Dynamique évolutive du cycle phénologique foliaire : le cas d'une méta-population de chênes sessiles le long d'un gradient altitudinal

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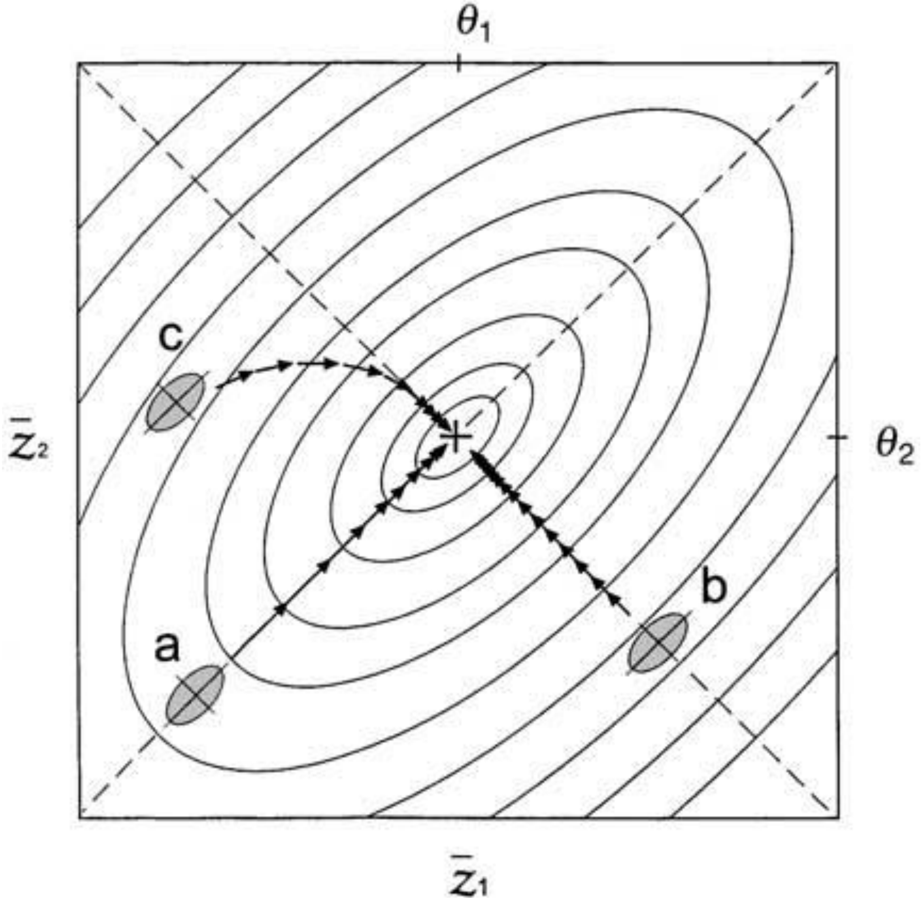
COLLOQUE FRANCOPHONE PHÉNOLOGIE 2015, Clermont Ferrand

« MeCC »

The rate of adaptation is conditioned by the pattern of multivariate genetic variation



Simpson 1953
Schluter 1996
Arnold *et al.* 2001
Etc.

DORMANCY

LEAF UNFOLDING

Temperature dependent

A focal trait: suspected to respond strongly to climate

- **How much more than the other traits?**
- **Which interaction(s) with other traits for shaping local adaptation?**

LEAF SENESCENCE

Photoperiod dependent

GROWING SEASON

Leaf phenological cycle defined by three biologically relevant traits…

-Leaf unfolding / formation date (« *LU* »)

-Leaf senescence date (« *LS* »)

-Growing seasong length / duration (« *GS* »)

Two phenological *s.s.* traits
→ Interval scale

One « Duration » trait
→ Ratio scale

$GS_i = 0 \rightarrow w_i \approx 0$

Leaf phenological cycle defined by three biologically relevant traits…

-Leaf unfolding / formation date (« *LU* »)

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Two phenological *s.s.* traits
→ Interval scale

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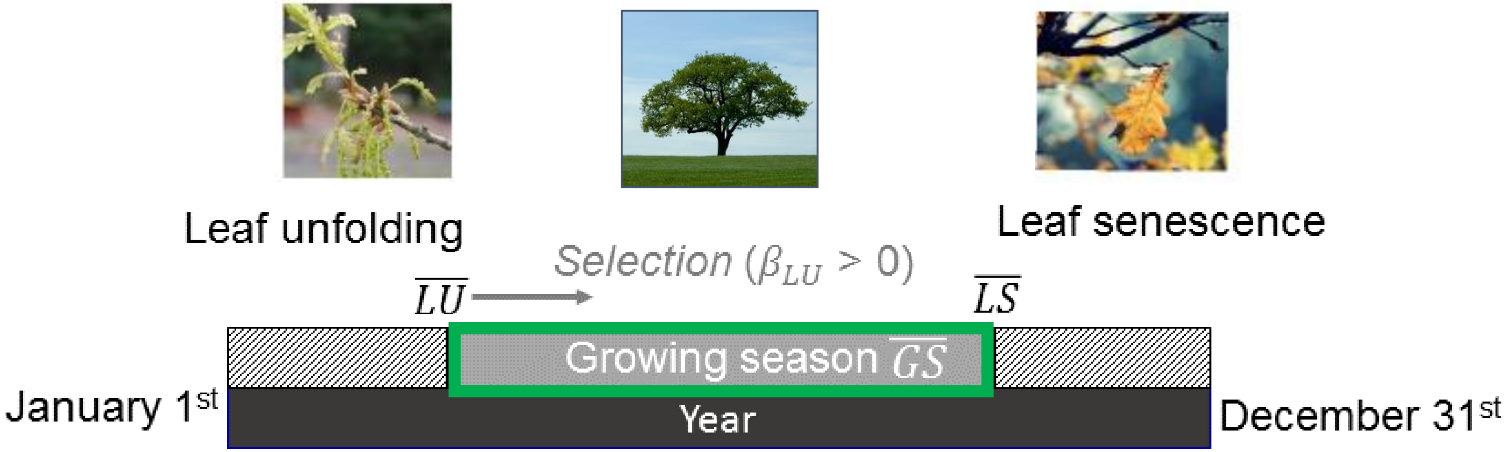
One « Duration » trait
→ Ratio scale

$GS_i = 0 \rightarrow w_i \approx 0$

…redundant information as $GS_i = LS_i - LU_i$

-*e.g.* regression slope $\boldsymbol{b}_{GS,LU} = \boldsymbol{b}_{LS,LU} - 1$

How to deal with this set of traits?



$$GS_i = LS_i - LU_i$$

$$\Delta\overline{GS} = \Delta\overline{LS} - \Delta\overline{LU}$$

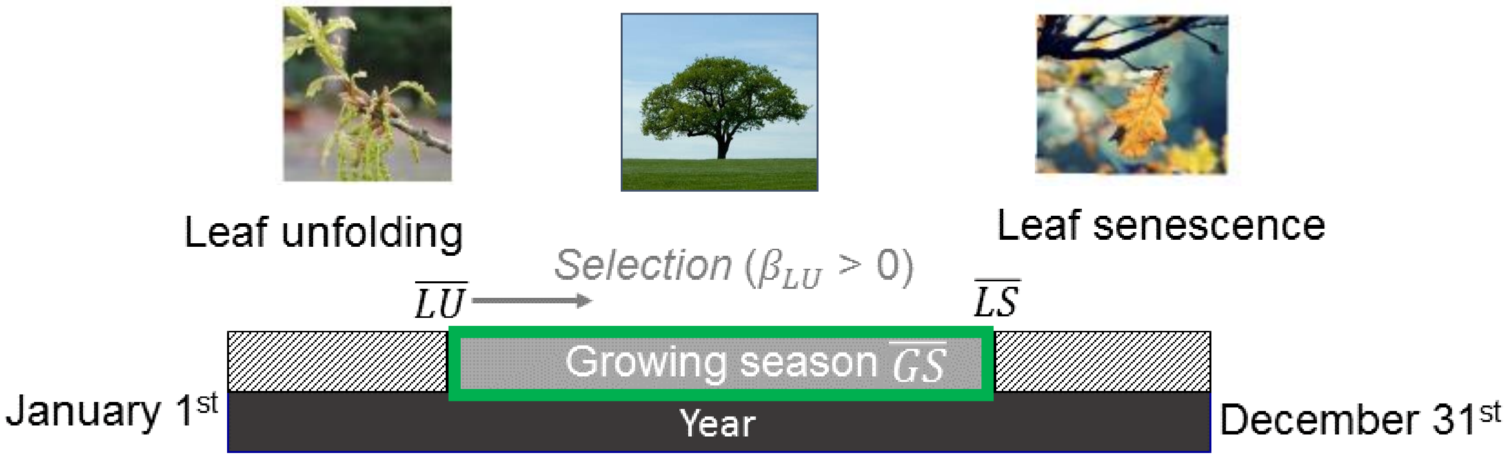
From the Lande's (1979) equation:

$$\Delta\bar{z} = \mathbf{G}\beta$$

$$\begin{bmatrix} \Delta\overline{LS} \\ \Delta\overline{LU} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G_{LS}} & \boldsymbol{G_{LS,LU}} \\ \boldsymbol{G_{LS,LU}} & \boldsymbol{G_{LU}} \end{bmatrix} \begin{bmatrix} \beta_{LS} \\ \beta_{LU} \end{bmatrix}$$

$$\begin{cases} \Delta\overline{LS} = \boldsymbol{G_{LS}}\,\beta_{LS} + \boldsymbol{G_{LS,LU}}\,\beta_{LU} \\ \Delta\overline{LU} = \boldsymbol{G_{LU}}\,\beta_{LU} + \boldsymbol{G_{LS,LU}}\beta_{LS} \end{cases}$$

How to deal with this set of traits?



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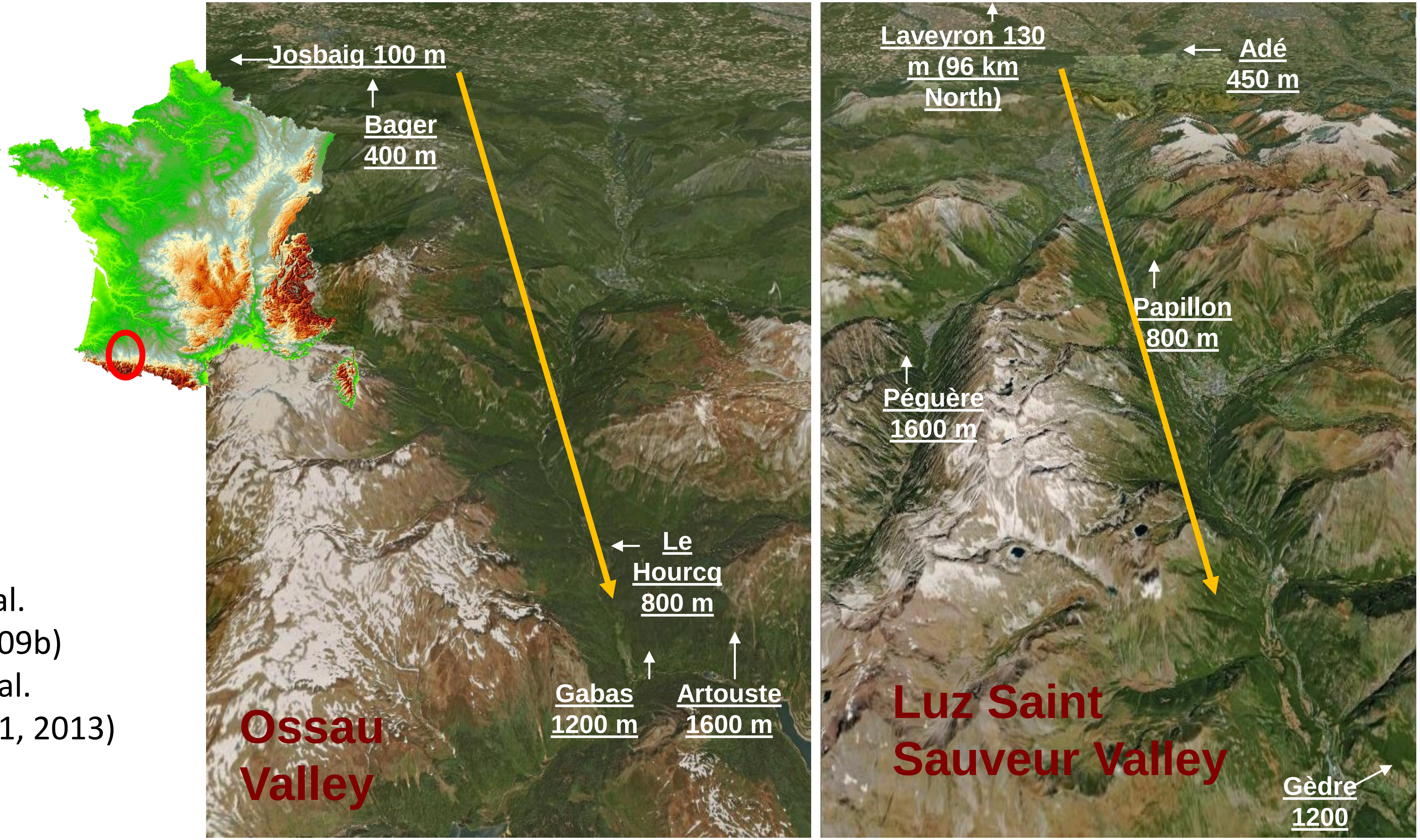
$$\boxed{\Delta\overline{GS} = \boldsymbol{G_{LS}}\,\beta_{LS} - \boldsymbol{G_{LU}}\,\beta_{LU} + \boldsymbol{G_{LS,LU}}(\beta_{LU} - \beta_{LS})}$$

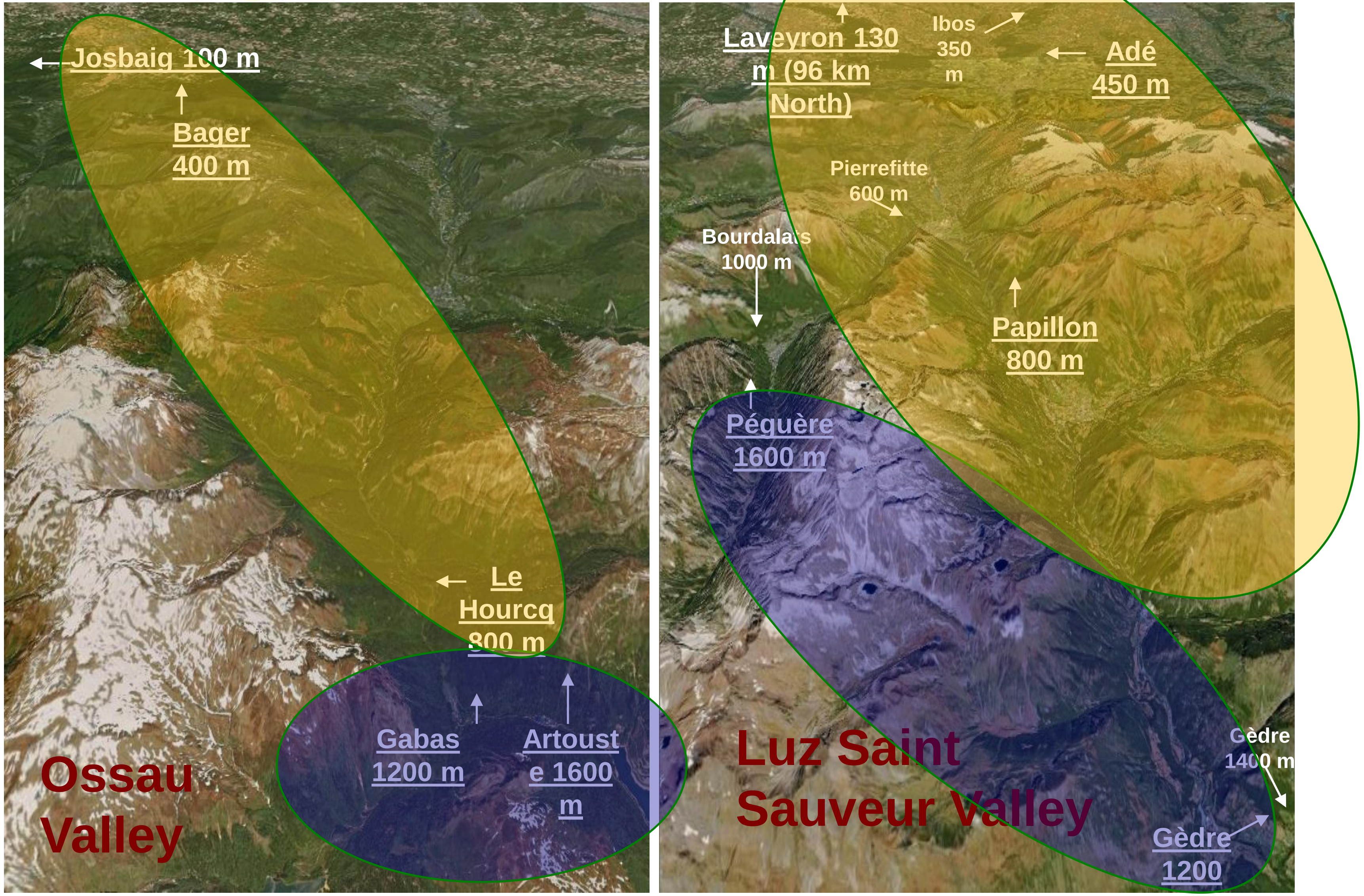
Study system: An altitudinal gradient, replicated in two Pyrenean valleys



Vitasse et al. (2009a, 2009b)
Alberto et al. (2010, 2011, 2013)

Post-Pleistocene colonization (- 11000-10000 yrs) colonization of the Pyrennees.

1) Genetic cline for bud burst



2) A 50% decrease of G_{LU} (bud burst)

Alberto *et al.* 2011 *J Evol Biol*

Study design in brief:

***In situ* monitoring**

10 populations monitored *in situ*
Altitude: 131 to 1630 m

Replicated phenological measures:
2005-2007
& 2009-2014 (2015)
→ 9 replicates

Common garden at the sea level (Toulenne)

Acorns from 152 mothers (*n* = 3321)
ca. 23 offspring / mother

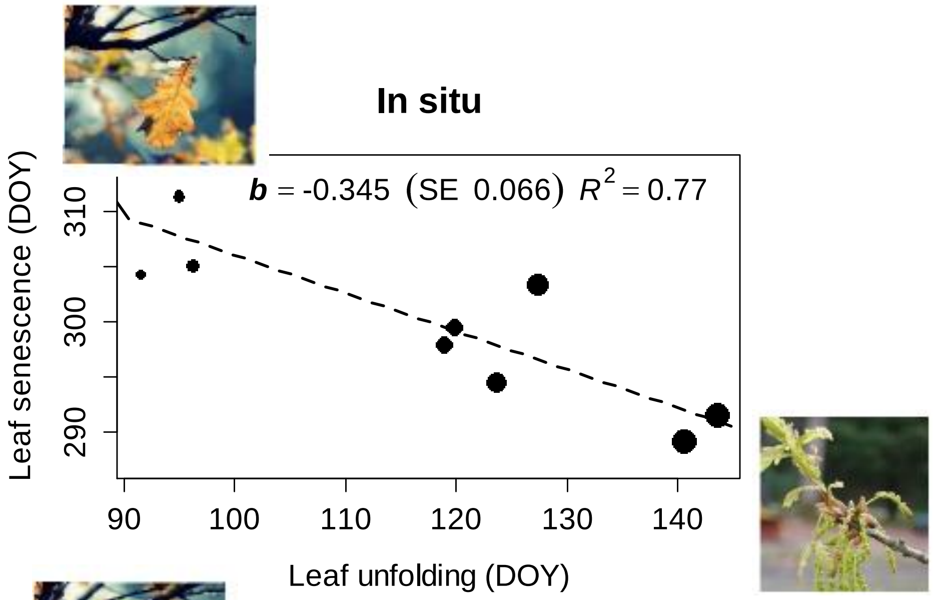
Replicated phenological measures:
2009-2014

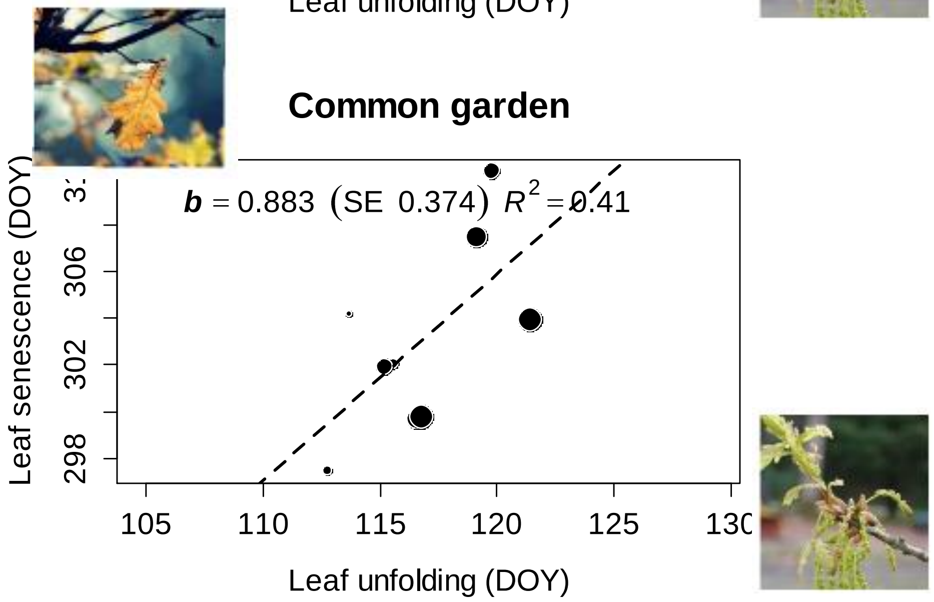
→ 6 replicates

Population differenciation

In situ

Common garden
Optimal conditions
(ca. 0 m. alt.)

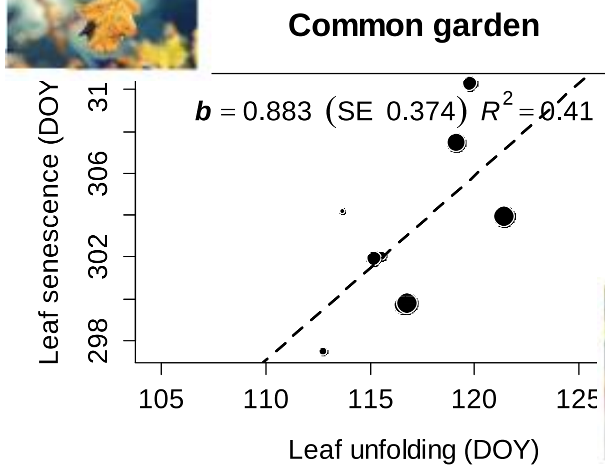




What happened?

Prediction (1/2)

$$\Delta\overline{GS} = G_{LS}\,\beta_{LS} - G_{LU}\,\beta_{LU} + G_{LS,LU}(\beta_{LU} - \beta_{LS})$$



$$\beta_{LU} > 0$$
$$\beta_{LS} \approx 0$$

$$\Delta\overline{GS} = (G_{LS,LU} - G_{LU})\beta_{LU}$$

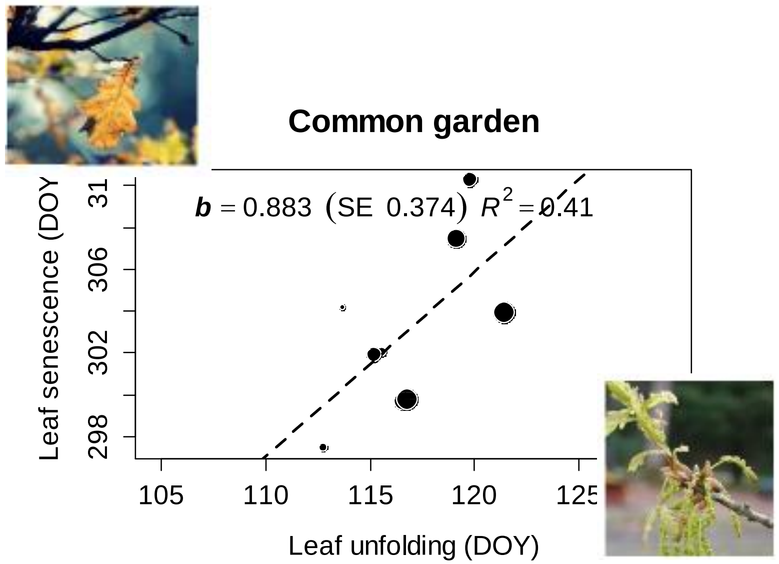
$$(G_{LS,LU} - G_{LU}) \geq 0$$

$$\frac{G_{LS,LU}}{G_{LU}} = \boldsymbol{b}_{\mathbf{G}} \geq 1$$ Total compensation in *GS*

$$0 < \boldsymbol{b}_{\mathbf{G}} < 1$$ Partial compensation in *GS*

Prediction (1/2)

$$\Delta\overline{GS} = G_{LS}\,\beta_{LS} - G_{LU}\,\beta_{LU} + G_{LS,LU}(\beta_{LU} - \beta_{LS})$$



$\beta_{LU} > 0$

$\beta_{LS} \approx 0$

$$\Delta\overline{GS} = (G_{LS,LU} - G_{LU})\beta_{LU}$$

$$(G_{LS,LU} - G_{LU}) \geq 0$$

$\frac{G_{LS,LU}}{G_{LU}} = \boldsymbol{b}_{\mathbf{G}} \geq 1$ Total compensation in *GS*

$0 < \boldsymbol{b}_{\mathbf{G}} < 1$ Partial compensation in *GS*

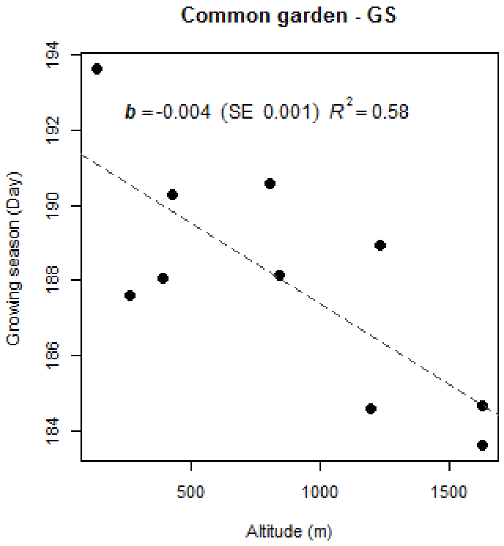
Potentially favorable covariance pattern (**G**-matrix orientation)

Prediction 1:

$\boldsymbol{b}_{\mathbf{G}} > 0$ determines bivariate populations divergence

Prediction (2/2)

$$\Delta\overline{GS} = G_{LS}\,\beta_{LS} - G_{LU}\,\beta_{LU} + G_{LS,LU}(\beta_{LU} - \beta_{LS})$$



As: $\Delta\overline{GS} < 0$ (ca. – 6 days)

$$G_{LS}\,\beta_{LS} - G_{LU}\,\beta_{LU} + G_{LS,LU}(\beta_{LU} - \beta_{LS}) < 0$$

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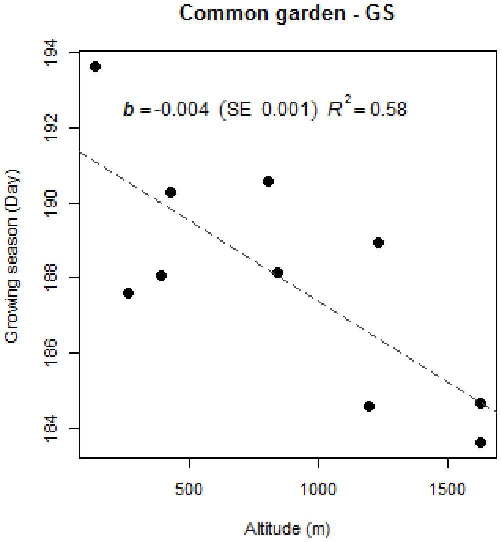


As: $\Delta\overline{GS} < 0$ (ca. – 6 days)

$$G_{LS}\,\beta_{LS} - G_{LU}\,\beta_{LU} + G_{LS,LU}(\beta_{LU} - \beta_{LS}) < 0$$

$$\frac{\beta_{LU}}{\beta_{LS}} > \frac{G_{LS} - G_{LU,LS}}{G_{LU} - G_{LU,LS}} = \boldsymbol{\theta}$$

$$\beta_{LU} > \boldsymbol{\theta}\beta_{LS}$$

Prediction 2:

The evolutionary dynamic of the phenological cycle is mostly driven by selection on *LU*,

then $\boldsymbol{\theta} > 1$

Statistics

'Animal' model – mixed-effect model

$$y_{ijklm} = B_{ij} + (Bp)_{ijk} + p_{ik} + a_{ijkl} + b_{ijkl} + e_{ijklm}$$

Population (common garden) effects (p_{ik})

Breeding values (a_{ijkl})
→ **G-matrix**

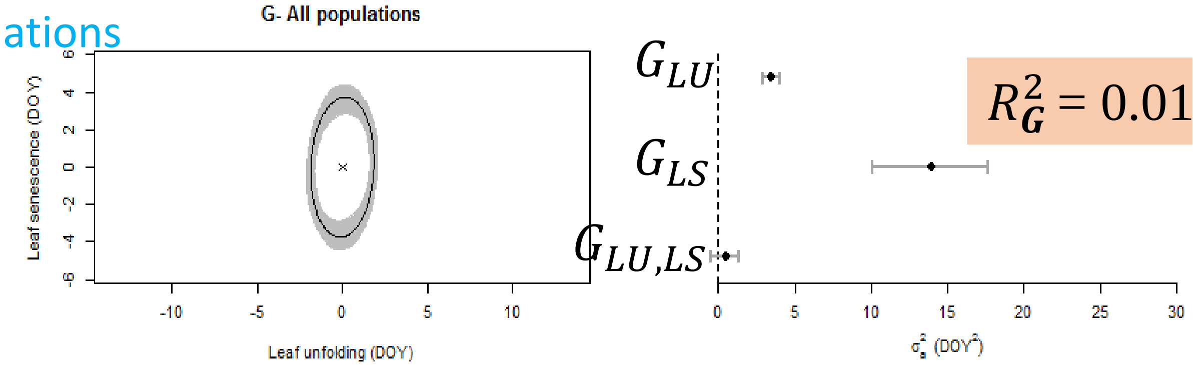
Permanent environmental effect (b_{ijkl})
→ **Replicated phenotypic values**

Within-individual (among-year) residuals (e_{ijklm})

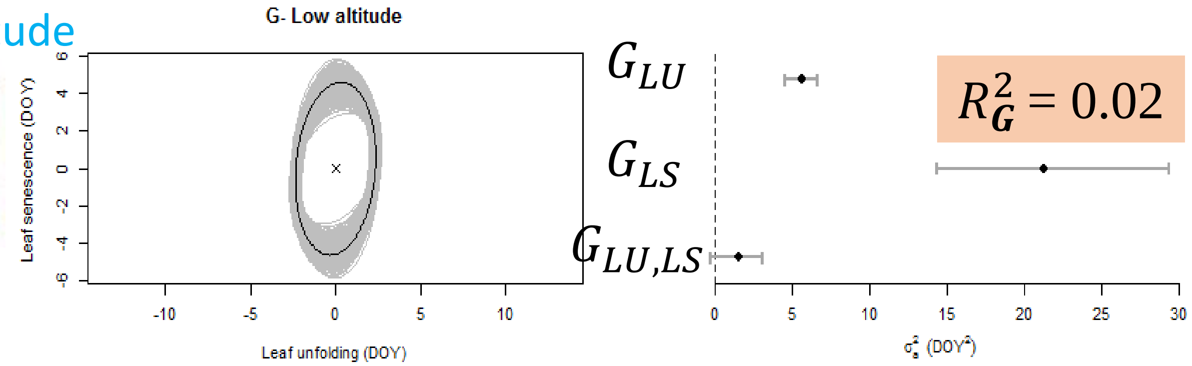
Bayesian estimations (MCMCglmm)

G-matrix estimates

All populations



Low altitude



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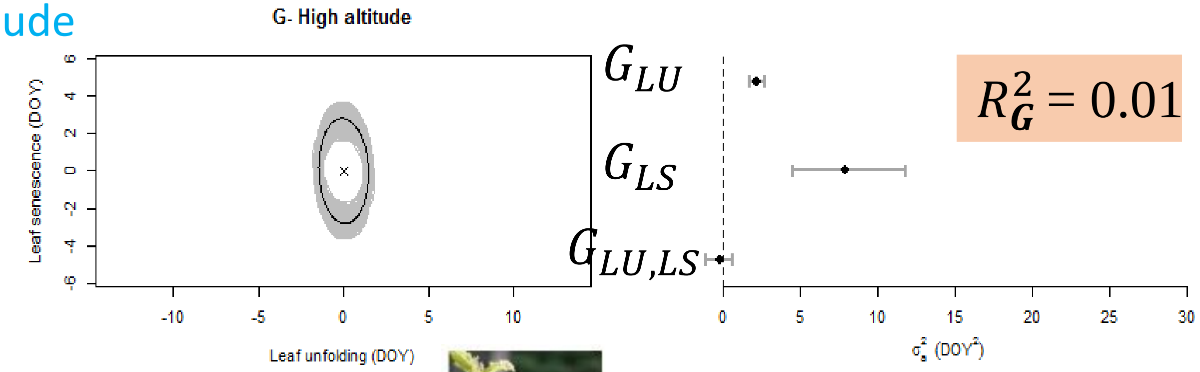


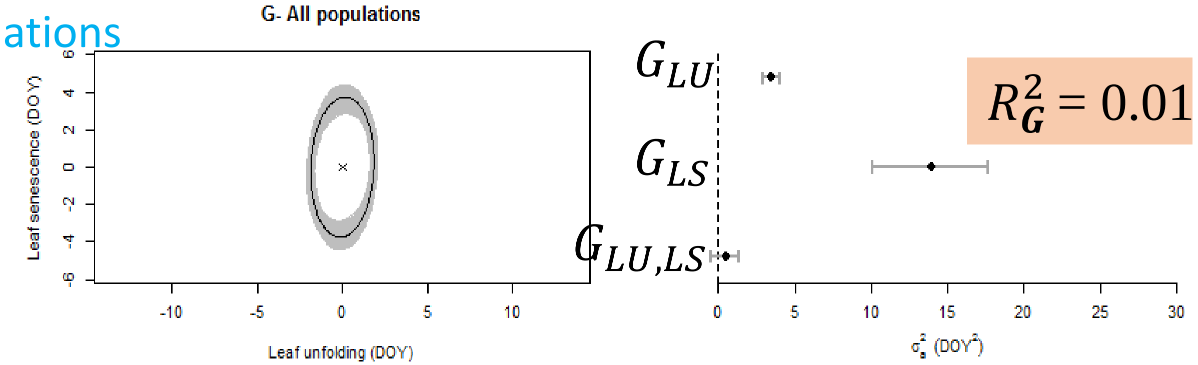
-Abundant genetic variance for both traits (more for senescence)

-Reduction of **G** by: 62% (*LU*), 67% (*LS*), *and* 47% (*GS*)

-No genetic constraints

G-matrix estimates

All populations



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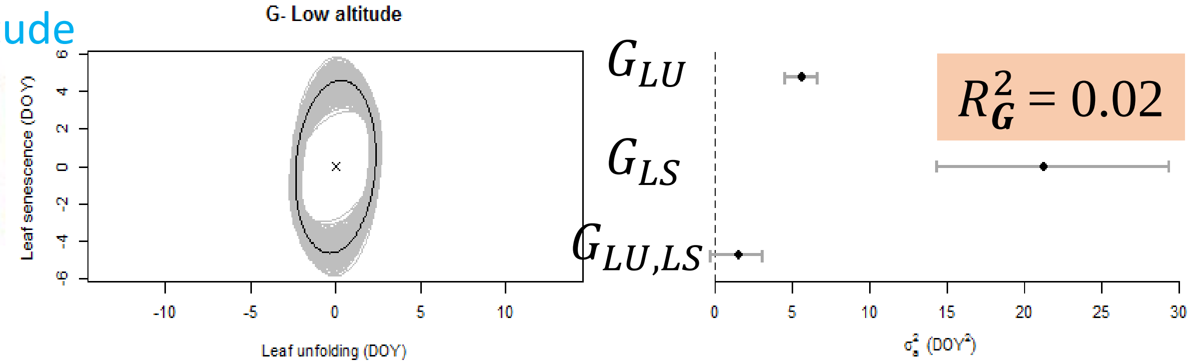

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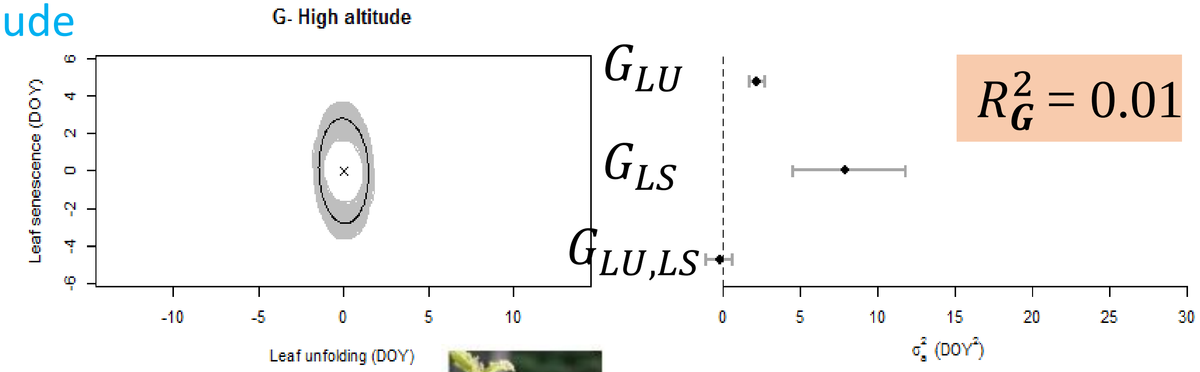

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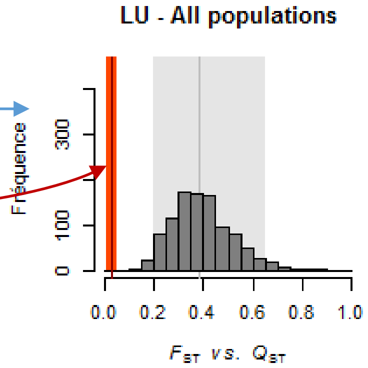
Prediction 1:
$\boldsymbol{b}_{\mathrm{G}} > 0$ determines bivariate populations divergence

NOT VALIDATED

F_{ST} – Q_{ST} comparisons

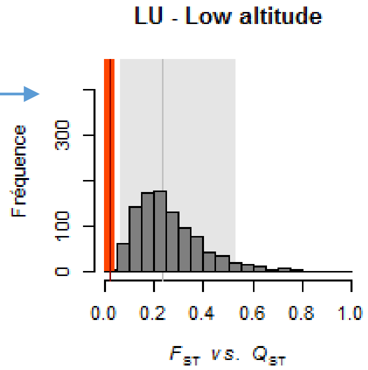
All populations →



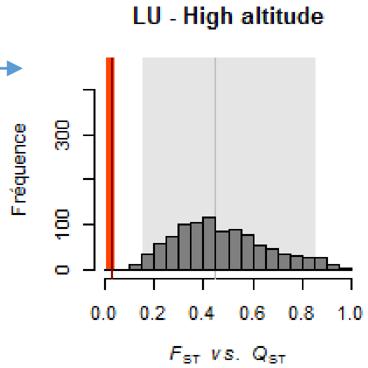
F_{ST}

reanalysis of 16 microsatellites from Alberto *et al.* (2010) Mol. Ecol.

Low altitude →



High altitude →



F_{ST} – Q_{ST} comparisons

All populations

Low altitude

High altitude

F_{ST}

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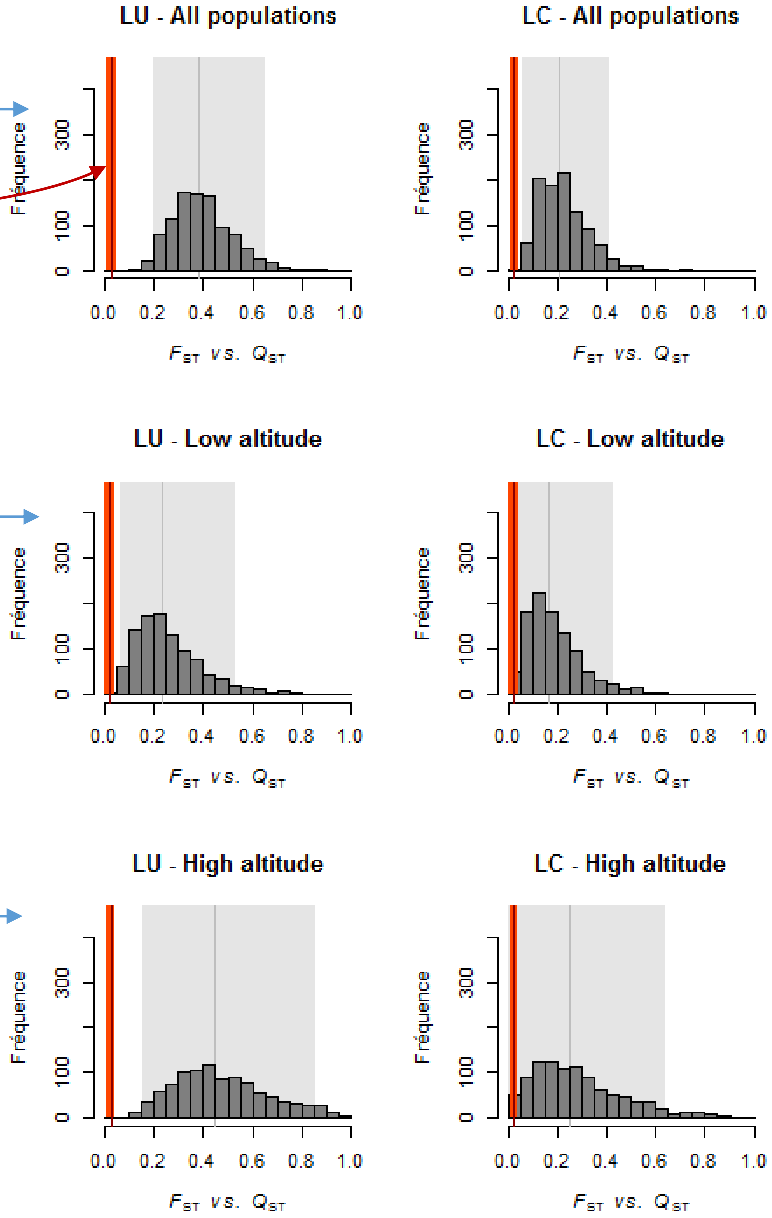


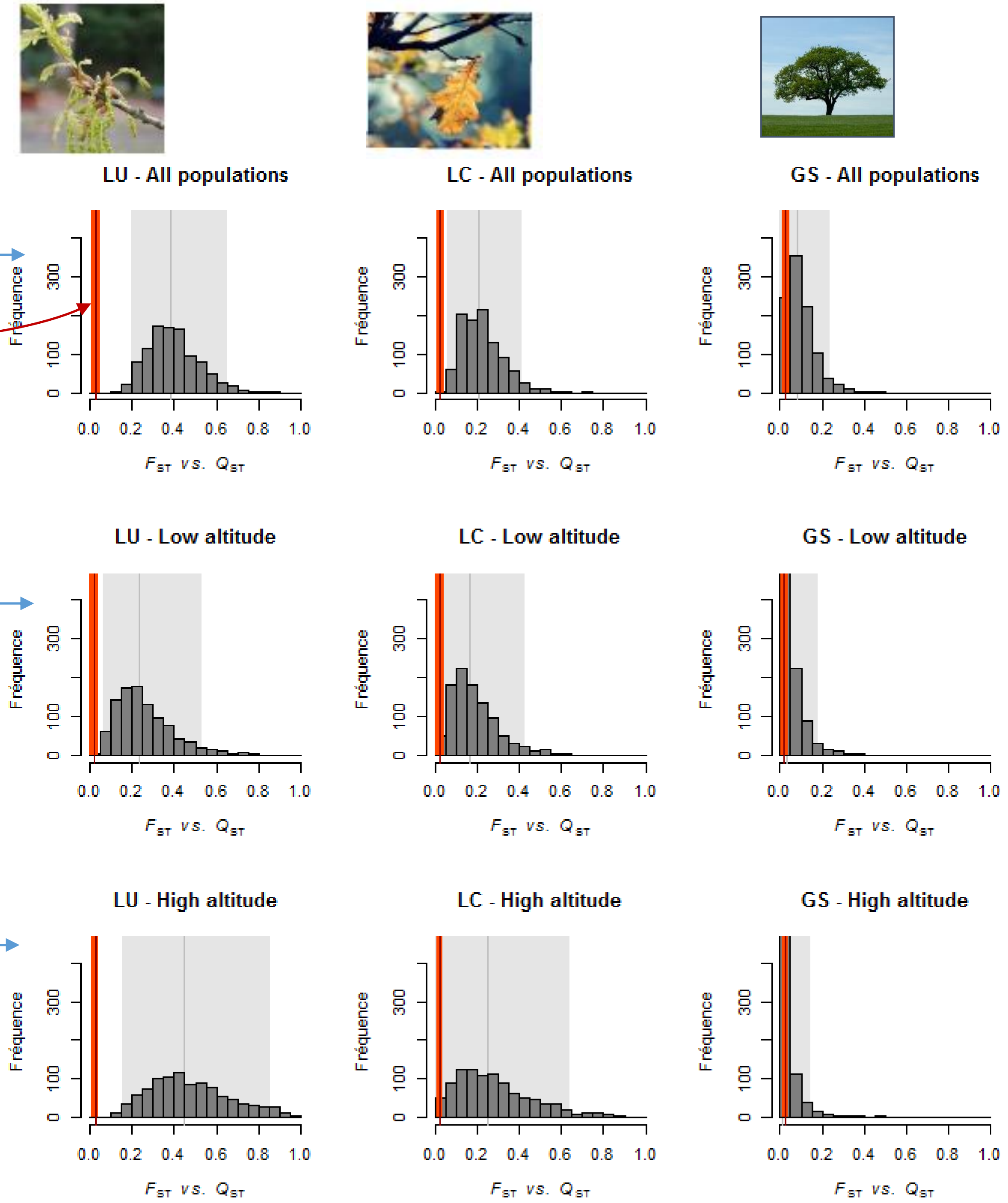
F_{ST} – Q_{ST} comparisons

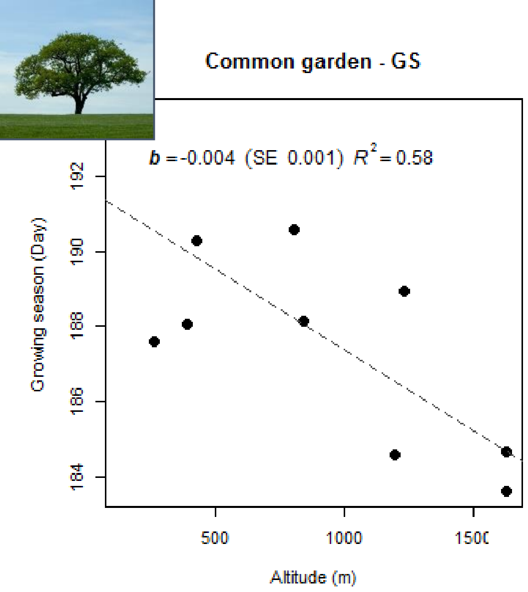
All populations →

F_{ST} reanalysis of 16 microsatellites from Alberto *et al.* (2010) Mol. Ecol.

Low altitude →

High altitude →

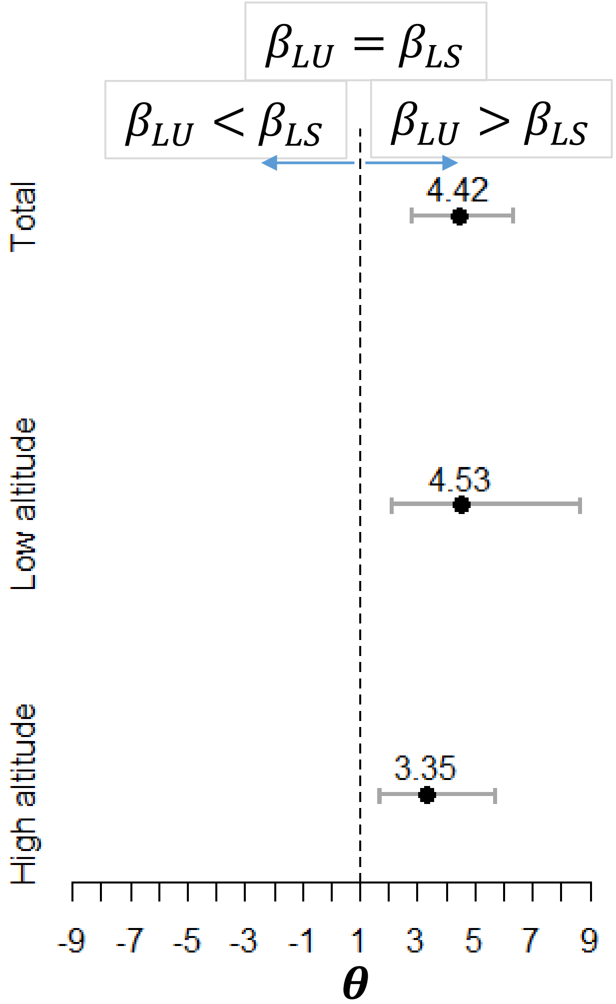




As: $\Delta\overline{GS} < 0$ (ca. – 6 days)

$$\frac{\beta_{LU}}{\beta_{LS}} > \frac{G_{LS} - G_{LU,LS}}{G_{LU} - G_{LU,LS}} = \boldsymbol{\theta}$$

$$\beta_{LU} > \boldsymbol{\theta}\beta_{LS}$$

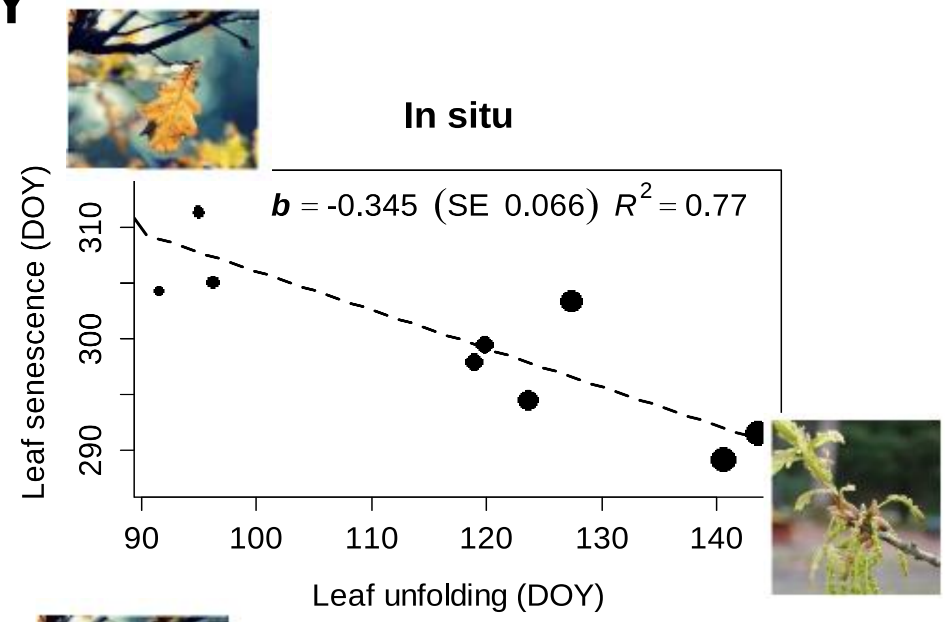


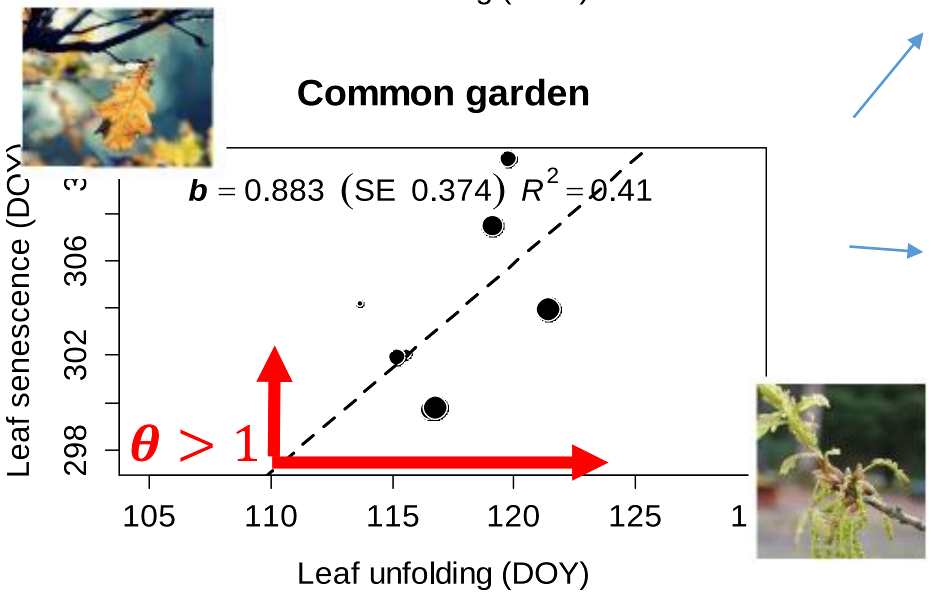
Prediction 2:

The evolutionary dynamic of the phenological cycle is mostly driven by selection on *LU*, then $\boldsymbol{\theta} > 1$

VALIDATED

SUMMARY

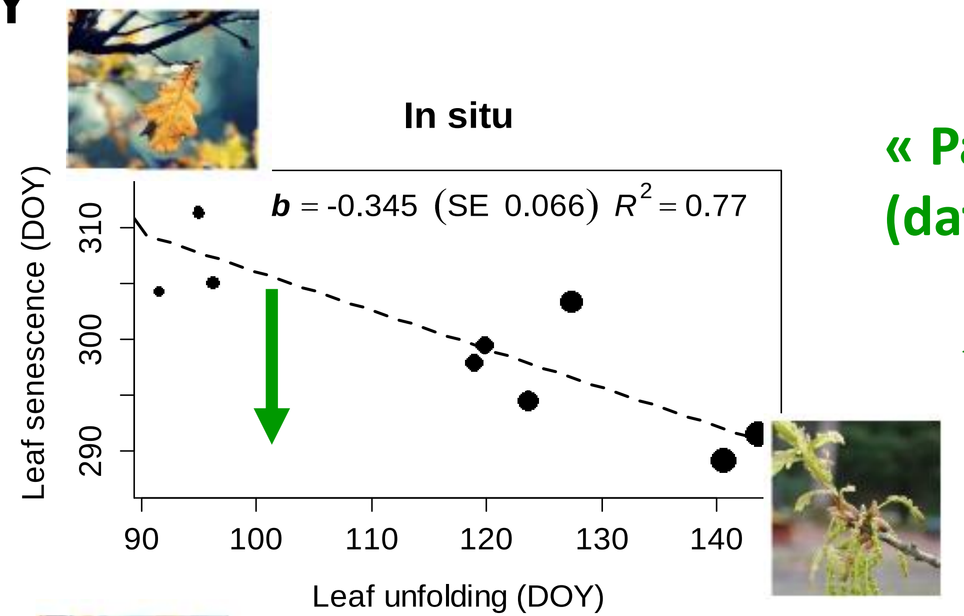


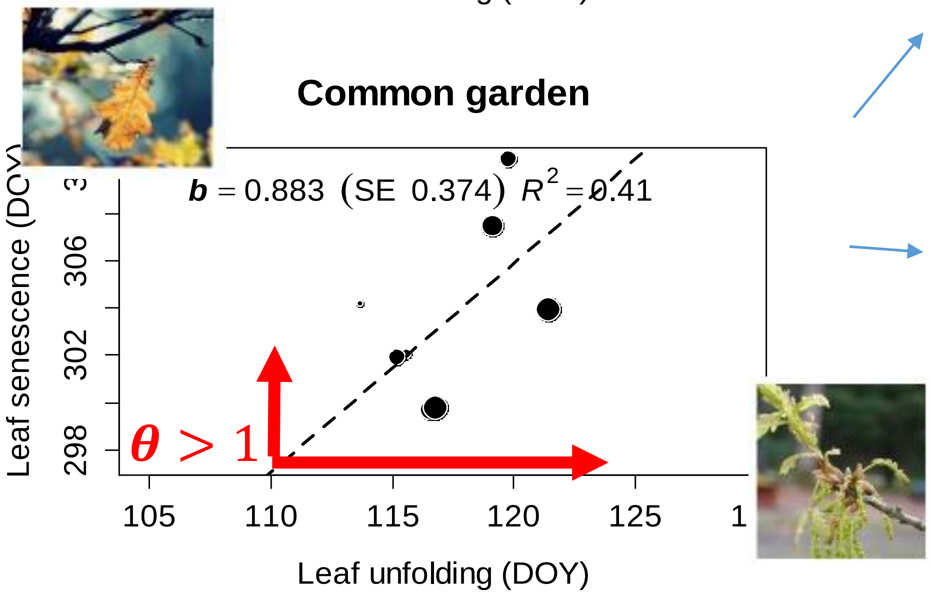


A pattern unlikely to result from genetic constraints

Selection acted in a direction minimizing the decrease of the growing season length, generating such covariation

SUMMARY





« Passive » plasticity of senescence takes over (date of 1st autumn frost)

A pattern unlikely to result from genetic constraints

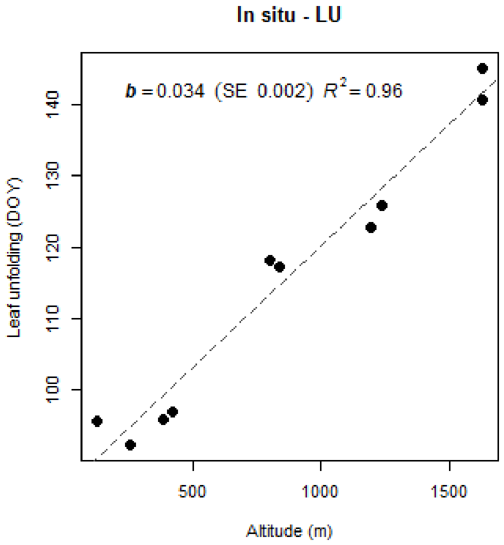
Selection acted in a direction minimizing the decrease of the growing season length, generating such covariation

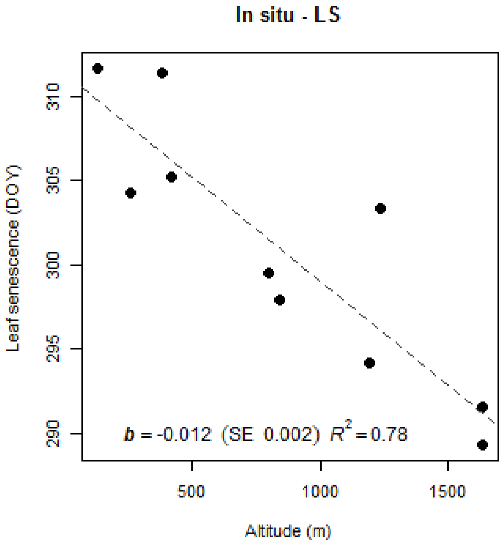

Merci

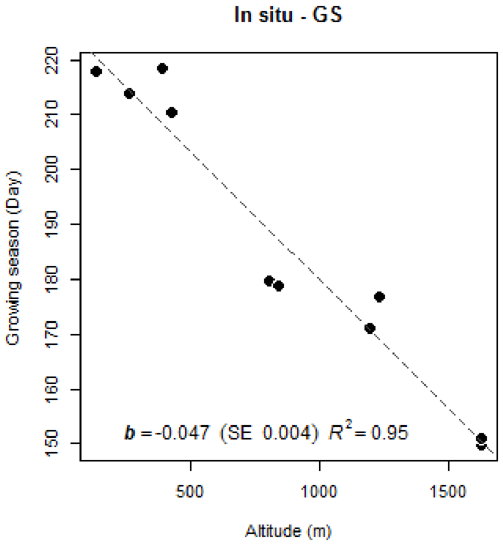
Population differenciation (1/2)

LS date – LU date

In situ





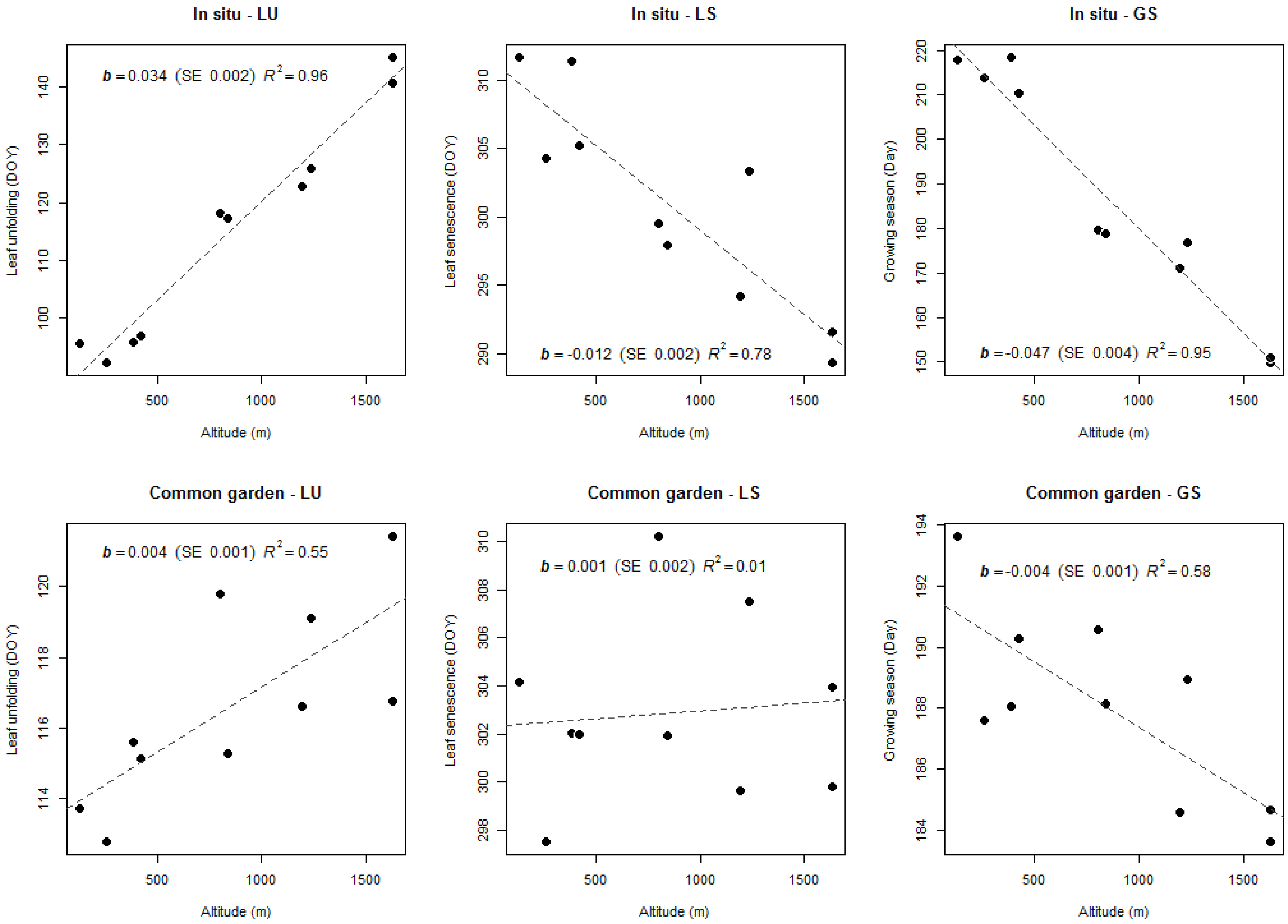


Population differenciation (1/2)

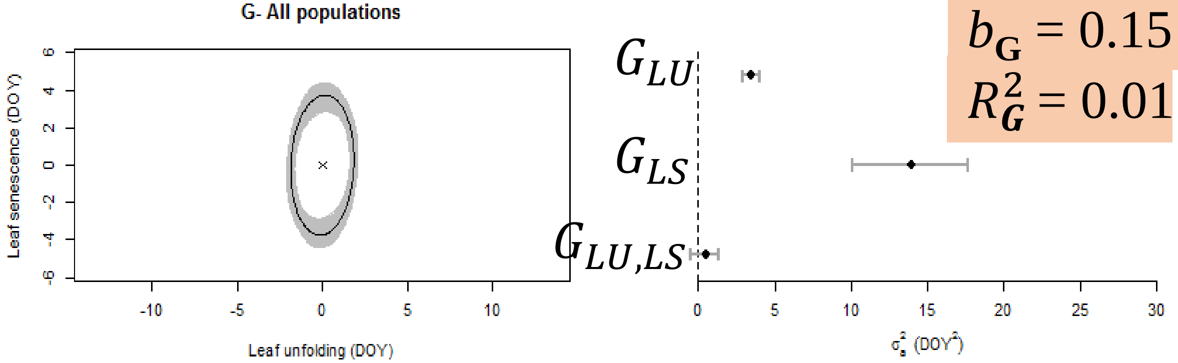
LS date – LU date

In situ

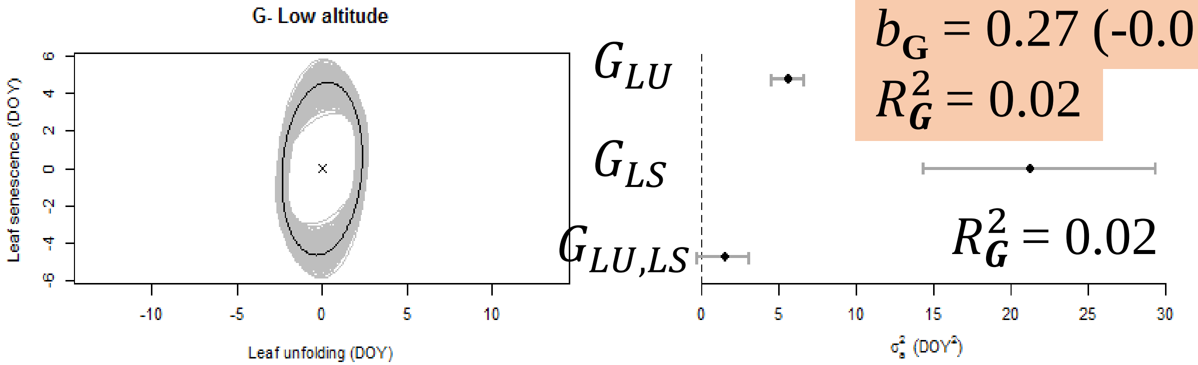
Common garden
Optimal conditions
(ca. 0 m. alt.)



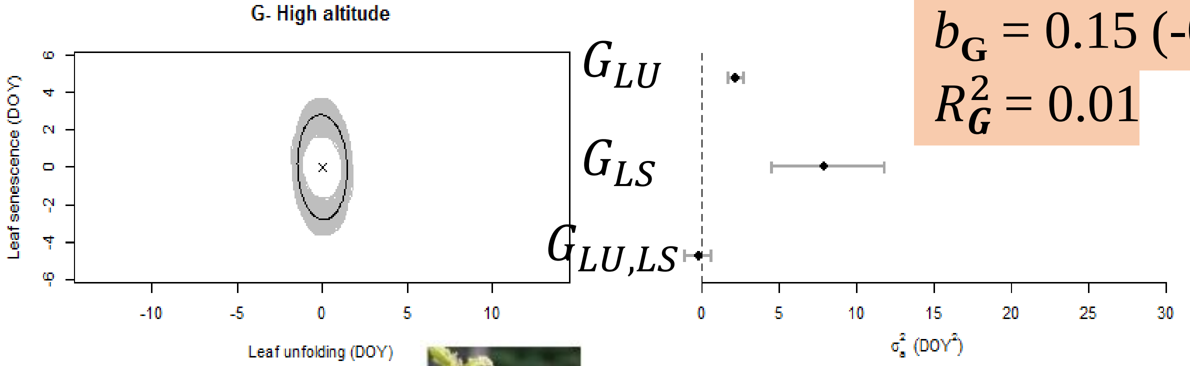
G-matrix estimates



$b_{\mathbf{G}}$ = 0.15 (-0.08, 0.39)
$R^2_{\boldsymbol{G}}$ = 0.01



$b_{\mathbf{G}}$ = 0.27 (-0.01, 0.61)
$R^2_{\boldsymbol{G}}$ = 0.02



$b_{\mathbf{G}}$ = 0.15 (-0.51, 0.26)
$R^2_{\boldsymbol{G}}$ = 0.01

-Abundant genetic variance for both traits (more for senescence)

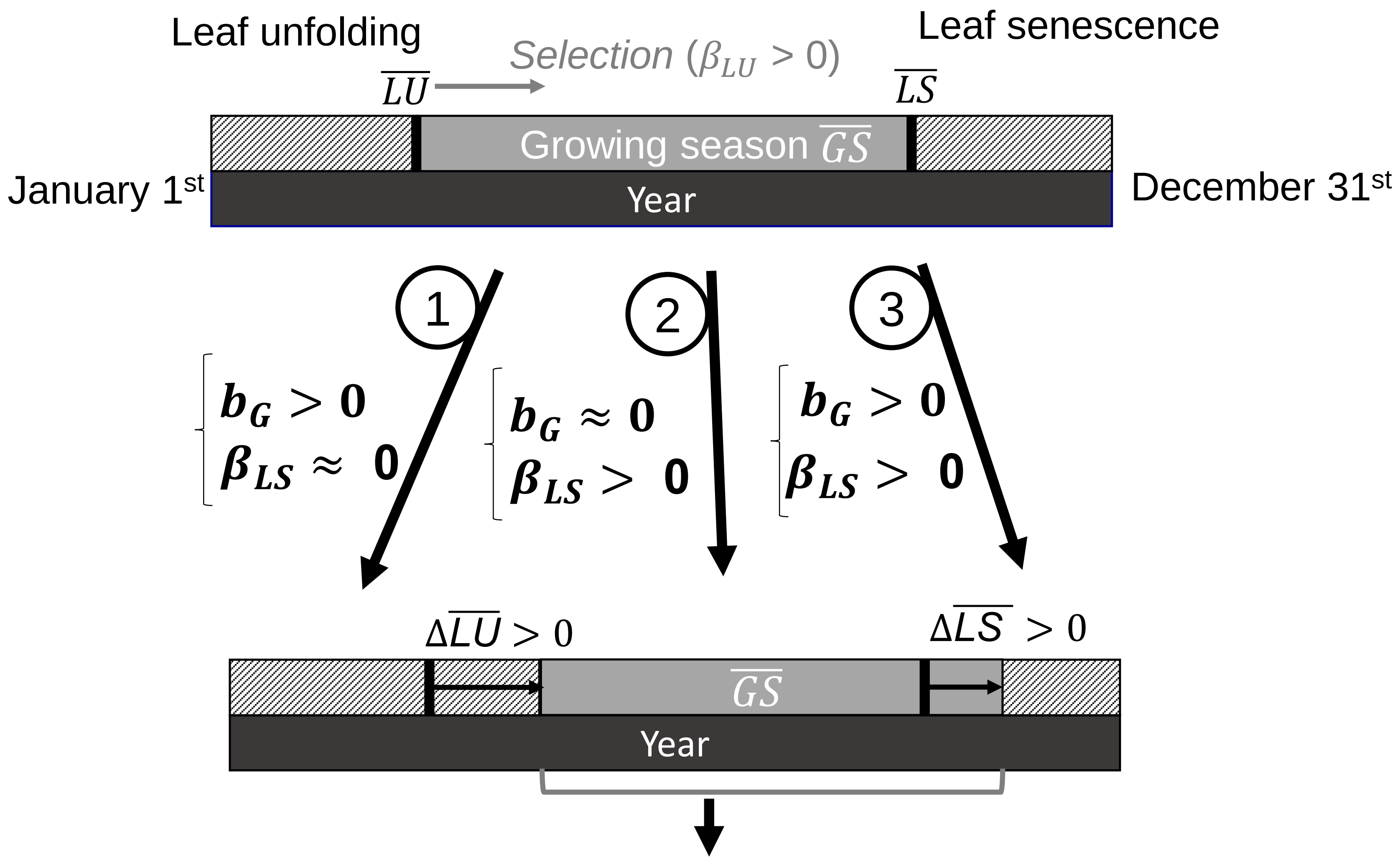
-Reduction of **G** by: 62% (*LU*), 67% (*LS*), *and* 47% (*GS*)

-No genetic constraints

Prediction 1:
$\boldsymbol{b}_{\mathbf{G}}$ > 0 determines bivariate populations divergence

NOT VALIDATED

Scenarios for compensation of delayed leaf unfolding date



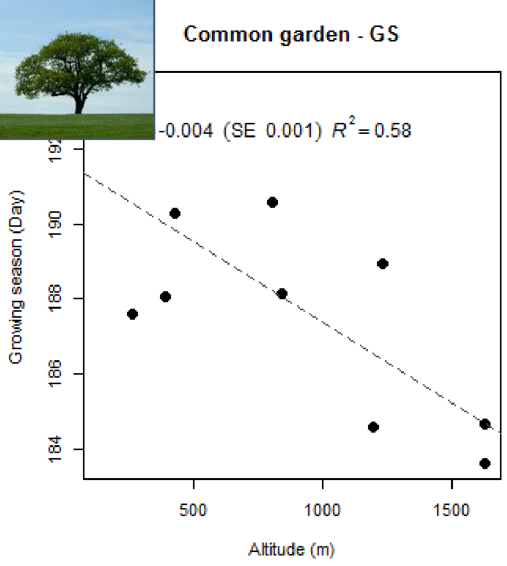
Partial compensation offset of the growing season length due to a positive genetic response on *LS*

$$\Delta\overline{GS} = -\Delta\overline{LU} + \Delta\overline{LS}$$

But…

Traits	Leaf unfolding timing (LU)			Leaf senescence timing (LS)			Growing season duration (GS)		
Components	**All populations**	**Low altitude**	**High altitude**	**All populations**	**Low altitude**	**High altitude**	**All populations**	**Low altitude**	**High altitude**
σ_p^2 (day^2)	4.65	3.43	3.7	7.09	8.94	4.9	2.75	1.3	0.41
	(1.41, 11.73)	(0.53, 11.78)	(0.39, 19.42)	(1.8, 19.57)	(0.03, 31.07)	(0, 34.81)	(0, 8.73)	(0, 7.7)	(0, 4.68)
σ_g^2 (day^2)	3.46	5.59	2.11	13.93	22.84	7.65	15.94	21.90	11.71
	(2.91, 3.99)	(4.54, 6.74)	(1.64, 2.61)	(10.13, 17.89)	(15.83, 29.67)	(4.32, 11.25)	(12.43, 19.55)	(15.15, 30.19)	(8.11, 15.61)
σ_m^2 (day^2)	0.01	0.02	0.01	1.04	0.75	0.56	0.13	0.41	0.18
	(0, 0.07)	(0, 0.2)	(0, 0.09)	(0, 4.51)	(0, 6.44)	(0, 4.04)	(0, 1.21)	(0, 4.92)	(0, 1.68)
σ_e^2 (day^2)	46.31	46.79	45.83	120.89	135.65	112.01	151.1	171.85	137.43
	(45.29, 47.41)	(45.02, 48.51)	(44.59, 47.01)	(116.56, 125.32)	(128.03, 143.49)	(106.27, 116.63)	(146.39, 156.85)	(162.91, 181.99)	(131.63, 143.58)
Q_{ST}	0.4	0.24	0.47	0.2	0.16	0.25	0.08	0.03	0.02
	(0.2, 0.66)	(0.08, 0.52)	(0.17, 0.86)	(0.07, 0.42)	(0.02, 0.42)	(0, 0.7)	(0, 0.21)	(0, 0.15)	(0, 0.18)
h^2	1	1	0.99	0.93	0.97	0.93	0.99	0.98	0.98
	(0.98, 1)	(0.97, 1)	(0.96, 1)	(0.72, 1)	(0.73, 1)	(0.59, 1)	(0.93, 1)	(0.79, 1)	(0.86, 1)
e (%)	-	-	-	-	-	-	0.05	0.06	0.03
							(0.04, 0.06)	(0.04, 0.08)	(0.02, 0.05)

Most – 90%– of the within population variance is among year, i.e. within individual…



As: $\Delta\overline{GS} < 0$ (ca. – 6 days)

$$\frac{\beta_{LU}}{\beta_{LS}} > \frac{G_{LS} - G_{LU,LS}}{G_{LU} - G_{LU,LS}} = \boldsymbol{\theta}$$

$$\beta_{LU} > \boldsymbol{\theta}\beta_{LS}$$

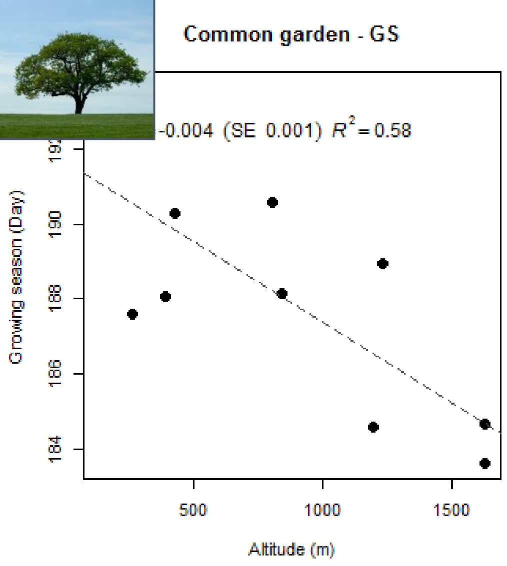
Components	All populations	Low altitude	High altitude
b_p	0.77 (0.08, 1.43) - 0.46	1.29 (0.05, 2.25) - 0.75	0.86 (-0.23, 1.88) - 0.63
b_a	0.15 (-0.08, 0.39) - 0.01	0.27 (-0.01, 0.61) - 0.02	-0.09 (-0.51, 0.26) - 0.01
b_d	-0.25 (-49.27, 42.89) - 0.27	-0.66 (-52.48, 38.02) - 0.25	-0.07 (-37.07, 40.96) - 0.13
b_ε	0.2 (0.16, 0.23) - 0.01	0.15 (0.08, 0.21) - 0.01	0.23 (0.18, 0.27) - 0.02
$\boldsymbol{\theta}$	4.42 (2.83, 6.37)	4.53 (2.11, 8.69)	3.35 (1.71, 5.72)

Make a figure in R with the line 1 as reference and the 95CI of theta.

Prediction 2:

The evolutionary dynamic of the phenological cycle is mostly driven by selection on *LU*,
then $\boldsymbol{\theta} > 1$

→ Average selection gradient on leaf unfolding date was ca. 4.59 times stronger than the analogue for leaf senescence date



As: $\Delta\overline{GS} < 0$ (ca. – 6 days)

$$\frac{\beta_{LU}}{\beta_{LS}} > \frac{G_{LS} - G_{LU,LS}}{G_{LU} - G_{LU,LS}} = \boldsymbol{\theta}$$

$$\beta_{LU} > \boldsymbol{\theta}\beta_{LS}$$

Components	All populations	Low altitude	High altitude
b_p	0.77 (0.08, 1.43) - 0.46	1.29 (0.05, 2.25) - 0.75	0.86 (-0.23, 1.88) - 0.63
b_a	0.15 (-0.08, 0.39) - 0.01	0.27 (-0.01, 0.61) - 0.02	-0.09 (-0.51, 0.26) - 0.01
b_d	-0.25 (-49.27, 42.89) - 0.27	-0.66 (-52.48, 38.02) - 0.25	-0.07 (-37.07, 40.96) - 0.13
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Part II. Analysis of thermal reaction norms

Which contribution of phenotypic plasticity on Leaf unfolding date?

Modeling within individual variance in Leaf unfolding time as a function of annual spring temperature *T*:

$$Z_{ijk} = a_j + \beta_j T_{ik} + e_{ijk}$$

With
-Jean-Paul Soularue
-Thomas Caignard

Study design in brief:

***In situ* monitoring**

10 populations monitored *in situ*
Altitude: 131 to 1630 m

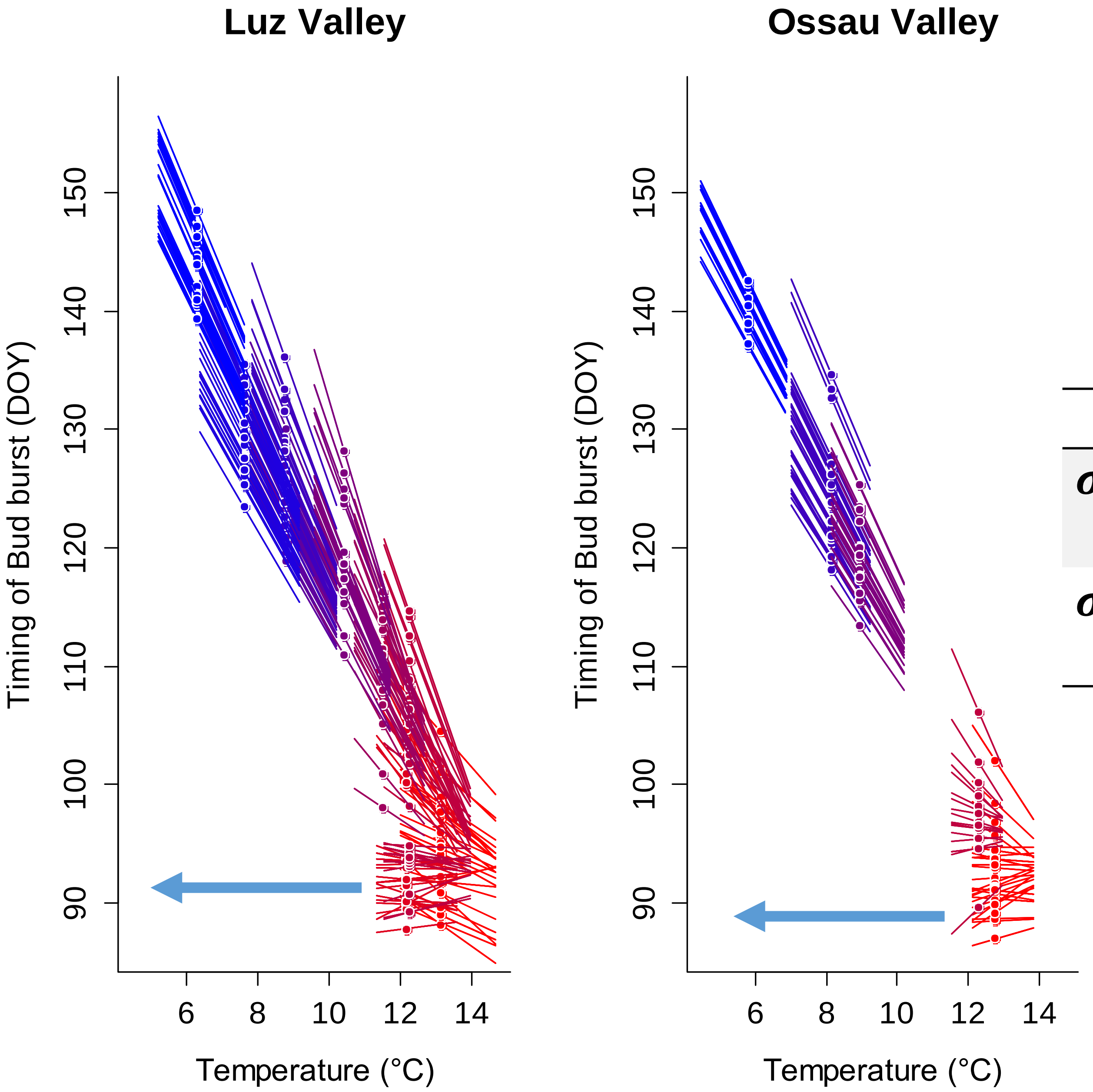
Replicated phenological measures:
2005-2007
& 2009-2014 (2015)
→ 9 replicates

Common garden at the sea level (Toulenne)

Acorns from 152 mothers (*n* = 3321)
ca. 23 offspring / mother

Replicated phenological measures:
2009-2014
→ 6 replicates

IN SITU

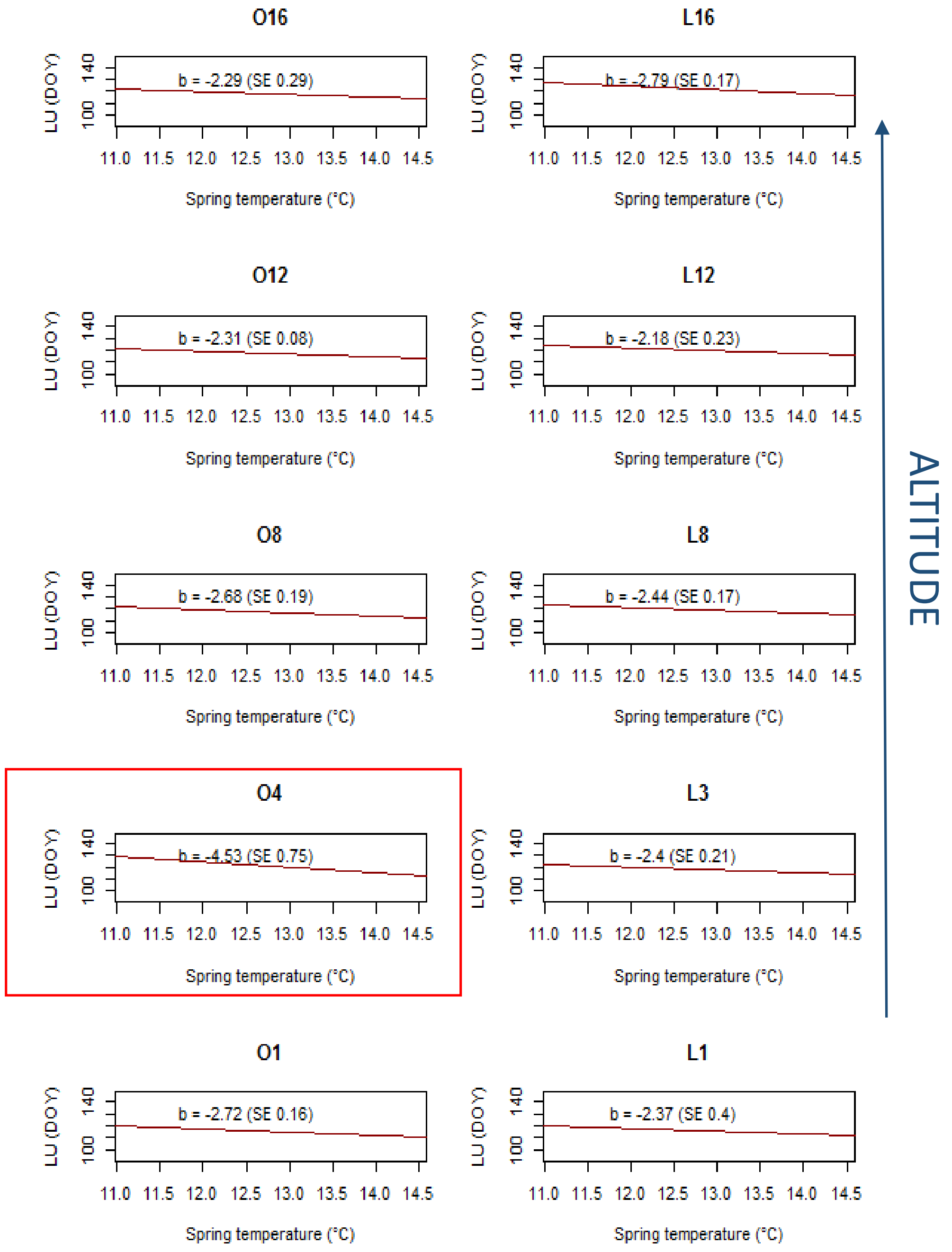


Average individual slope becomes more negative (i.e. steeper) by 0.43 (0.30, 0.56) DOY/ °C when site temperature decreases by 1 °C along the gradient.
(contextual model-based estimation)

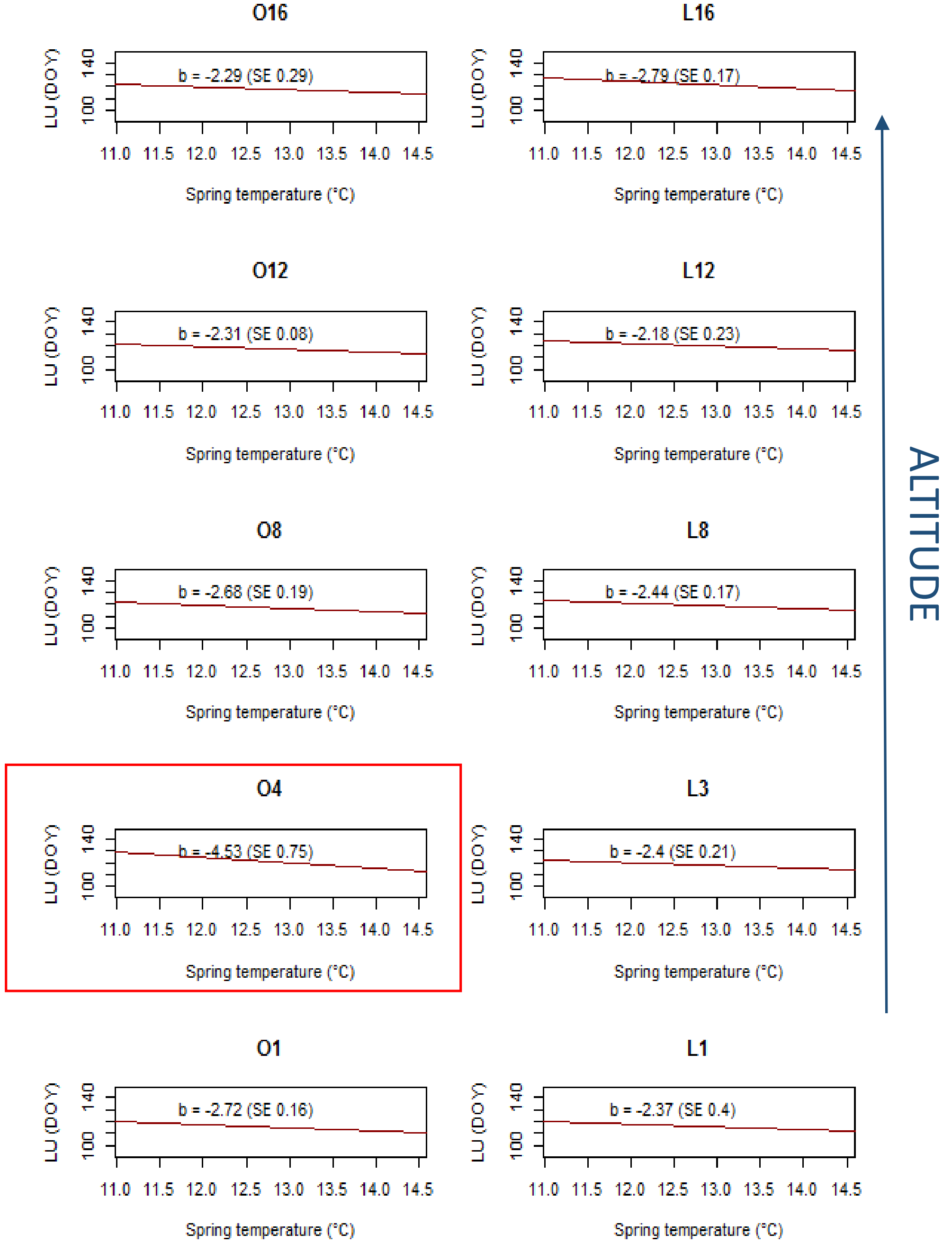
	Total	Low altitude	High altitude
σ_a^2	17.43 (14.00, 22.31)	28.20 (20.80, 35.39)	5.47 (3.17, 8.43)
σ_b^2	1.87 (0.72, 3.01)	2.9 (1.28, 4.93)	0.46 (0.16, 1.02)

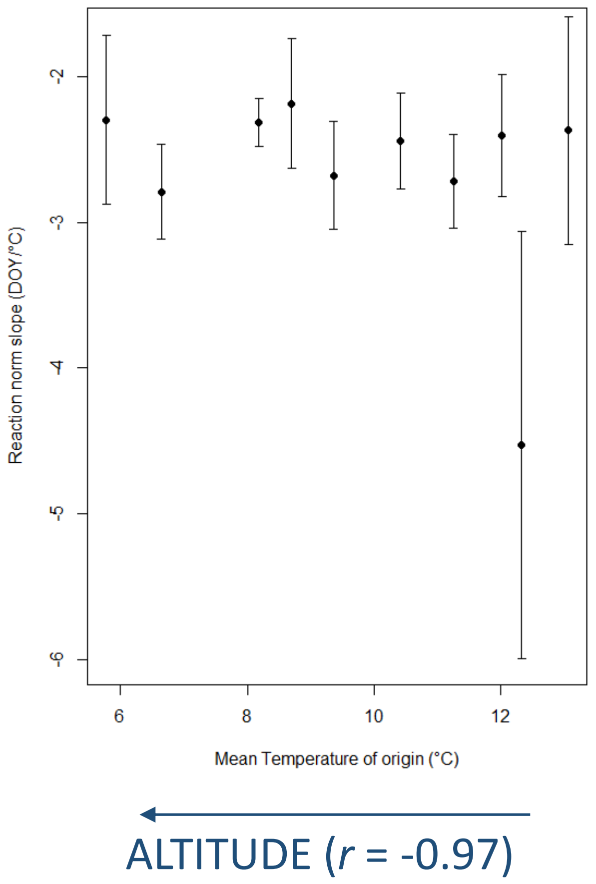
Soularue *et al.* In prep.

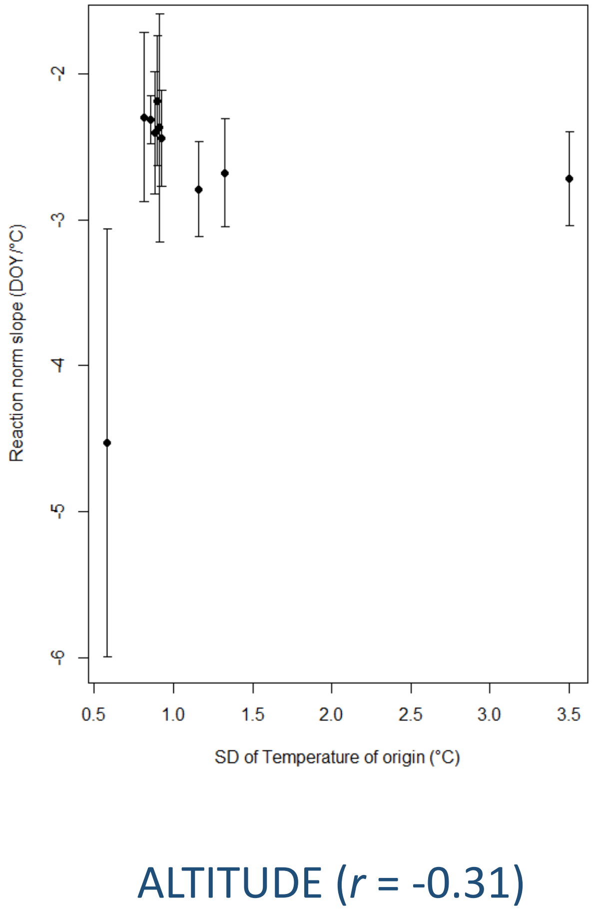
COMMON GARDEN



COMMON GARDEN







Estimating among population & genetic variances in slope and elevation

Methods

Random-regression animal model

$$y_{jklm} = B_j + \beta_o T_l + (Bp)_{jk} + p_k + \beta_k(p)T_l + a_{jkm} + \beta(a)_{jkm}T_l + b_{jkm} + \beta(b)_{jkm}T_l + \varepsilon_{jkml}$$

- $p_k + \beta_k(p)T_l$: Population deviation
- $a_{jkm} + \beta(a)_{jkm}T_l$: Breeding values
- $b_{jkm} + \beta(b)_{jkm}T_l$: Non genetic individual level deviation to the reaction norm
- ε_{jkml}: Ultimate deviation from individual reaction norm

Variance components

Component	Total	Low altitude	High altitude
$(a)\ \sigma_p^2$	6.587 (1.783, 17.446)	5.276 (0.651, 29.674)	21.951 (1.159, 410.52)
$(b)\ \sigma_p^2$	0.029 (0, 0.137)	0.44 (0.038, 1.788)	1.889 (0.228, 9.537)
$(a)\ \sigma_g^2$	4.97 (4.242, 5.658)	7.754 (6.359, 9.216)	3.169 (2.447, 3.943)
$(b)\ \sigma_g^2$	0.057 (0.004, 0.136)	0.121 (0.017, 0.289)	0.006 (0, 0.045)
$(a)\ \sigma_m^2$	0.017 (0, 0.144)	0.052 (0, 0.424)	0.026 (0, 0.2)
$(b)\ \sigma_m^2$	0.009 (0, 0.071)	0.014 (0, 0.122)	0.003 (0, 0.035)
$(a)\ h^2$	0.997 (0.971, 1)	0.993 (0.946, 1)	0.992 (0.937, 1)
$(b)\ h^2$	0.867 (0.357, 1)	0.9 (0.387, 1)	0.629 (0.014, 1)
$(a)\ Q_{ST}$	0.401 (0.197, 0.657)	0.256 (0.062, 0.666)	0.78 (0.336, 1)
$(b)\ Q_{ST}$	0.206 (0, 0.668)	0.658 (0.253, 0.957)	0.994 (0.934, 1)
σ_e^2	41.51 (40.488, 42.785)	38.885 (37.195, 40.62)	42.163 (40.721, 43.605)

Little, but ≠ 0, $\mathbf{V}_G$ in the slope

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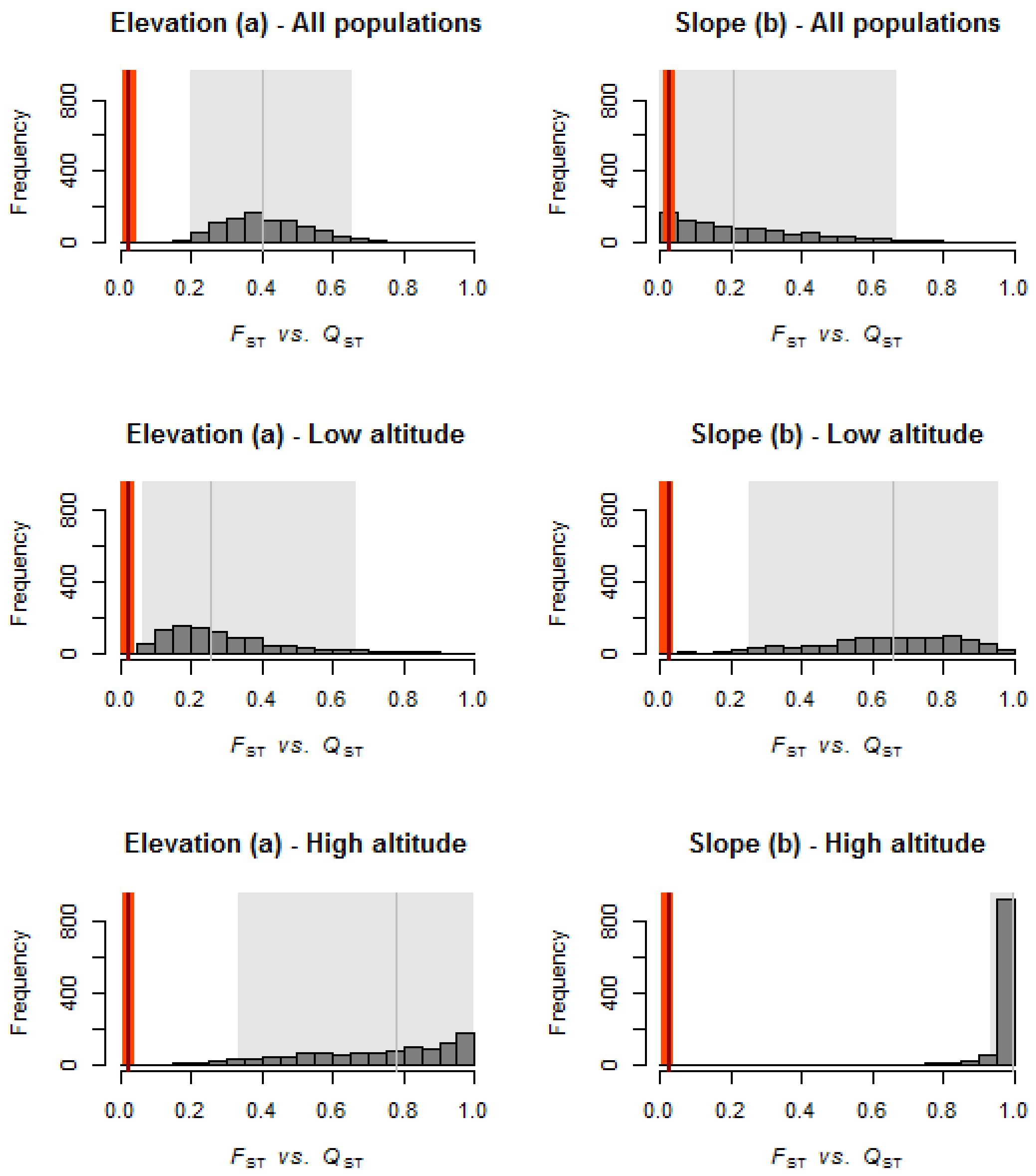
F_{ST} – Q_{ST} comparisons

$$Q_{ST} = \sigma_p^2 / (\sigma_p^2 + 2\sigma_g^2)$$



σ_p^2 low

σ_g^2 high

σ_p^2 increases

σ_g^2 higher

σ_g^2 very low


Merci


Traits	Leaf unfolding timing (LU)			Leaf senescence timing (LS)			Growing season duration (GS)		
Components	**All populations**	**Low altitude**	**High altitude**	**All populations**	**Low altitude**	**High altitude**	**All populations**	**Low altitude**	**High altitude**
σ_p^2 (day²)	4.65	3.43	3.7	7.09	8.94	4.9	2.75	1.3	0.41
	(1.41, 11.73)	(0.53, 11.78)	(0.39, 19.42)	(1.8, 19.57)	(0.03, 31.07)	(0, 34.81)	(0, 8.73)	(0, 7.7)	(0, 4.68)
σ_a^2 (day²)	3.46	5.59	2.11	13.93	22.84	7.65	15.94	21.90	11.71
	(2.91, 3.99)	(4.54, 6.74)	(1.64, 2.61)	(10.13, 17.89)	(15.83, 29.67)	(4.32, 11.25)	(12.43, 19.55)	(15.15, 30.19)	(8.11, 15.61)
σ_m^2 (day²)	0.01	0.02	0.01	1.04	0.75	0.56	0.13	0.41	0.18
	(0, 0.07)	(0, 0.2)	(0, 0.09)	(0, 4.51)	(0, 6.44)	(0, 4.04)	(0, 1.21)	(0, 4.92)	(0, 1.68)
σ_e^2 (day²)	46.31	46.79	45.83	120.89	135.65	112.01	151.1	171.85	137.43
	(45.29, 47.41)	(45.02, 48.51)	(44.59, 47.01)	(116.56, 125.32)	(128.03, 143.49)	(106.27, 116.63)	(146.39, 156.85)	(162.91, 181.99)	(131.63, 143.58)
Q_{ST}	0.4	0.24	0.47	0.2	0.16	0.25	0.08	0.03	0.02
	(0.2, 0.66)	(0.08, 0.52)	(0.17, 0.86)	(0.07, 0.42)	(0.02, 0.42)	(0, 0.7)	(0, 0.21)	(0, 0.15)	(0, 0.18)
h^2	1	1	0.99	0.93	0.97	0.93	0.99	0.98	0.98
	(0.98, 1)	(0.97, 1)	(0.96, 1)	(0.72, 1)	(0.73, 1)	(0.59, 1)	(0.93, 1)	(0.79, 1)	(0.86, 1)
e (%)	-	-	-	-	-	-	0.05	0.06	0.03
							(0.04, 0.06)	(0.04, 0.08)	(0.02, 0.05)