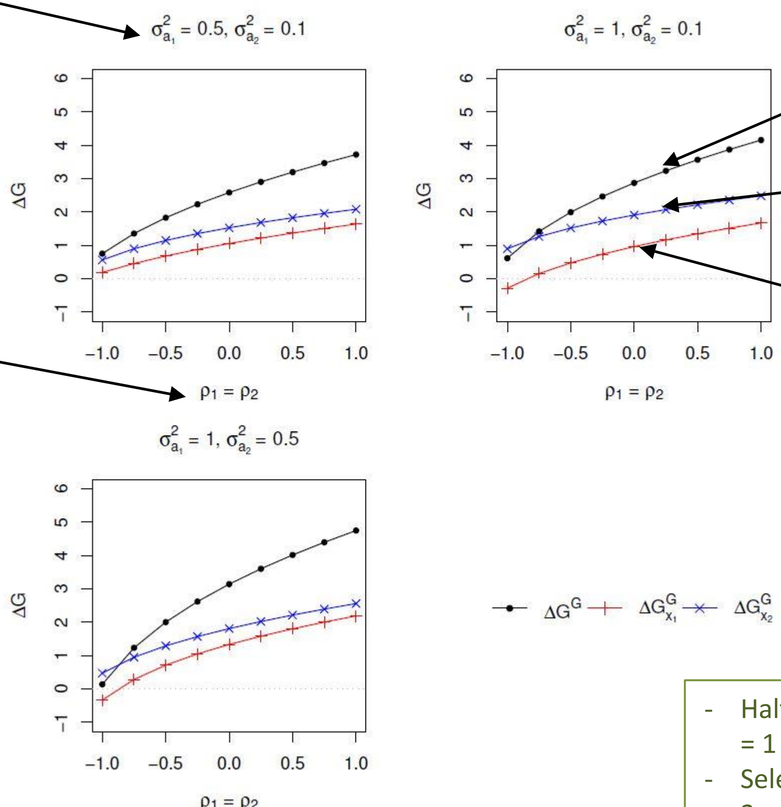
- ***pure stands performances are positively correlated to both direct and associate effects***
- ***and correlation between direct and associate effects are negative***

## SGMA: expected response to selection of the mixture performance ($\Delta G^G$) and of species contributions to the mixture ($\Delta G^G_{x1}$ and $\Delta G^G_{x2}$)

Selection on observed mixture performances: $y_{1r.}$ and $y_{2s.}$

Ratio
(var assoc effects) / (var direct effects)

Cor ($v_1$, $a_1$) = cor ($v_2$, $a_2$)




Expected response of the mixture performance ($\Delta G^G$)

Expected response of the contribution of species 2 ($\Delta G^G_{x2}$)

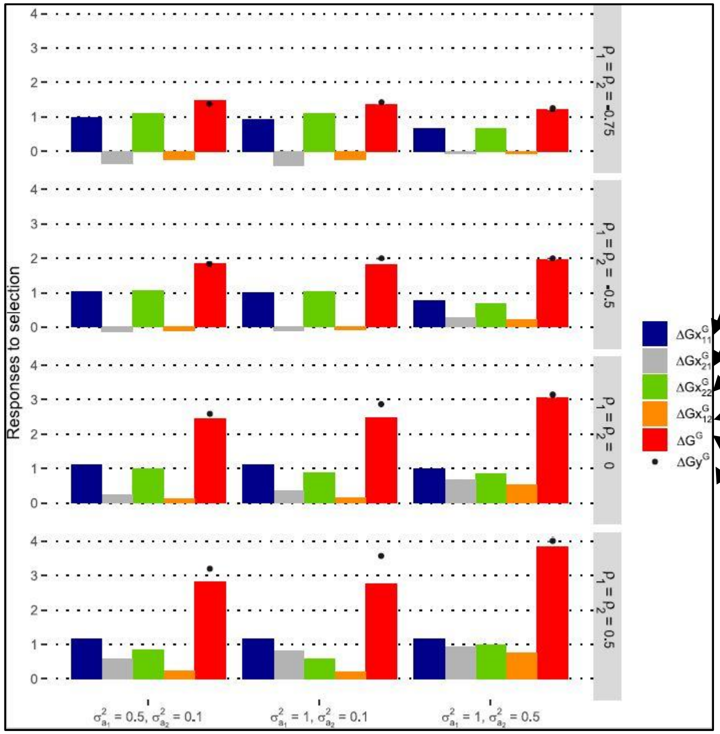
Expected response of the contribution of species 1 ($\Delta G^G_{x1}$)

- Half-sib family selection in both species ($\phi$ = 1 and $\Theta$ = 1, see paper)
- Selection rate 20% SGMA
- 3 replicates (m= 3)

⇨***Selection only on the overall performance of the mixture (i.e. on GMA = v + a) may lead to unequal responses of species contributions (largest response for the species whose genetic variance is the largest)***

# SGMA: expected response to selection of the mixture performance and of species contributions to the mixture

## Selection on two indices aiming to equate expected responses of species contributions (index weights provided by nonlinear constraint optimisation)




$\Delta G^G_{x11}$ Expected response of species 1 contribution with selection on species 1 index

$\Delta G^G_{x21}$ Expected response of species 2 contribution with selection on species 1 index

$\Delta G^G_{x12}$ Expected response of species 1 contribution with selection on species 2 index

$\Delta G^G_{x22}$ Expected response of species 2 contribution with selection on species 2 index

$\Delta G^G$ Expected cumulated response of overall mixture performance with parallel selection on indices in species 1 and 2

$\Delta G_y^G$ Expected cumulated response of overall mixture performance with parallel selection on $y_{1r.}$ in species 1 and o $y_{2s.}$ in species 2

- Half-sib family selection in both species (ϕ = 1 and Θ = 1)
- Selection rate 20%
- 3 replicates (m= 3)

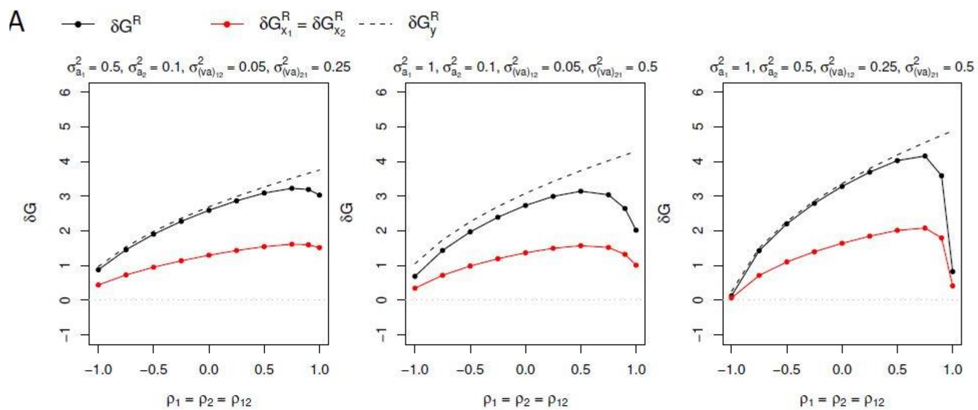
**Non linear constraint optimisation:**
$\Delta G^G$ maximum
under the constraint $\Delta G^G_{x11} + \Delta G^G_{x12} = \Delta G^G_{x21} + \Delta G^G_{x22}$

***⇨Selection in both species on indices equating expected cumulated responses of species contributions is expected to result in only very small loss on the cumulated response of overall mixture performance (compared to selection on overall mixture performance in the two species)***

# SRMA: expected response to selection of the mixture performance and of species contributions to the mixture

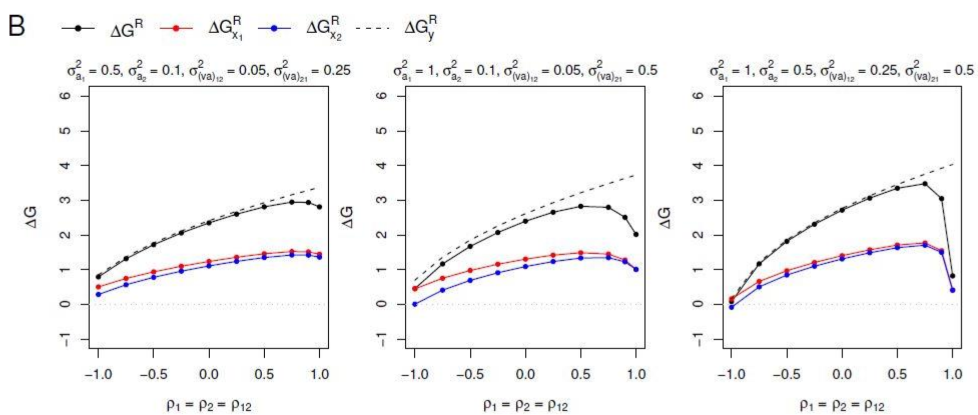
## Selection on an index aiming to equate expected responses of species contributions before recombination

Selection differentials (expected responses before recombination)




$\delta G^R_y$ Expected response of the mixture performance with selection on $y_{1r2s.}$
$\delta G^R$ Expected response of the mixture performance with selection on the index
$\delta G^R_{x1} = \delta G^R_{x2}$ Expected response of species contributions

Expected responses after recombination




$\Delta G^R_y$ Expected response of the mixture performance with selection on $y_{1r2s.}$
$\Delta G^R$ Expected response of the mixture performance with selection on the index
$\Delta G^R_{x1}$ Expected response of species 1 contribution
$\Delta G^R_{x2}$ Expected response of species 2 contribution

- Half-sib family selection in both species ($\phi = 1$ and $\Theta = 1$)
- Families of a species tested in mixture with a single family from the other species
- Selection rate 10%
- 3 replicates (m= 3)

⇨Selection on an index equating expected responses of species contributions before recombination is able to provide near equal expected responses after recombination

↳ The loss on expected gain of overall mixture performance is small

# Which selection scheme ?

**Selection on pure stands:**

- ***Assets:***
  Obviously easier to implement
- ***Drawbacks:***
  Efficient only if pure stands performance are positively correlated to direct and associate effects and cor (direct, associate ) < -0.5
  ↳ Would likely need to select on traits different than for pure stand cropping and to assess covariances between pure stands and direct and associate effects in mixture

**SRMA:**

- ***Assets:***
  Direct identification of mixtures of family progenies with outstanding performances
  → *Straighforward follow-up to release mixtures for farming usage*
- ***Drawbacks:***
  Direct and associate effects are not assessable, or only with poor accuracy
  → imprecise control of responses to selection

**SGMA:**

- ***Drawbacks:***
  Need of a test for specific mixture ability subsequent to the SGMA scheme
  → *Additional step towards release of mixtures for farming usage*
- ***Assets:***
  Direct and associate effects are directly assessable
  → *more efficient control of responses to selection*
  SGMA especially more efficient than SRMA if associate effects are large and cor(direct, associate) > -0.5

***⇨ Whatever the method, need to control the responses to selection of species contributions as soon as the variances of direct effects and of associate effects are different in the two (or more) species, i.e. always***

# More than two species (or components) ?

**SRMA:**

$\Delta G^R = \Theta_R\, i_R / \sigma_{yR} \Sigma_k \text{cov}(g_k, A_{gk})$

The variance between tested mixtures ($\sigma^2_{yR}$) increases very rapidly

→ *SRMA is poorly efficient as soon as 3 components in the mixture*

**SGMA:**

$\Delta G^G = \Theta_G\, i_G \Sigma_k 1 / \sigma_{yG} \text{cov}(g_k, A_{gk})$

The variance between tested mixtures ($\sigma^2_{yG}$) does not increase with the number of species

However, cov ($g_k$, $A_{gk}$) depends on an increasing number of number of covariances which may be negative if compensation effects are mainly negative → little propect of improvement in this case

↳ *Need experiments to assess these covariances and thus the feasability of SGMA*

➩ ***Diversity within species:***

more efficient to target unimodal distribution with fairly large variability (one component per species)

than

plurimodal distribution (several components per species with narrow within variability) ??