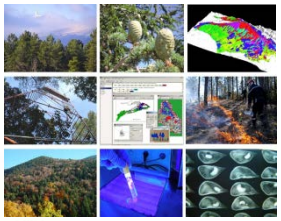
How drought and late frost interact to shape adaptive landscape for budburst phenology along an altitudinal gradient of *Fagus sylvatica* ?

Sylvie Oddou-Muratorio

Kevin Liautaud, Hendrik Davi

BIOADAPT 2013 -projet MeCC



Ecologie des Forêts Méditerranéennes (URFM)

Capsis

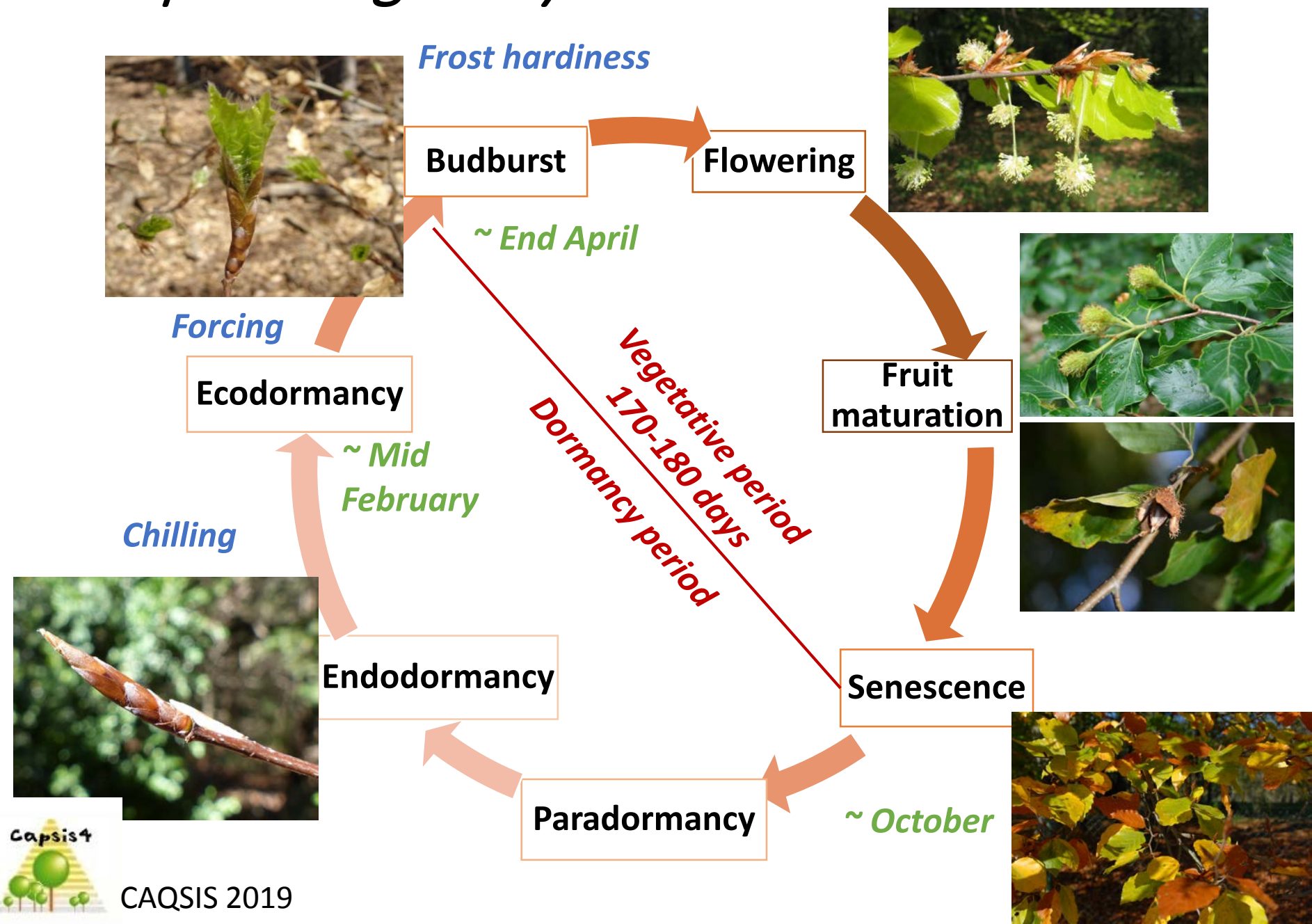
Computer-aided projection of strategies in silviculture

The role of phenological traits in population response to climate change (CC)

- Recent shifts in the dates of major phenological events (Parmesan 2006) in particular budburst in plant (Fu et al. GCB 2014)
- Major issues : Underlying mechanisms ? Phenotypic plasticity or evolution ?
- Budburst date (BBday) of deciduous plants is an event integrated within a complex phenological cycle (Chuine et Regnières 2017) and a trait that evolves under a double constraint (Bennie et al. 2010):
  1. avoiding late frost
  2. maximizing the duration of vegetation period.

Beech phenological cycle

Pictures: O Gilg, F Bonne & F Jean



CAQSIS 2019

What is the adaptive value of BBday ?

1) Direct approach = **Phenotypic selection analysis**, ie BBday-fitness relationship *(Lande et Arnold 1983)*

- Flowering date(Geber et Griffen 2003)
- Selection towards early flowering (Munguia-Rosas et al. 2011)

Adaptive landscape

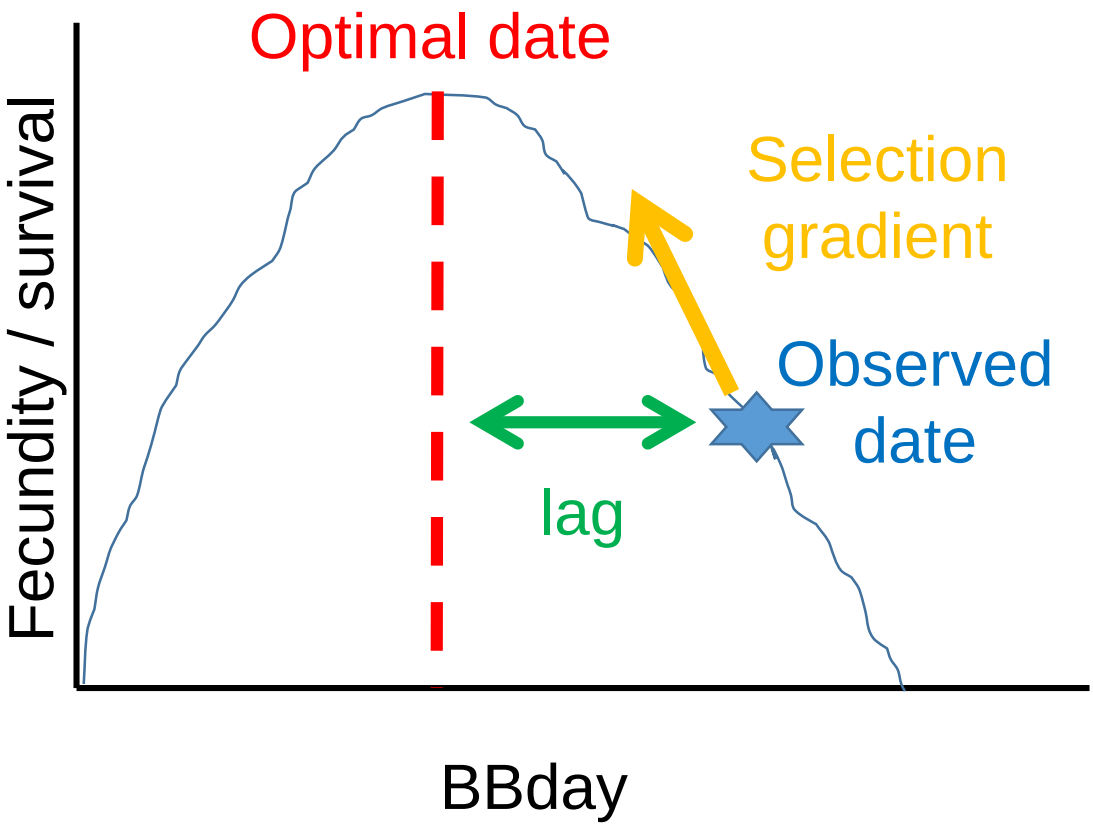


Schéma de O Ronce

What is the adaptive value of BBday ?

2) Indirect approach = **genetic clines** as the signature of local adaptation driven by BBday.

- Co-gradient versus counter-gradient
- counter-gradient ↔ maladaptive plasticity (Connover & Shultz 2003) ?

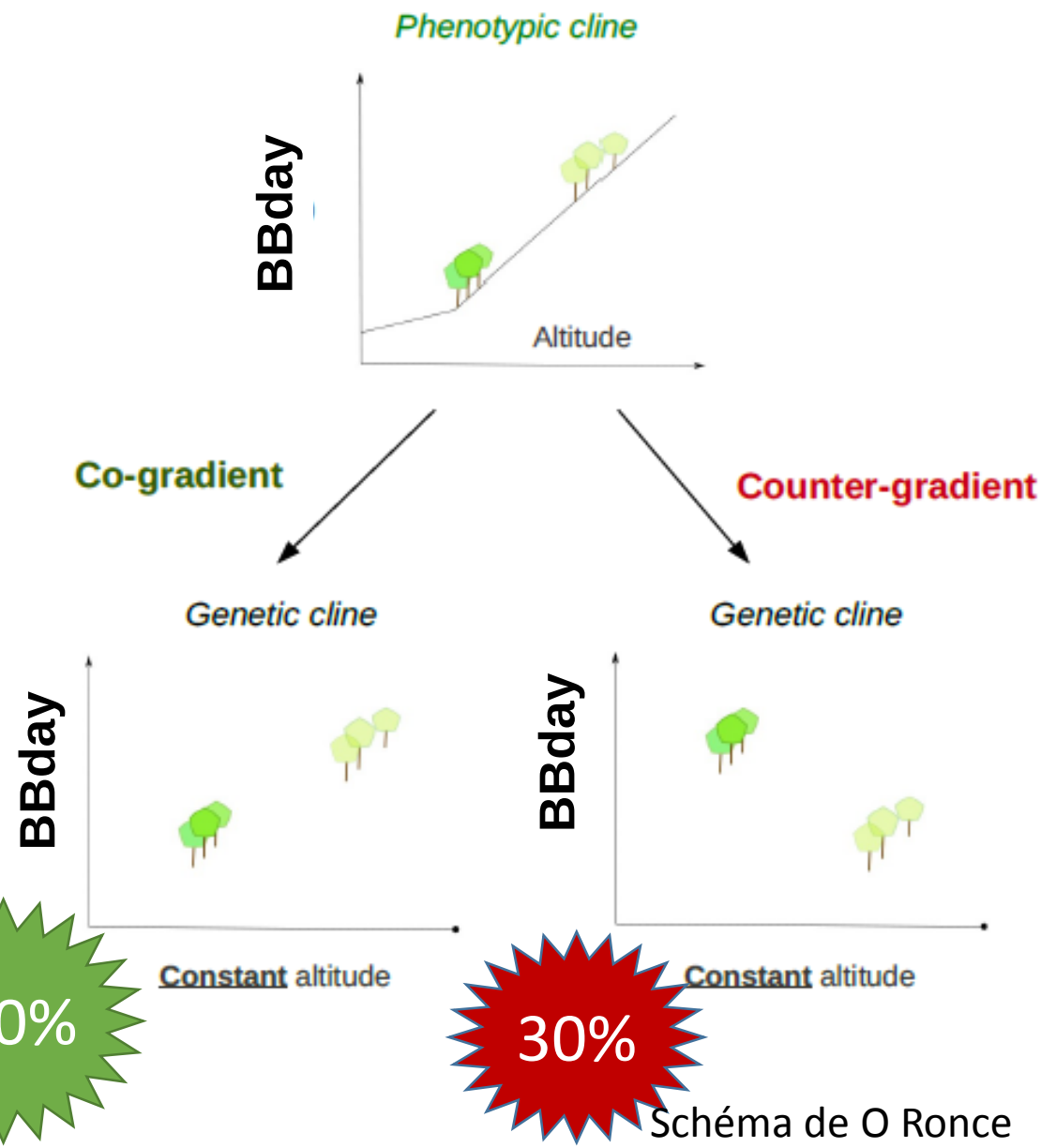
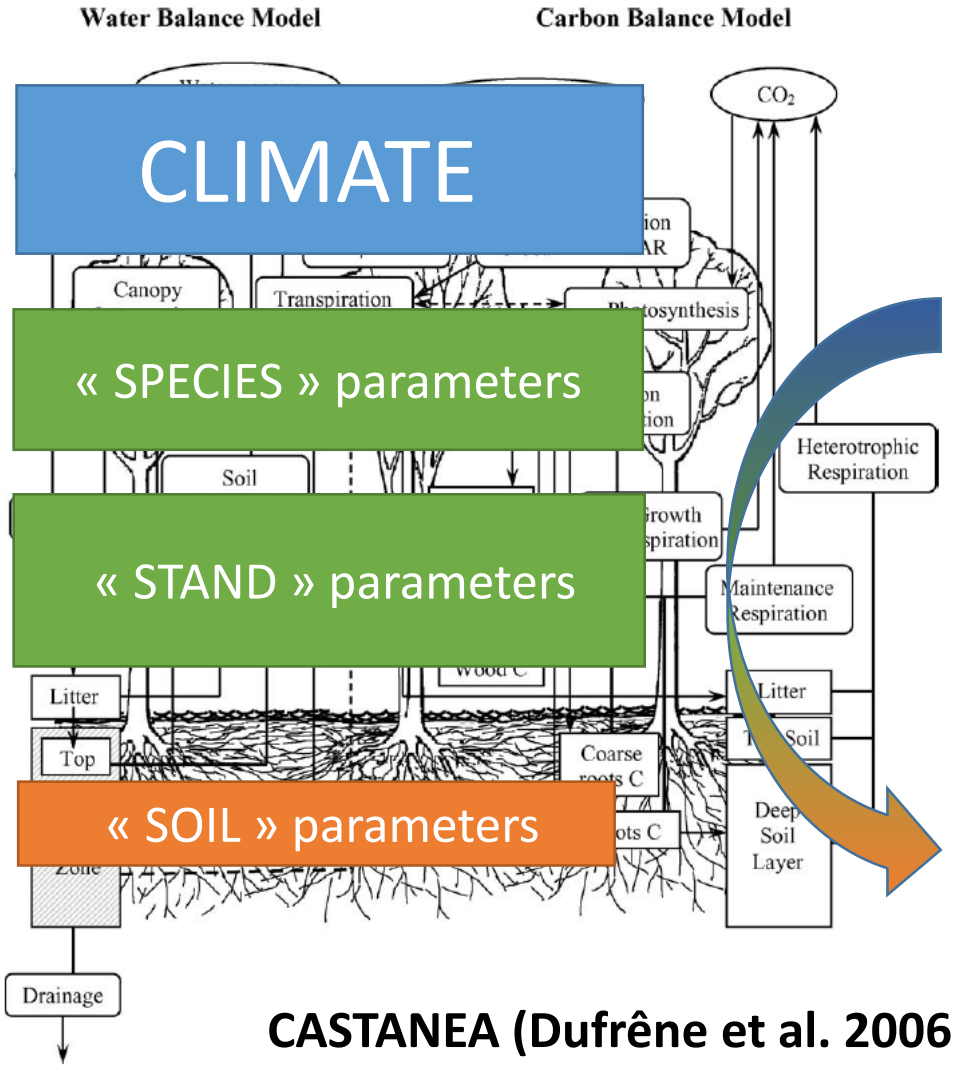


Schéma de O Ronce

What is the adaptive value of BBday ?

3) *in silico* direct approach using process-based models



CLIMATE

« SPECIES » parameters

« STAND » parameters

« SOIL » parameters

CASTANEA (Dufrêne et al. 2006)

Mean tree
- Photosynthesis
- Respiration
- C Allocation
- Budburst

FITNESS :
- Mortality through C starvation
- Mortality through hydraulic failure
- Growth
- Reproduction

Objectives of this study

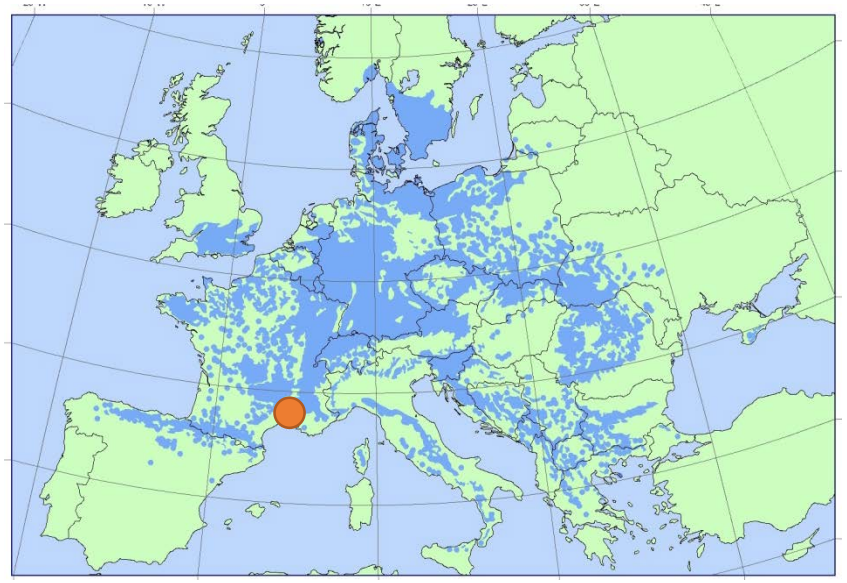
I. What is the **shape of adaptive landscapes** for BBday under current climate ?
   - Do they differ among **fitness components** ?
   - How **far** are extant populations from their optimal budburst date ?
   - How do landscapes/lags **vary** with altitude, Soil Water Content (SWC), tree age/size, species sensitivity to late frost?

II. What is the **type/intensity of selection** on BBday ? How does the selection gradients **vary** with altitude, SWC, tree age/size, species sensitivity to late frost?

III. How will **climate change** affect fitness landscapes, optimal budburst date and selection gradients ?

Studied species and site

Beech under mountain-Mediterranean climate



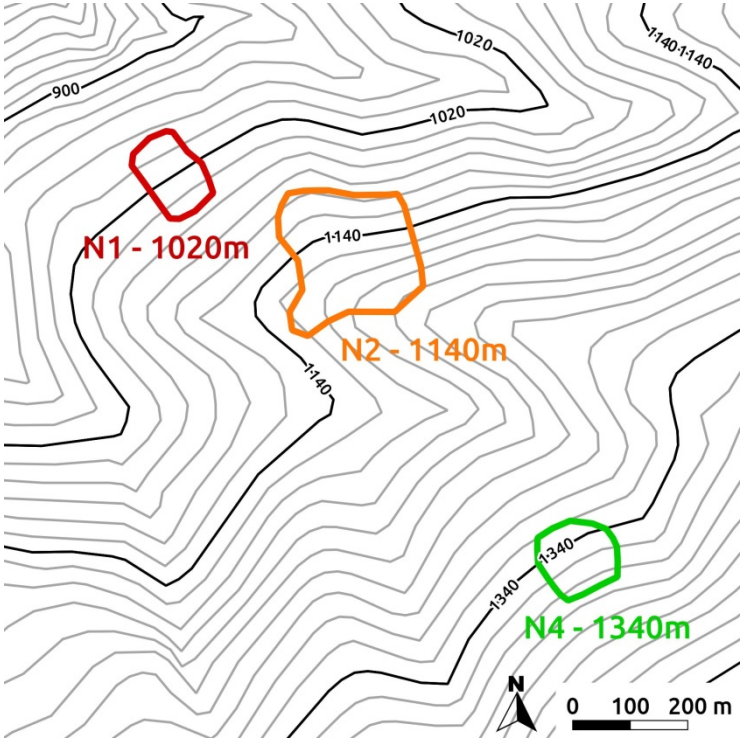
Major constraints :

High altitude : Duration of growing season

Low altitude : Water stress

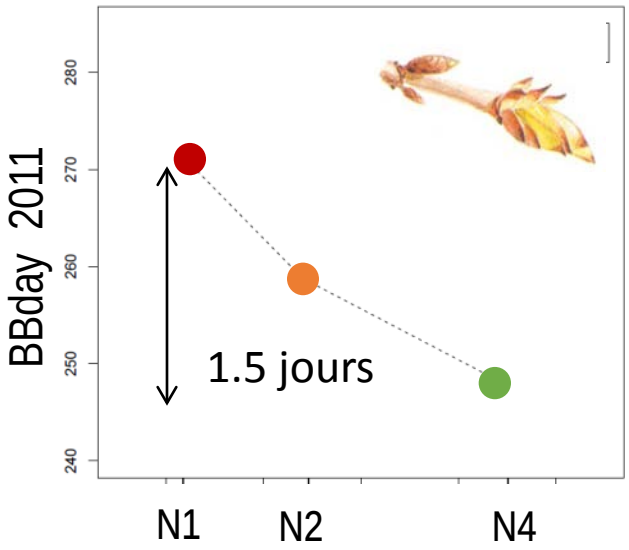
Genetic differentiation of phenological traits along an altitudinal gradient

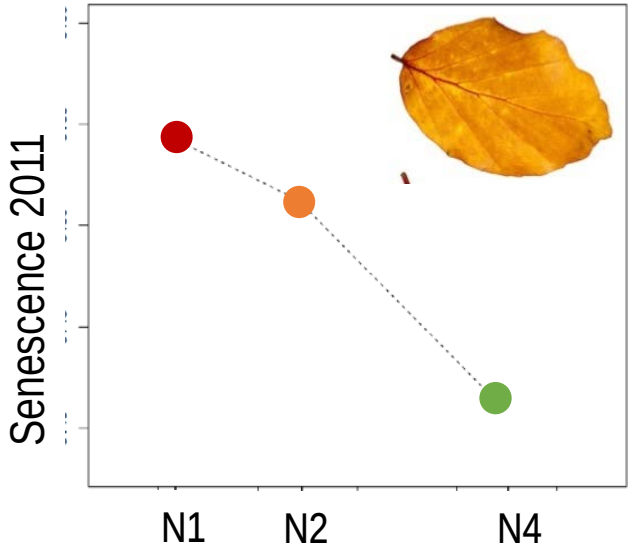
Common garden, Aix en Provence

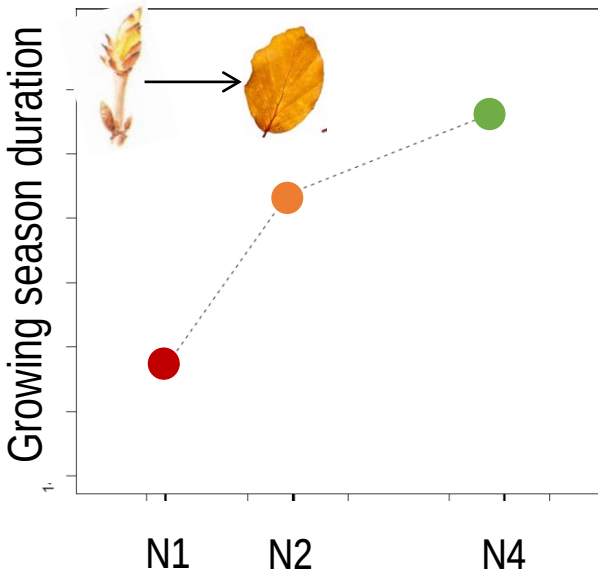


3 altitudes ×20 mother-trees ×100 offspring ~5600 seedlings

Genetic differentiation of phenological traits along an altitudinal gradient







CntG

CoG

CntG

J. Gaüzère PhD thesis (2014)

- Genetic clines on phenological traits
- Due to selection, not to genetic drift (Ovaskainen et al. 2011)

Methods

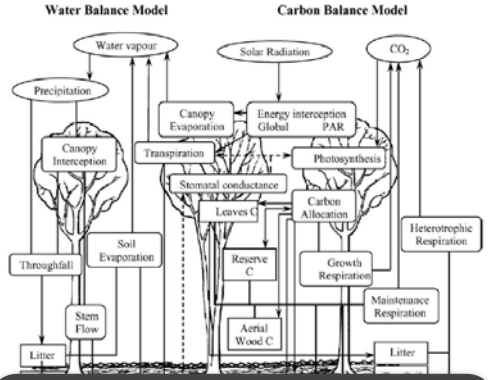
Module CastaneaOnly

« SPECIES » prm

« TREE » prm

« SOIL » prm

Climate



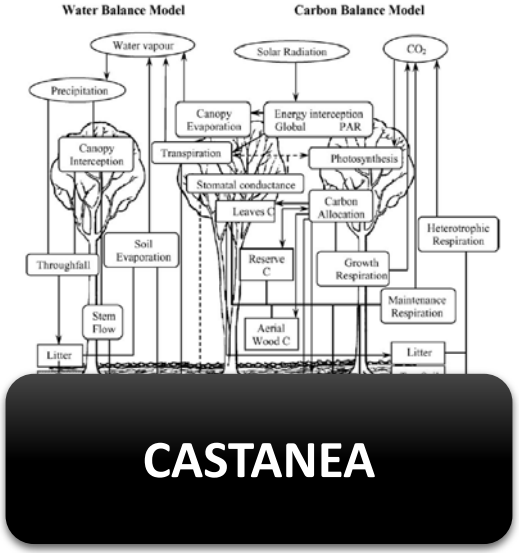
Process-based "library" CASTANEA

FITNESS

BBday

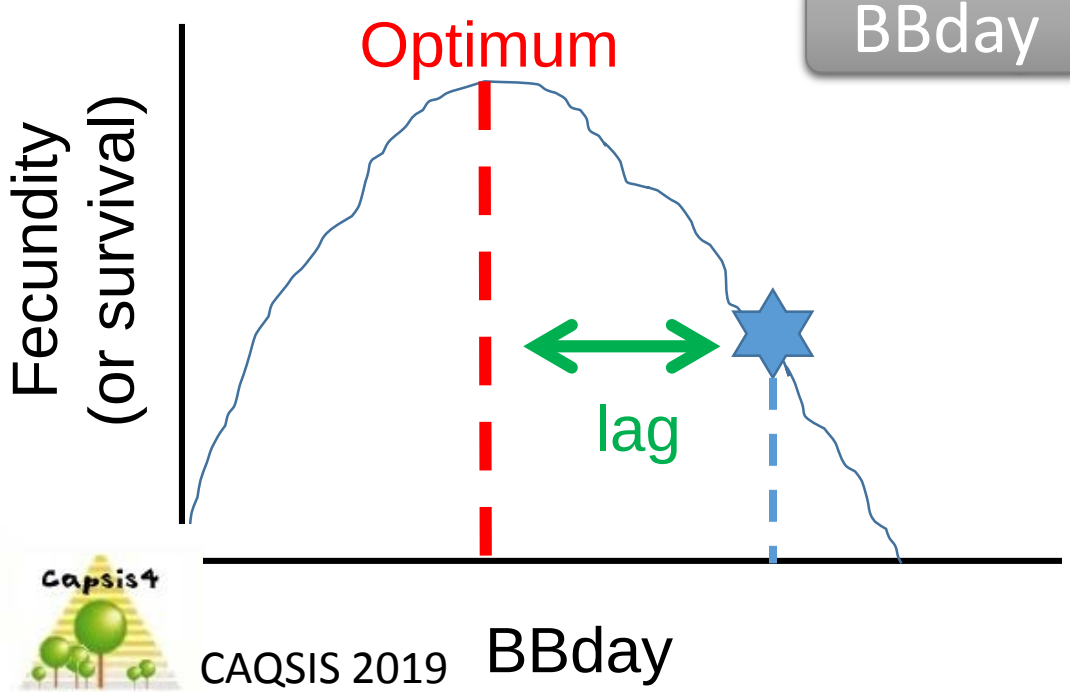
CAQSIS 2019

Methods



BBday

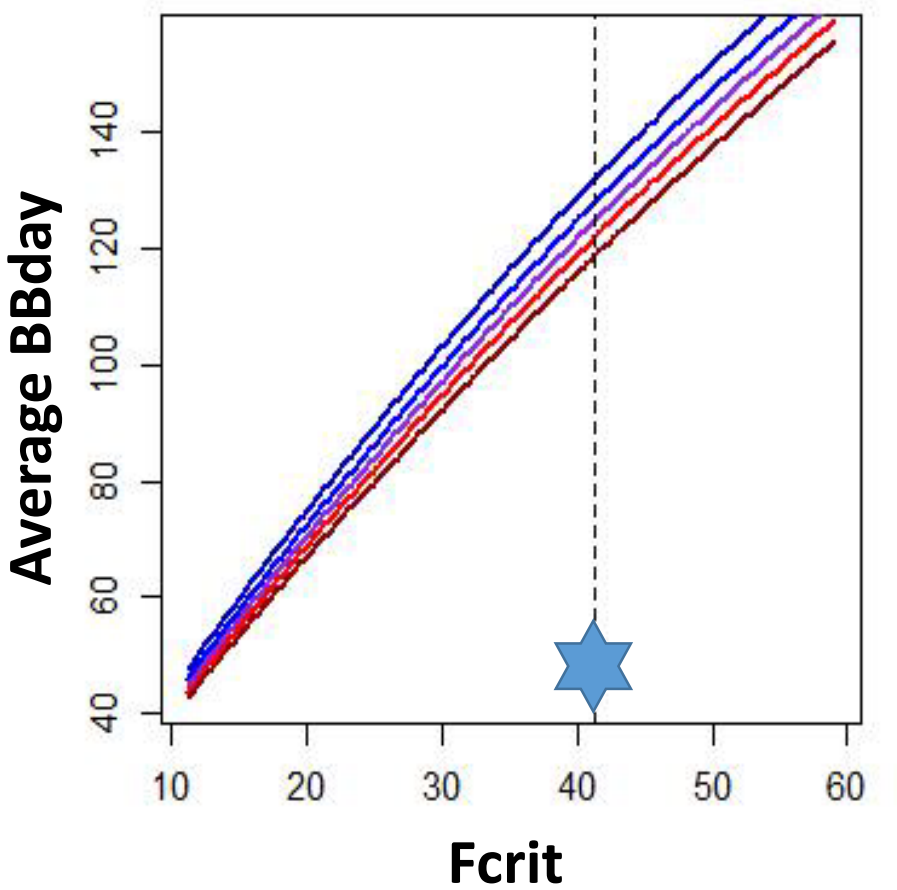
Adaptive landscape

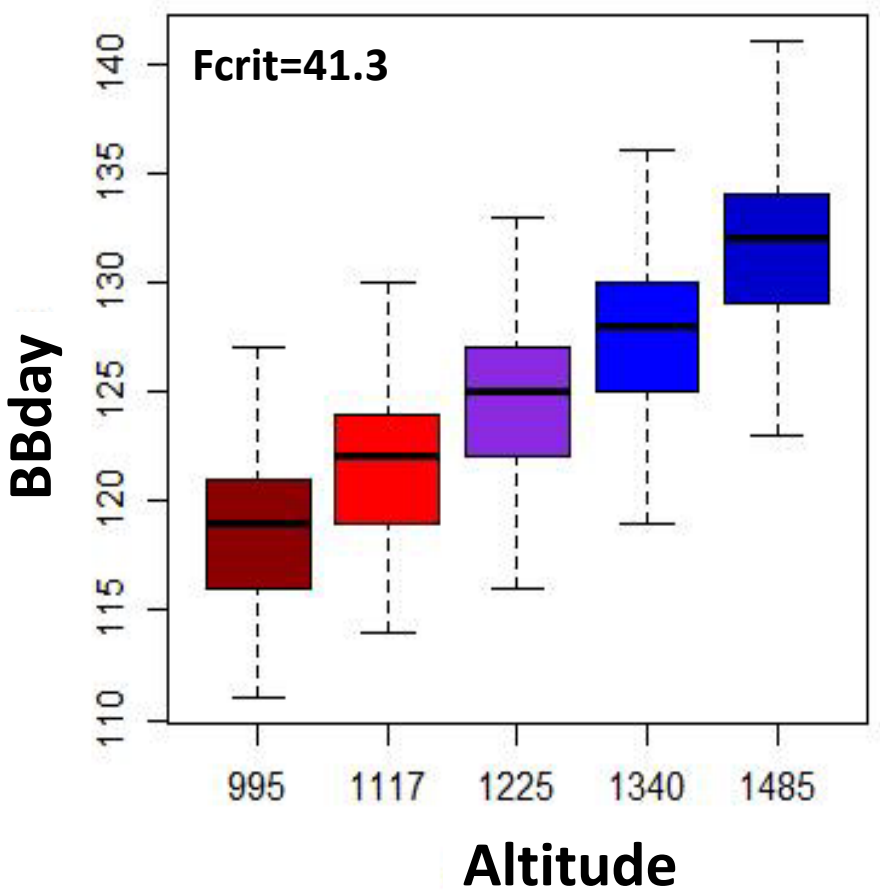


Phenological model: UNICHILL
(<Phenofit)
Variable parameter= sum of forcing temperatures (Fcrit)

Range of F_{crit} = [11 – 60] → computation of mean(Bbday) over x years

«realised» Bbday = BBday(altitude, Fcrit=41.3)



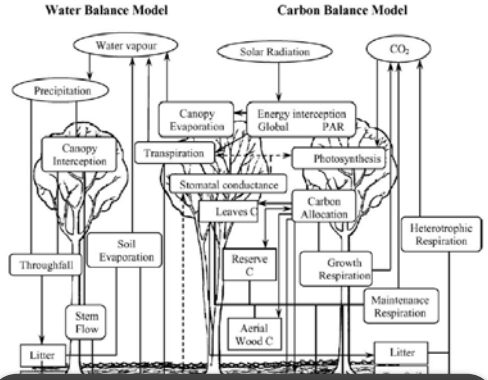


Average realized BBday : between the 29th of April [N1] to the 11th of May [N5] → 12-days lag

Among-year variation :

- [N1] between the 21th of April to the 7th of May → 17-days range
- [N5] between the 3d of May to the 21th of May → 19-days range

Methods



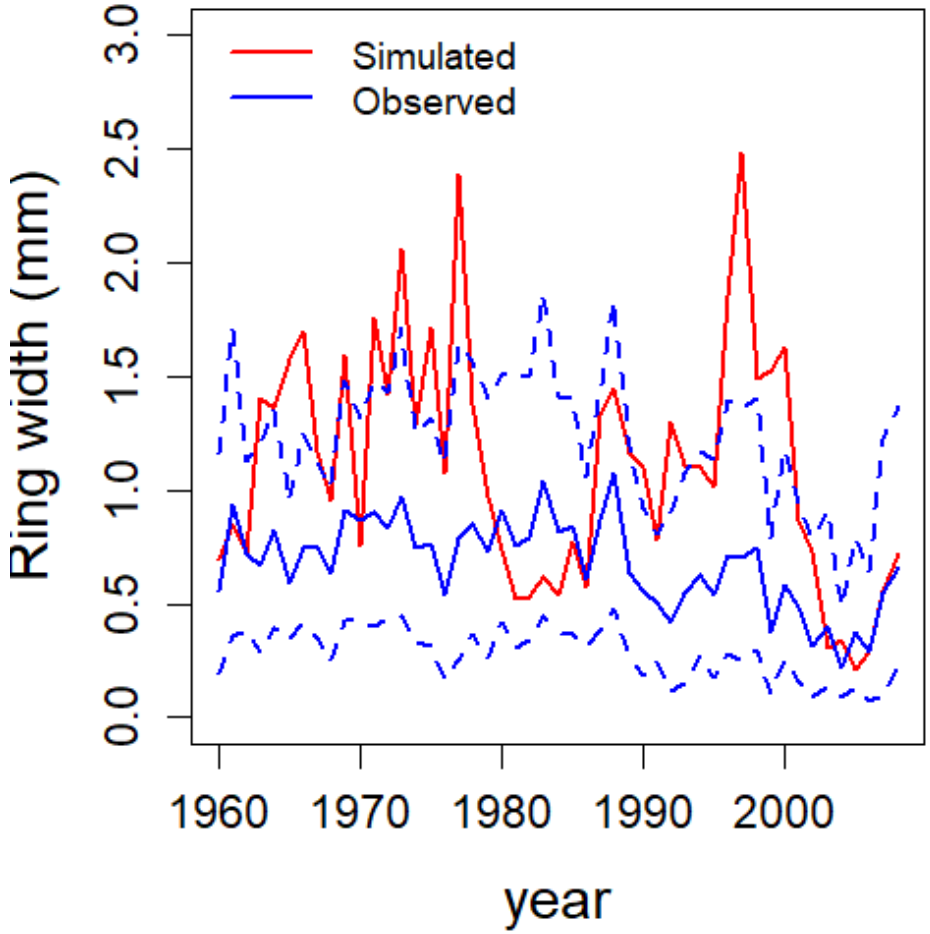
CASTANEA → **FITNESS**

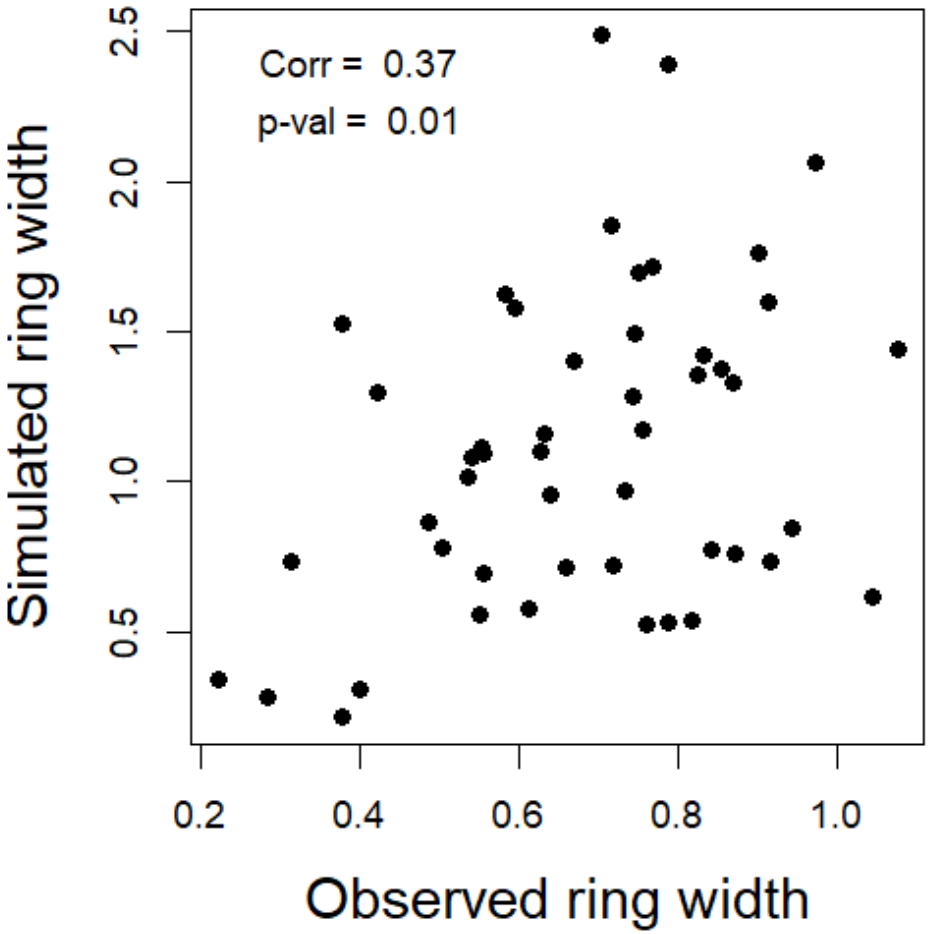
Reproductive output : sum of seeds produced [SumSeed]

Growth/Biomass : sum of wood ring area [SumWoodArea]

Safety margin from carbon starvation : minimal level of carbon storage [MinStorage]

Risk of hydraulic failure : max percentage of loss of conductance [maxPLC]





Trend to overestimate ring width

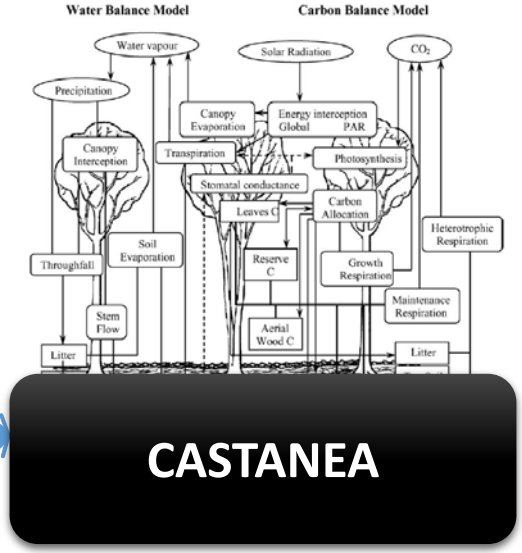
Methods

« SPECIES » prm

« TREE » prm

« SOIL » prm

Climate



CASTANEA

Species parameter related to frost hardiness [IFROST]

- Strong : LAI=LAImax ∀ $N_{lateFrost}$ [IFROST=0]
- Weak : LAI=LAImax- b $N_{lateFrost}$ [IFROST=1]
- **In between** (2d flush) LAI=LAImax- b $N_{lateFrost}$ +$LAI_{reflush}$ [IFROST=3]

AGE: {age, diameter, height} at simulation initiation (60, **90**, 110)

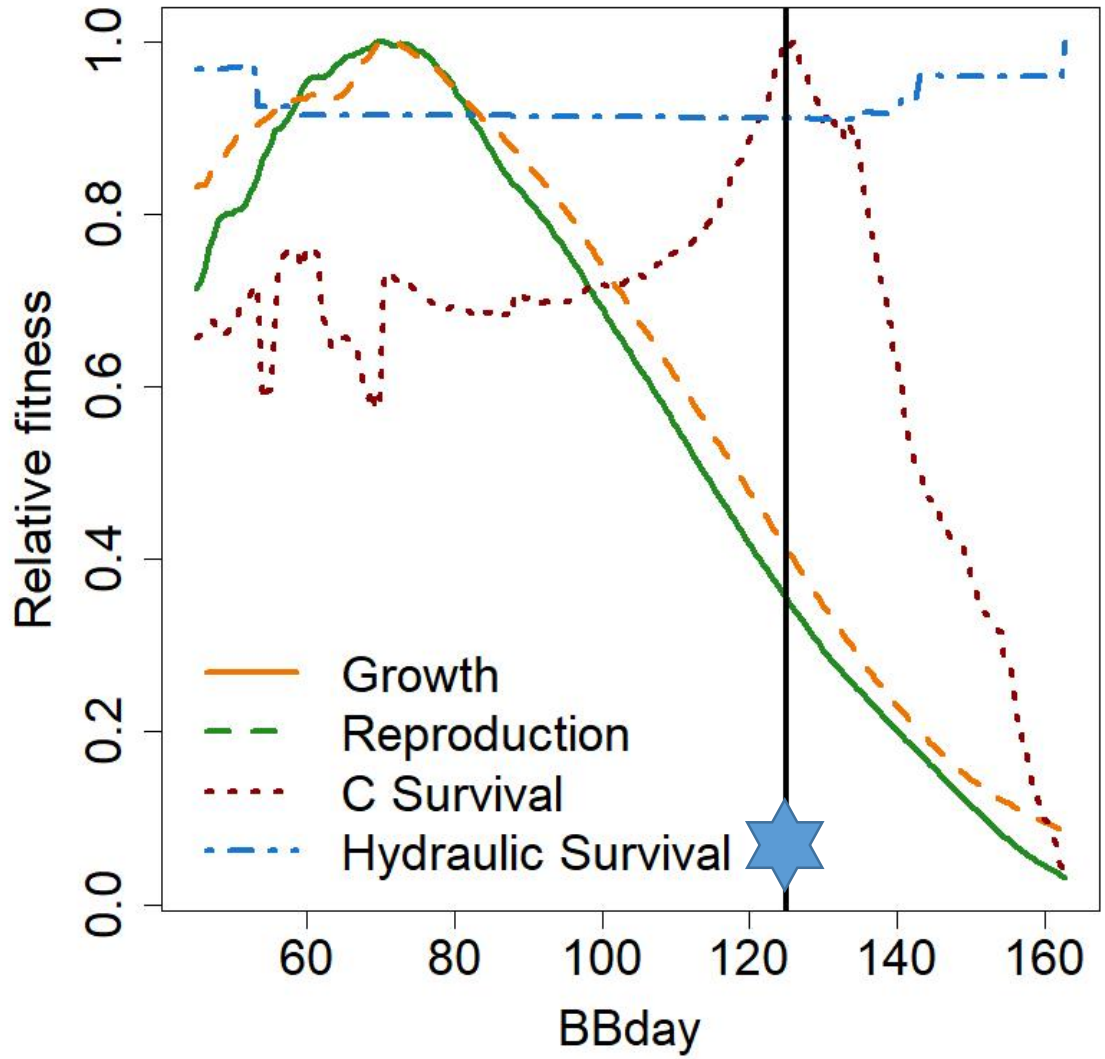
Soil water content (SWC) : 4 levels (45, **60**, 100 et 145 mm)

Altitude : 5 plots, from 995 m to 1485 m (N1 to N5)

Comparison btw **current climate** (**1959-2015**) & **future climate** (2045-2099, scenario RCP4.5 et RCP8.5)

I. Adaptive landscape for the whole population, all fitness components

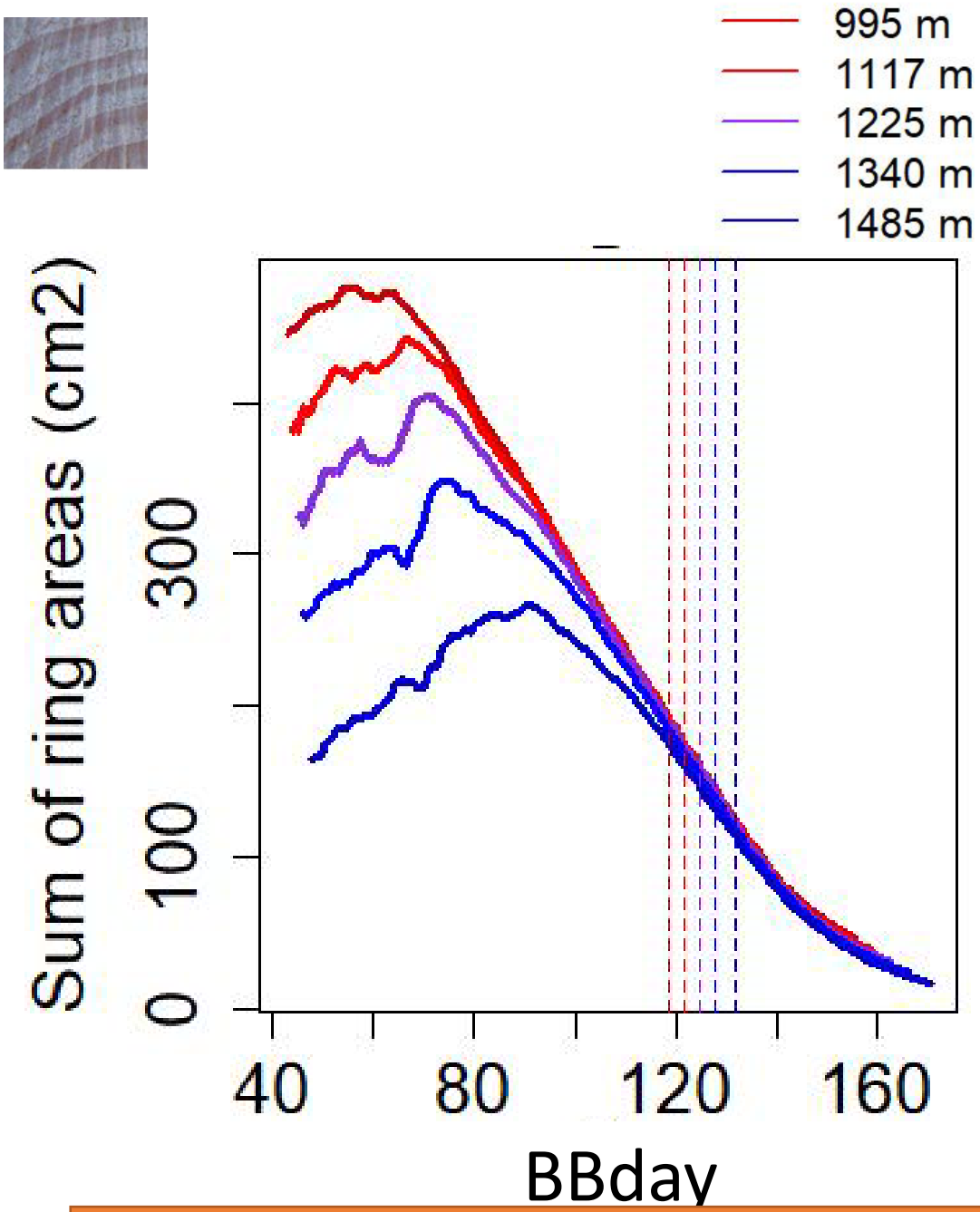
- BBday optima exist for the different fitness components
- BBday values maximizing growth and reproduction differ from those maximizing survival



IFROST3; Age : 90 ; SWC= 60 mm; Current climate

I. Altitude effect on adaptive landscapes

- Growth increases towards lower altitudes
- Optimal BBday advances with decreasing altitude
- Realized BBday advances with decreasing altitude
- Budburst is always too late as compared to the optimum

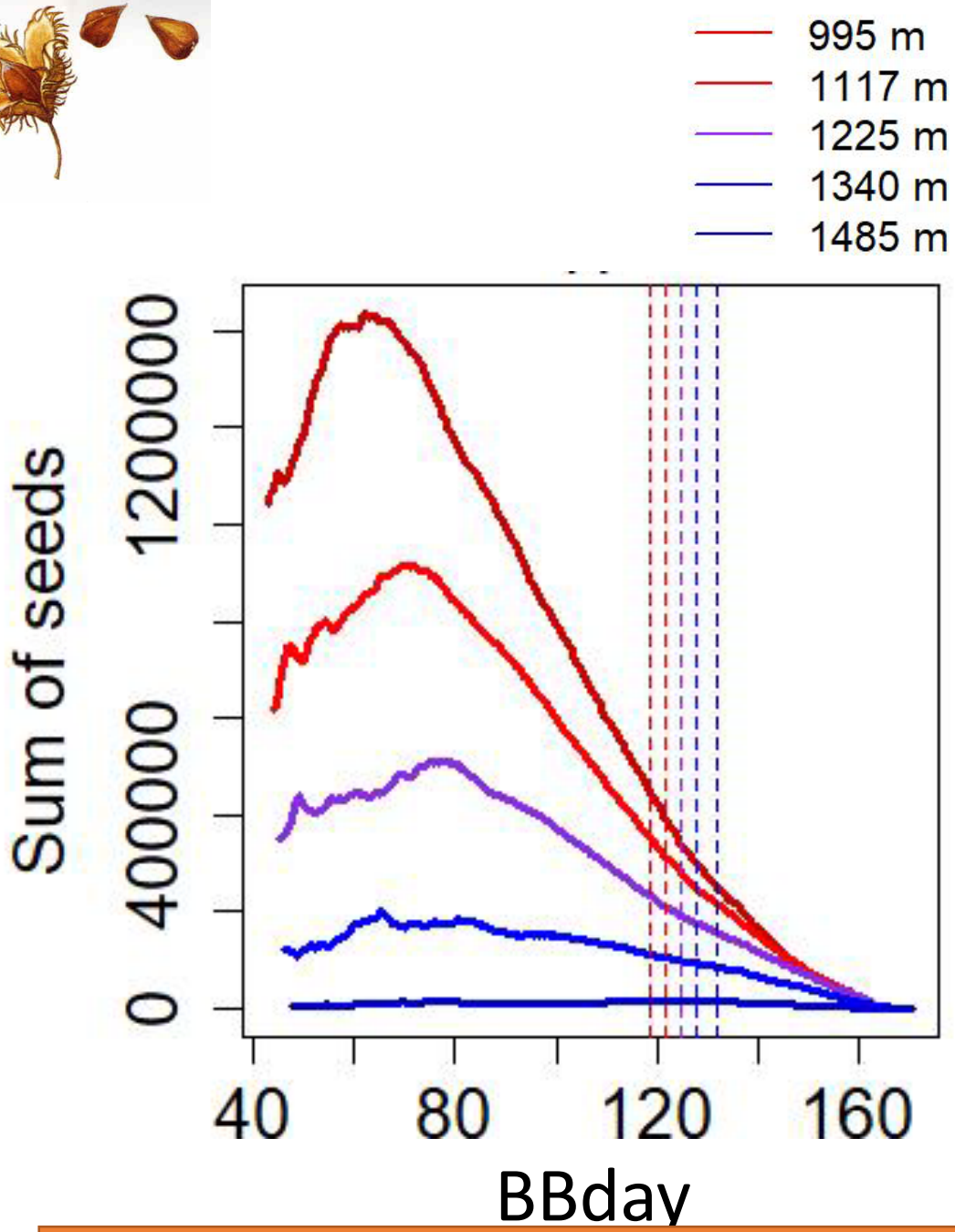


IFROST3; Age : 90 ; SWC= 60 mm; Current climate

I. Altitude eff
on ad
scapes

Same shape

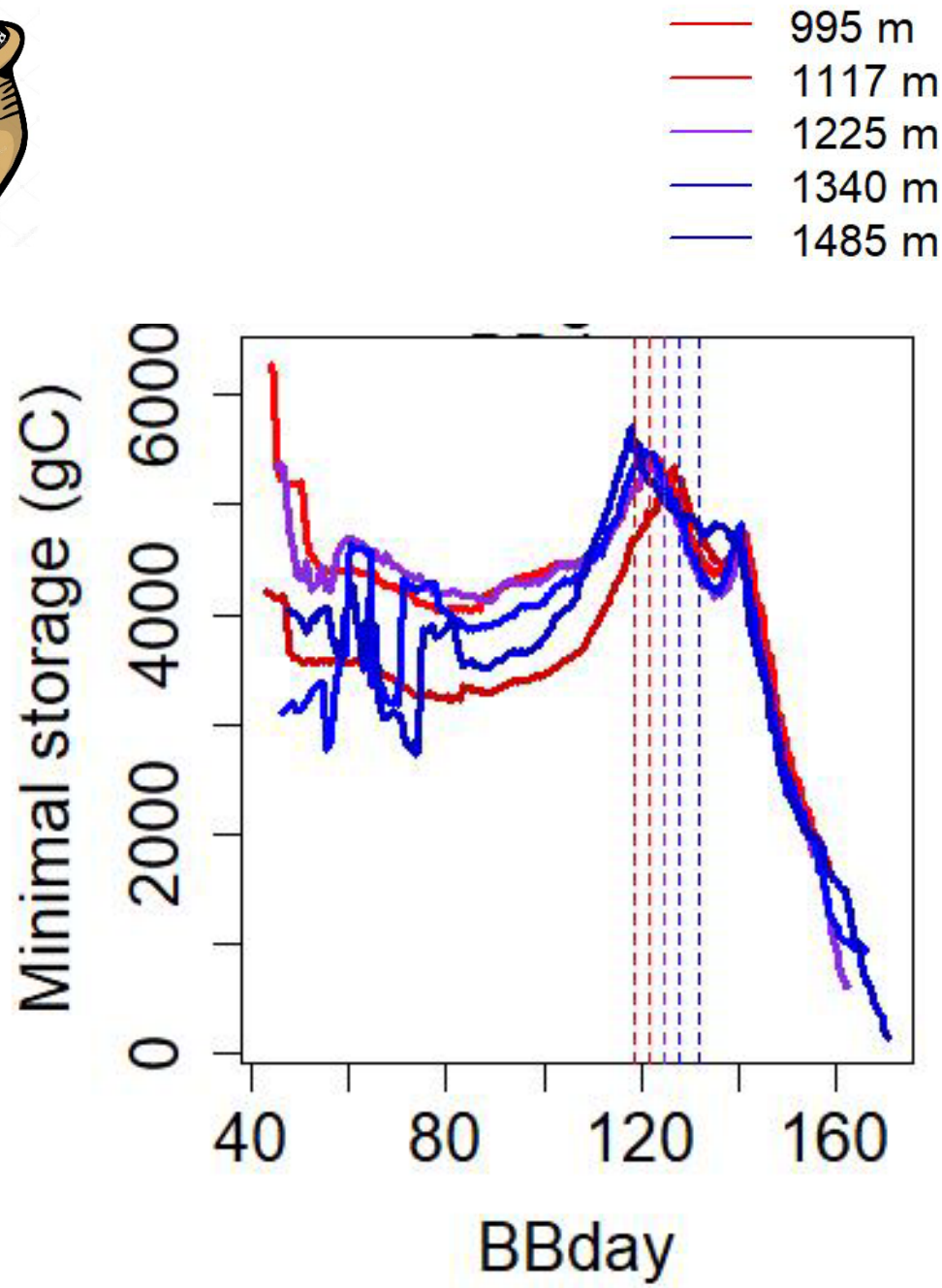
- Reproductive output increases at low altitudes
- Optimal BBday advances with decreasing altitude
- Realized BBday advances with decreasing altitude
- Budburst is always too late as compared to the optimum



IFROST3; Age : 90 ; SWC= 60 mm; Current climate

I. Altitude effect on adaptive landscapes

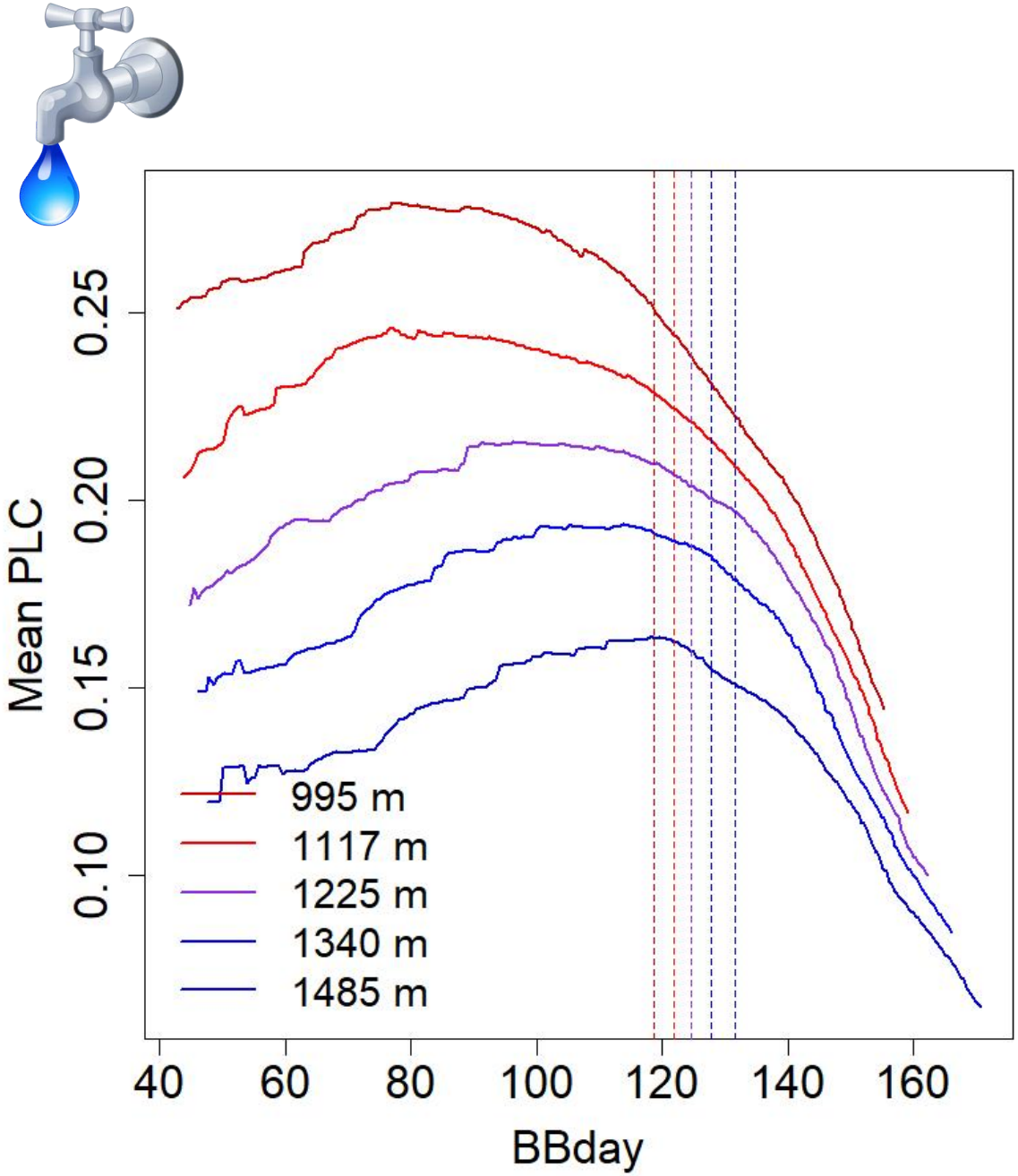
- Two peaks, with early budburst limited by late frosts
- Realized budburst is slightly too late compared to its optimum at high altitude
- Realized budburst is slightly too early compared to its optimum at low altitude



IFROST3; Age : 90 ; SWC= 60 mm; Current climate

I. Altitude effect on adaptive landscapes

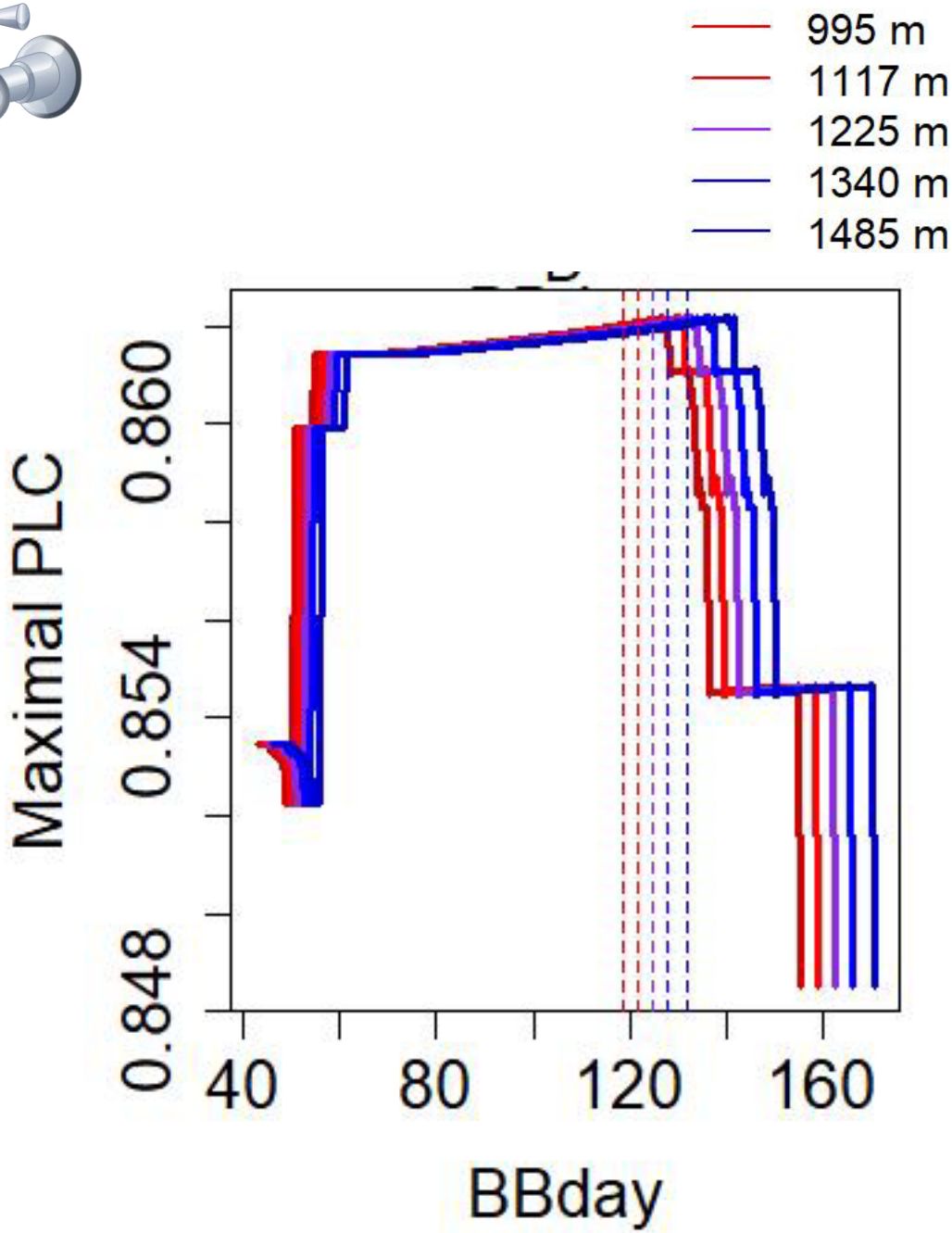
- Weak mean PLC as compared to lethal values (88%)
- PLC increases as altitude decreases



IFROST3; Age : 90 ; SWC= 60 mm; Current climate

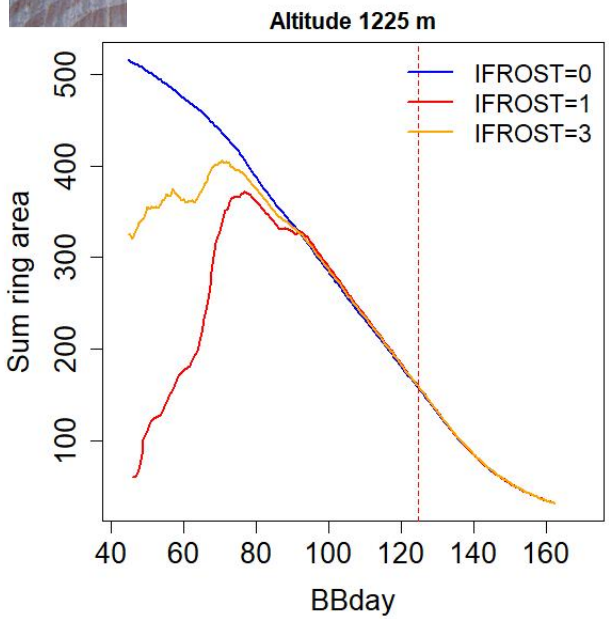
I. Altitude effect on adaptive landscapes

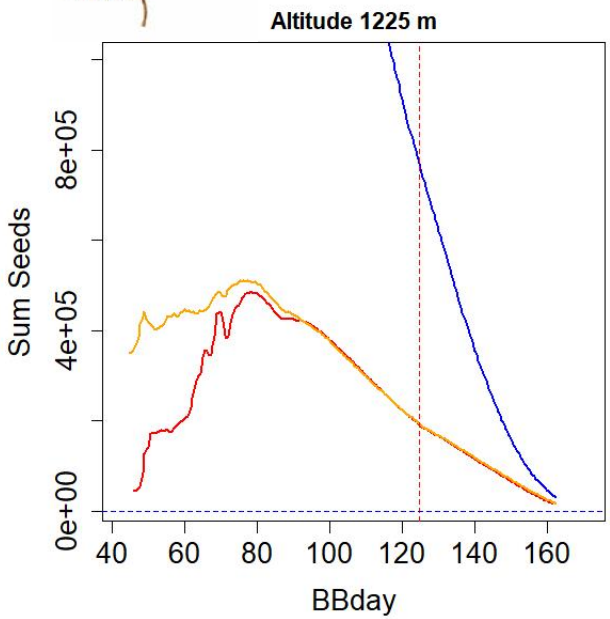
- maxPLC get closer from lethal values (88%)
- Later budburst increases the safety margin to hydraulic failure

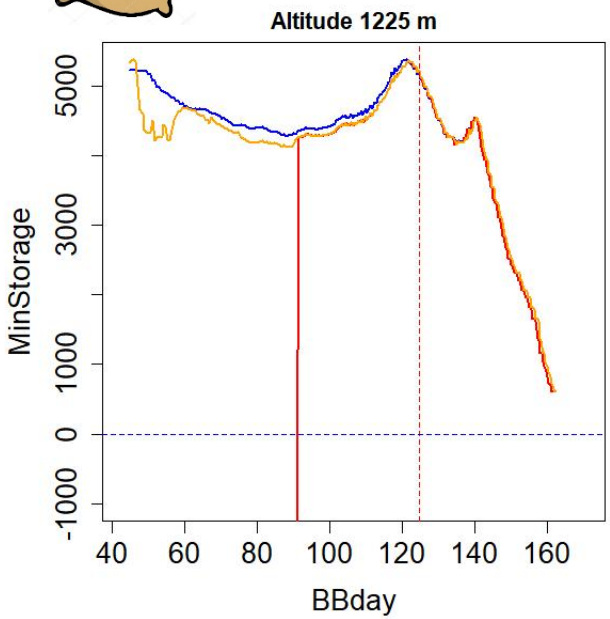


IFROST3; Age : 90 ; SWC= 60 mm; Current climate

I. Effect of frost hardiness on adaptive landscapes







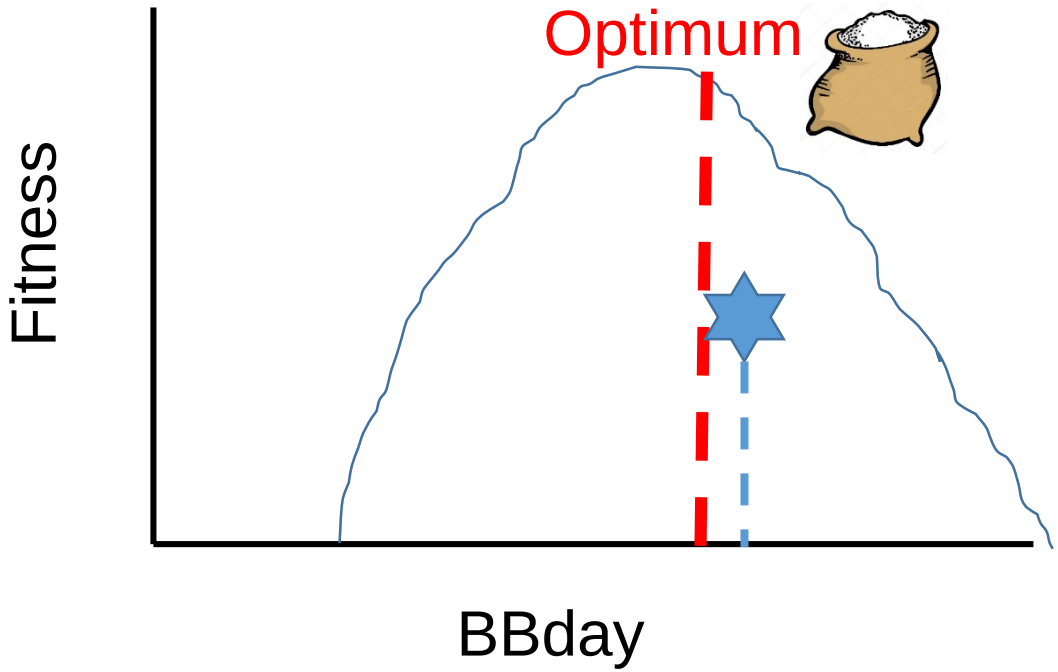
Late frosts are responsible for the decrease of fitness for very early budburst

CAQSIS 2019

Age : 90 ; SWC= 60 mm; Current climate

Conclusions I. : shape of adaptive landscapes

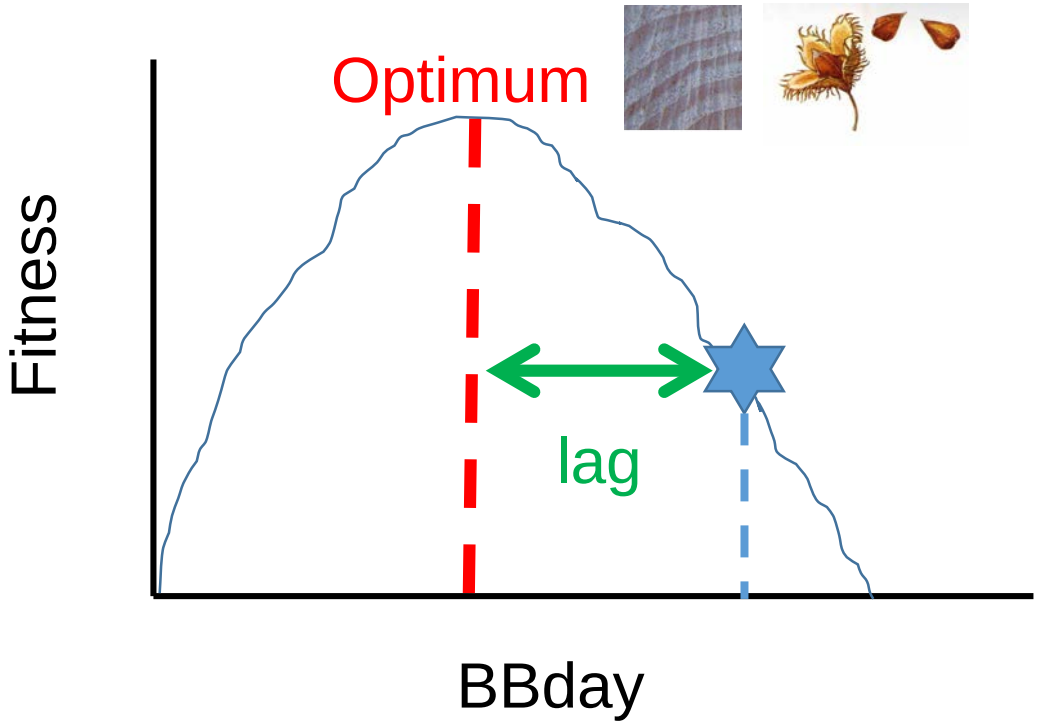
The shape of adaptive landscape vary among fitness components



- The realized BBday is
  - Close to the optimum for minimal reserve

Conclusions I. : shape of adaptive landscapes

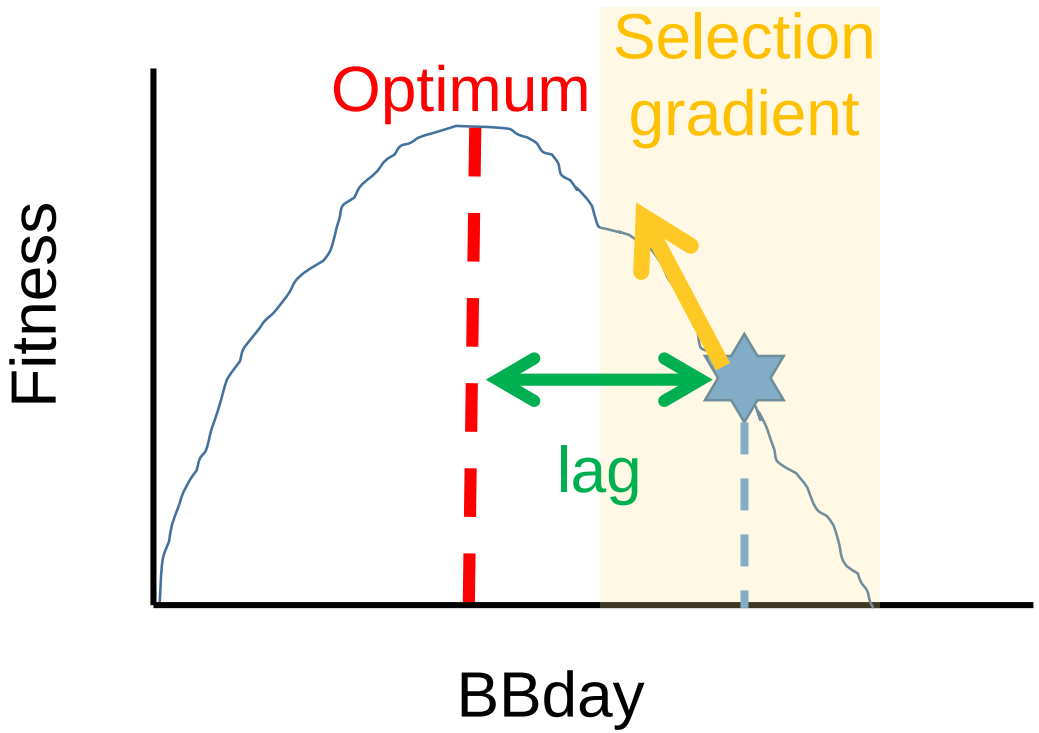
The shape of adaptive landscape vary among fitness components



- The realized BBday is
  - Close to the optimum for minimal reserve
  - Later than the optima for growth + reproductive output
  - Earlier than the optimum for maximum PLC

The shape of landscapes depend on frost hardiness, but is similar across SWC and age.

Part II : Selection gradients on BBday



Range of BBday defined by the variance in BBday observed within natural populations (σ^2_{BBday} =5)
Resampling of 100 individuals within $\mathcal{N}(\mu_{BBday}, \sigma^2_{BBday})$

Estimation of direct (β) and quadratic (γ) gradients (Lande&Arnold 1983) :

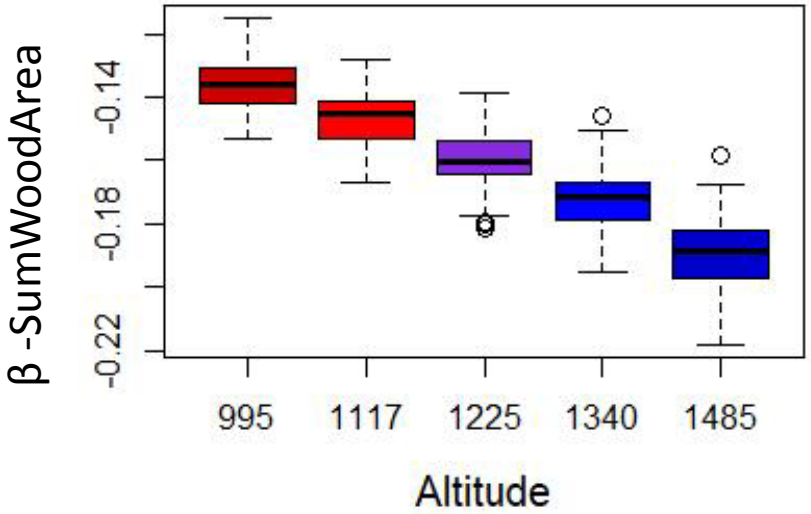
$$RelatFitness = \beta\ BBday_{sd}$$

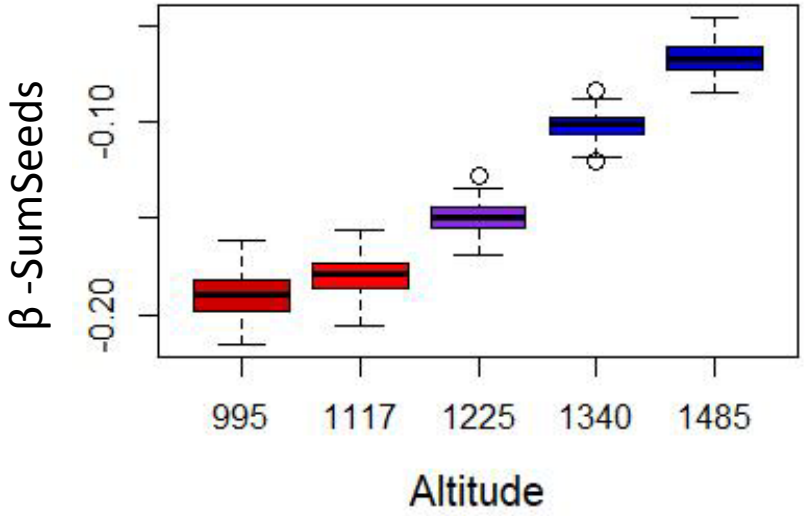
$$RelatFitness = \beta_2\ BBday_{sd} + 0.5\ \gamma\ Bbday_{sd}^2$$

with $RelatFitness = Fitness / \mu_{fitness}$ and $BBday_{sd} = BBday / \sigma_{BBday}$

II. Selection gradients on growth and reproductive output

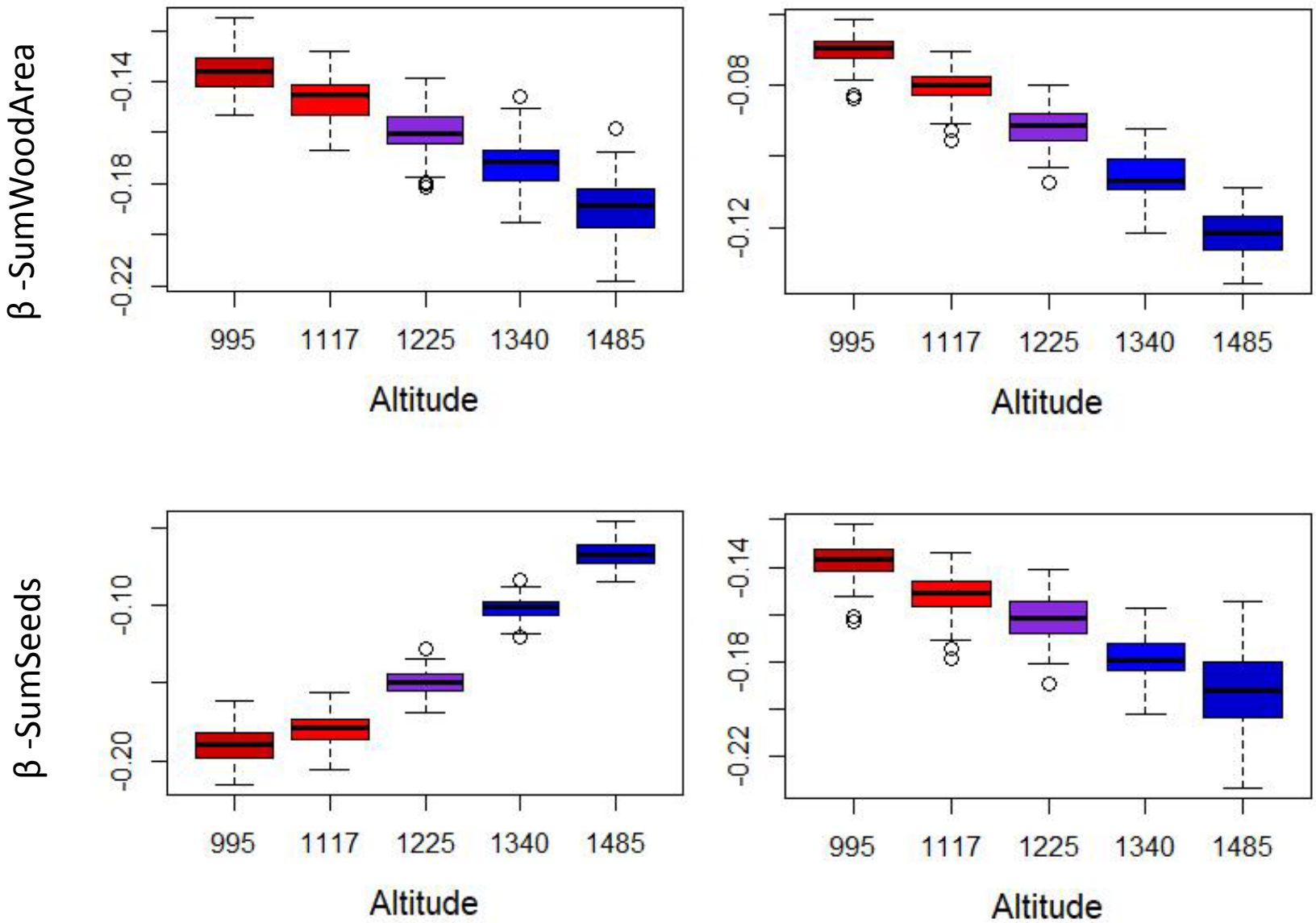
- Negative β-values ↔ selection towards early budburst
- Selection intensity increases with altitude for growth, reverse for reproductive output ?





IFROST3; Age : 90 ; SWC= 60 mm; Current climate

II. Selection gradients on growth and reproductive output

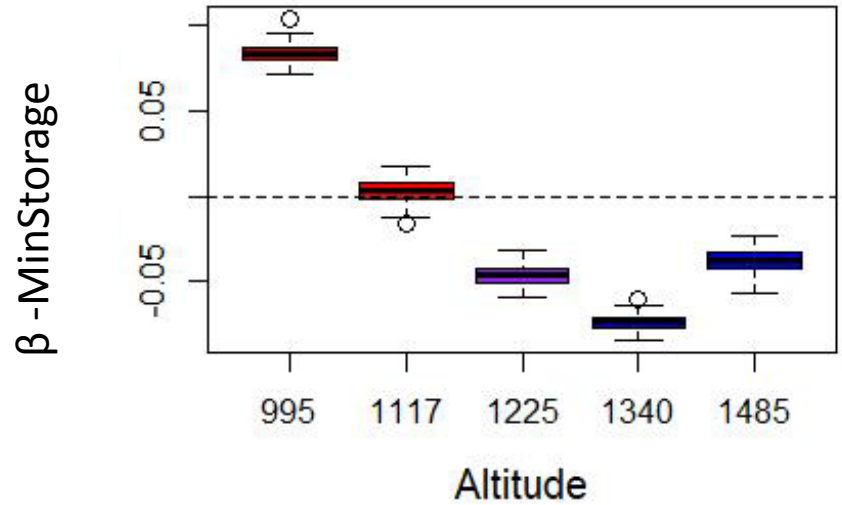


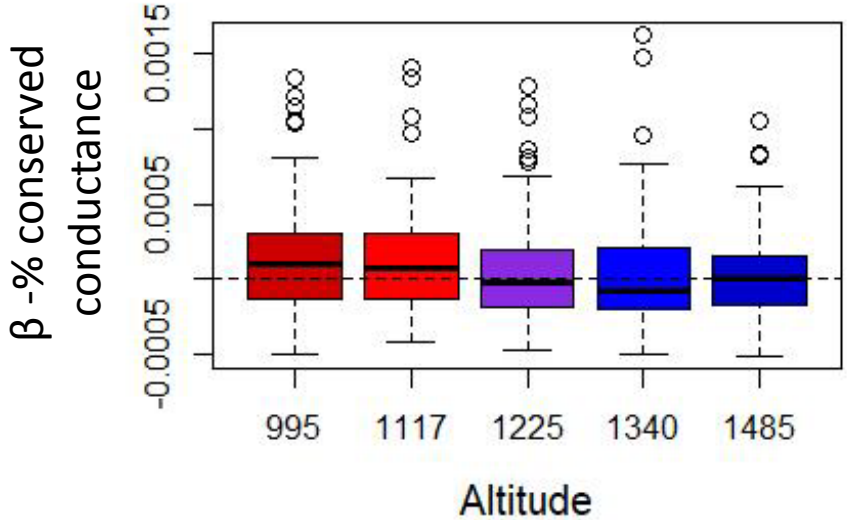
SWC= 60 mm

SWC= 145 mm

II. Selection gradients on survival components

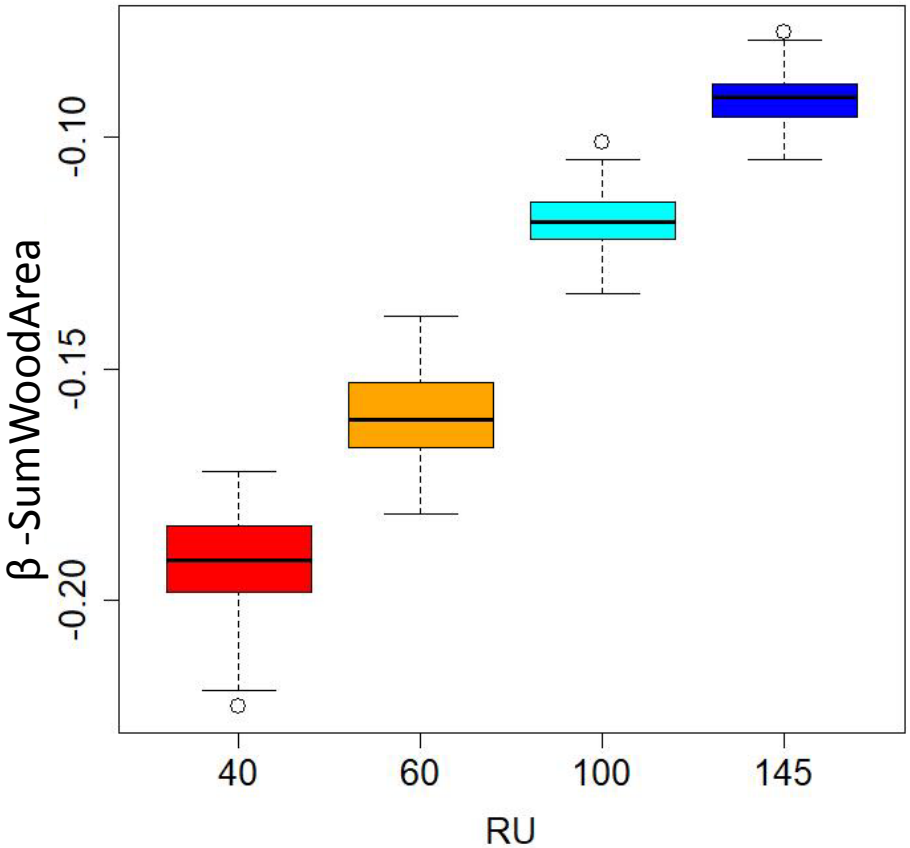
- Positive β-values ↔ selection towards late budburst
- Weaker β-values



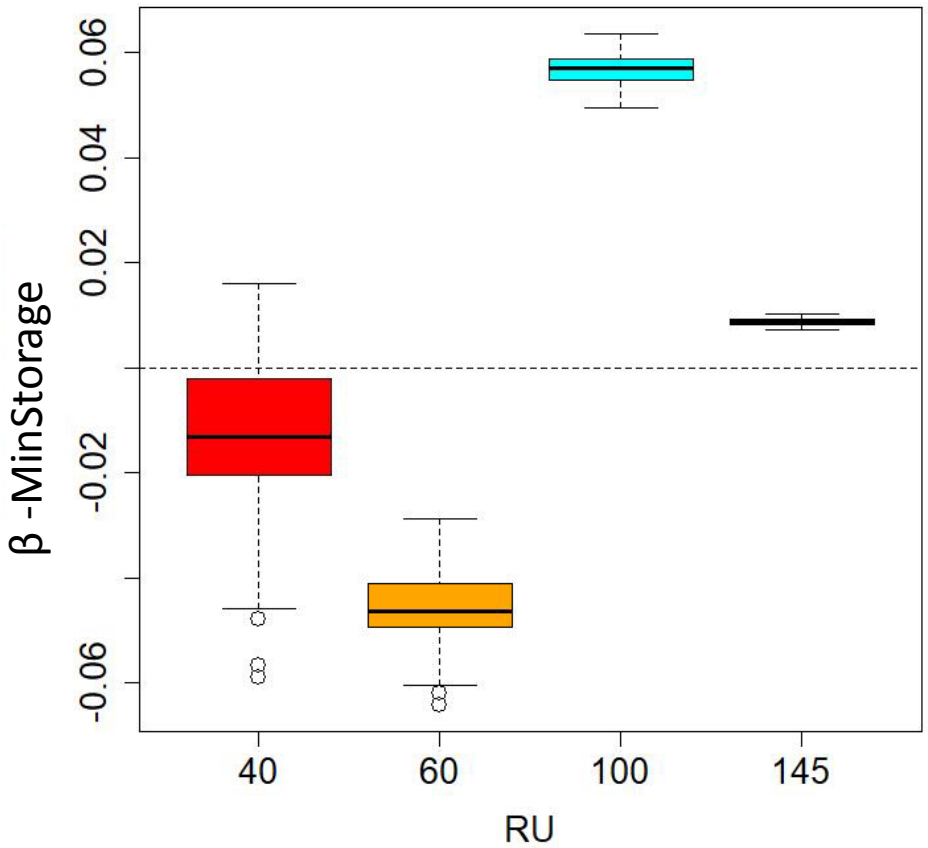


IFROST3; Age : 90 ; SWC= 60 mm; Current climate

II. Selection gradients vary with SWC



Selection is more intense at low SWC

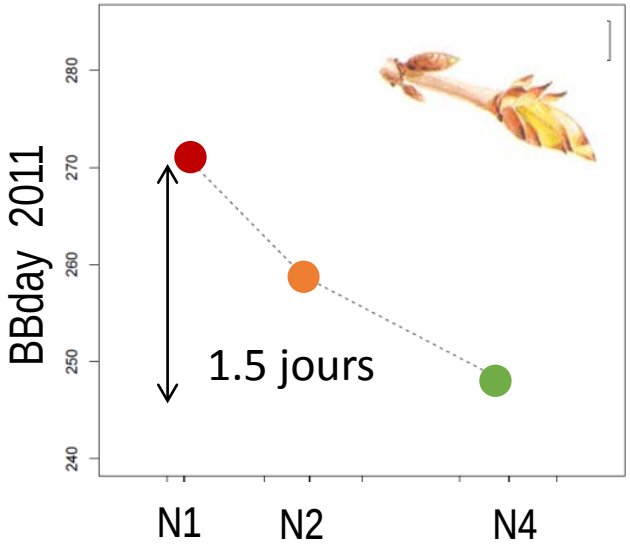


Selection change direction depending on SWC

IFROST3; Age : 90 ; Altitude 1225m; Current climate

Conclusions II. : selection gradients

- Experimental direct estimates of selection gradient on BBday : selection towards early budburst , intensity higher at plot N4 than N1
- Consistent with our in silico estimates of selection gradient on growth and reproductive output
- Selection at early life-stage may be driven by survival, and then at late life stage by other fitness components ?



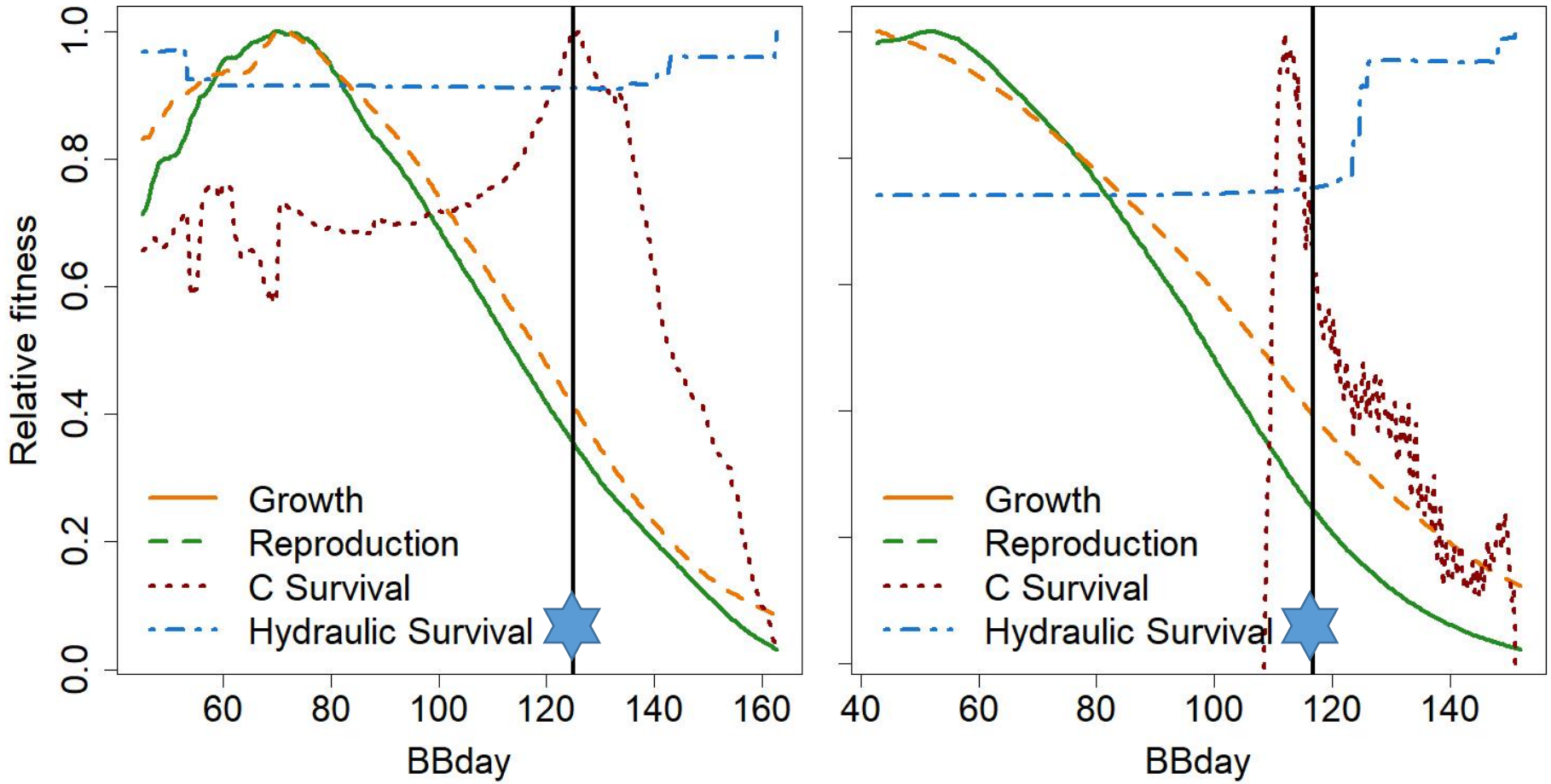
CntG

Response to selection is less constrained at high elevation
→ more rapid/efficient

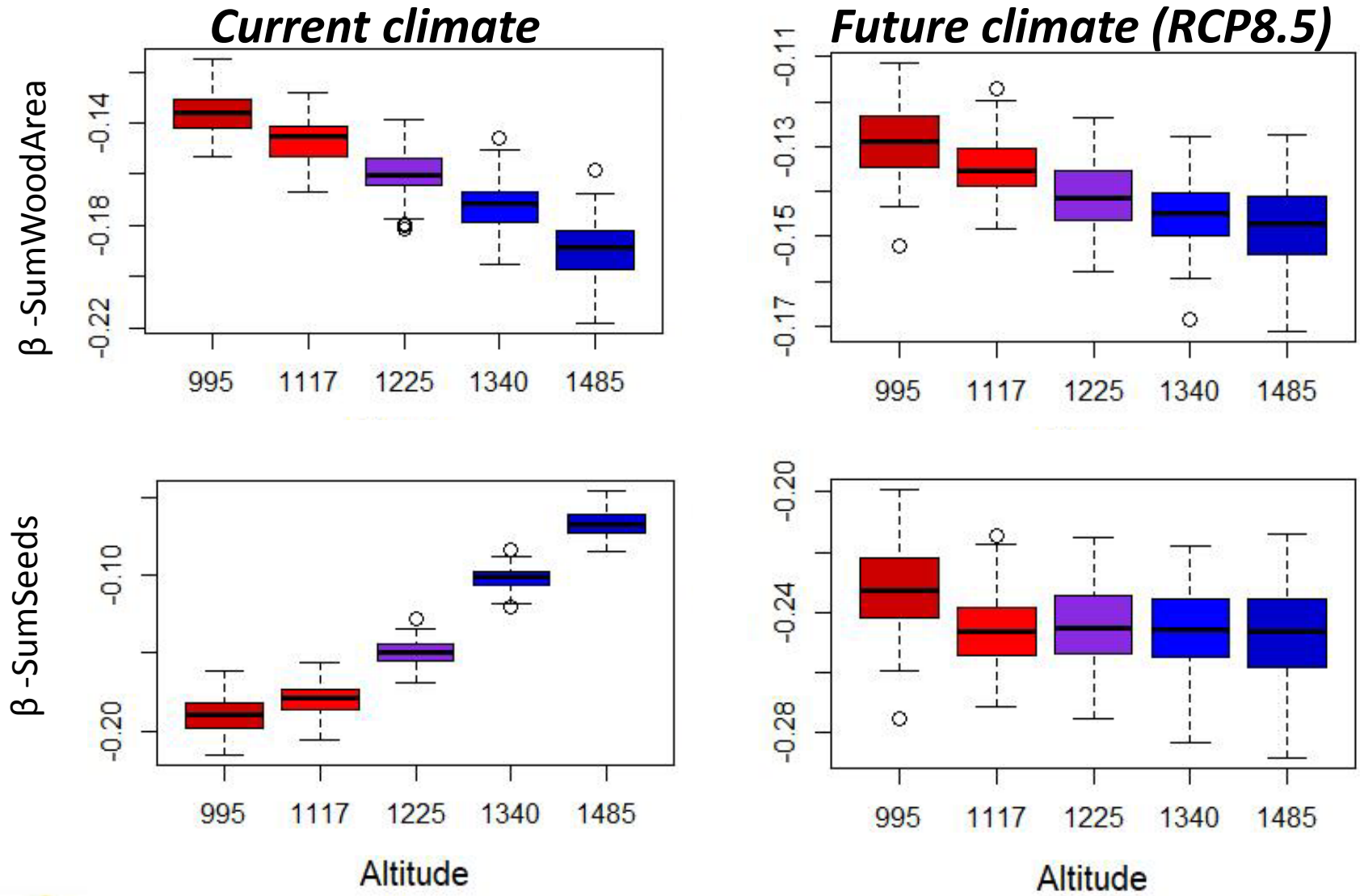
Part III : Effect of climate change

Adaptive landscape

Current climate ***Future climate (RCP8.5)***



III. Selection gradients on growth and reproductive output



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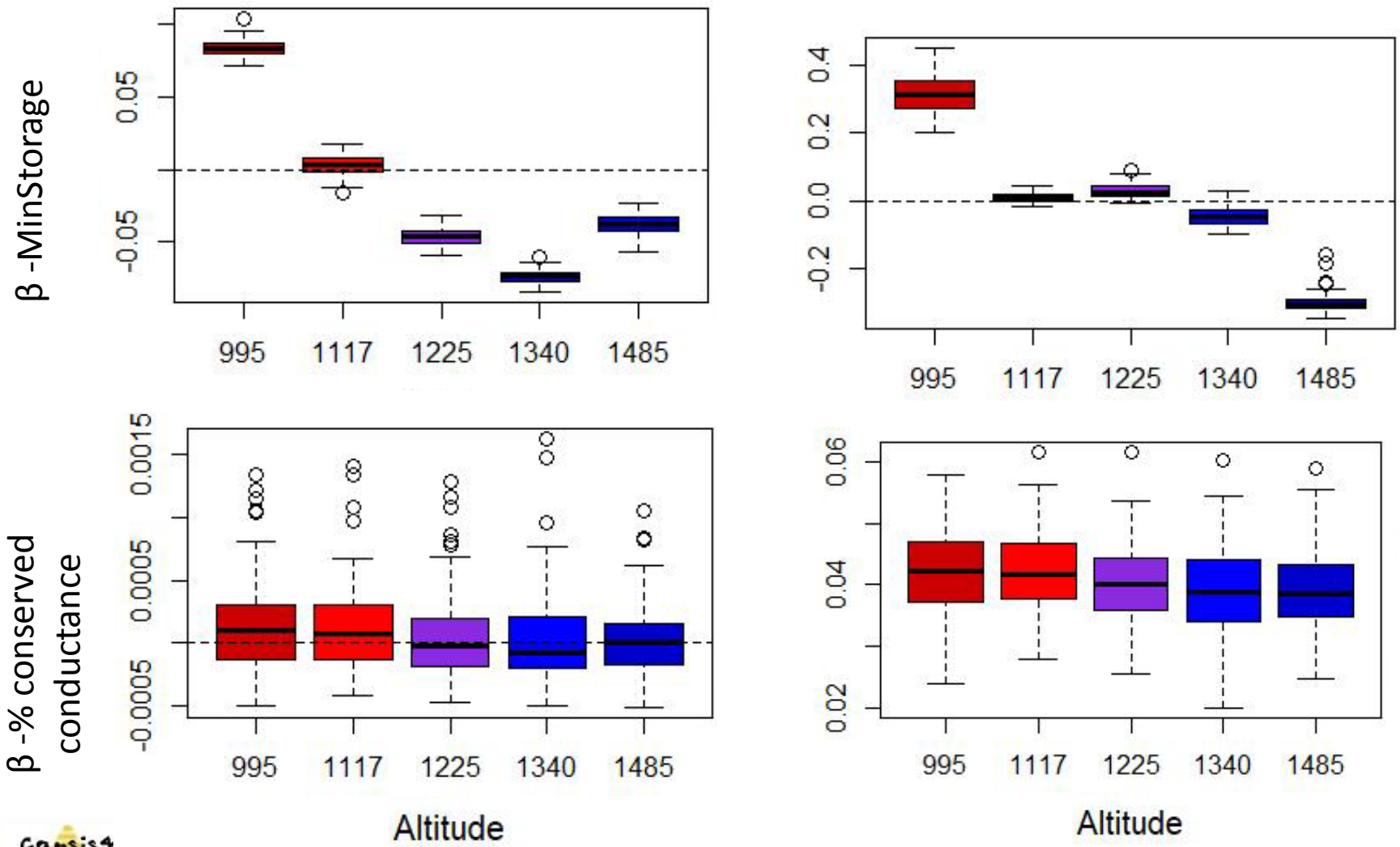
IFROST3; Age : 90 ; SWC= 60 mm

III. Selection gradients on on survival components

Current climate | **Future climate (RCP8.5)**

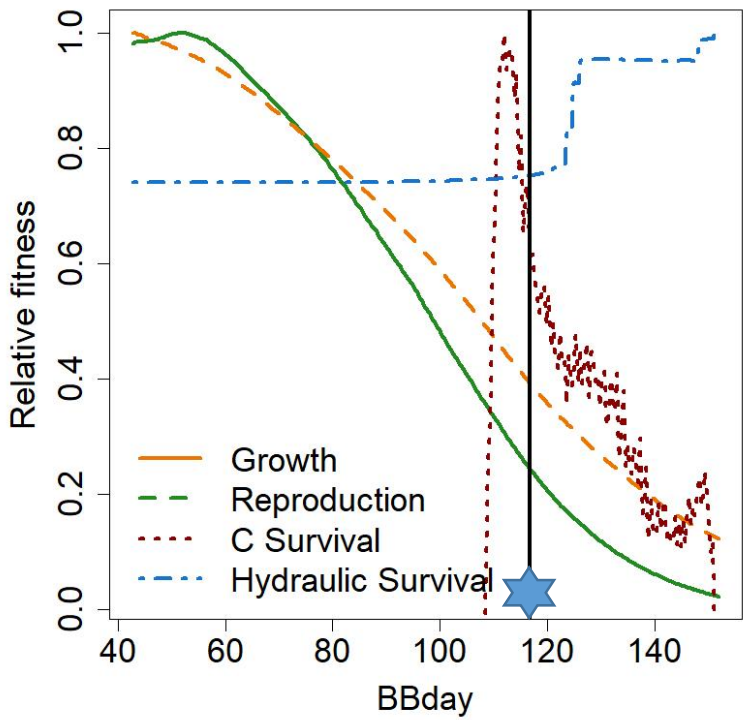


CAQSIS 2019

IFROST3; Age : 90 ; SWC= 60 mm

Conclusions III. : future climates

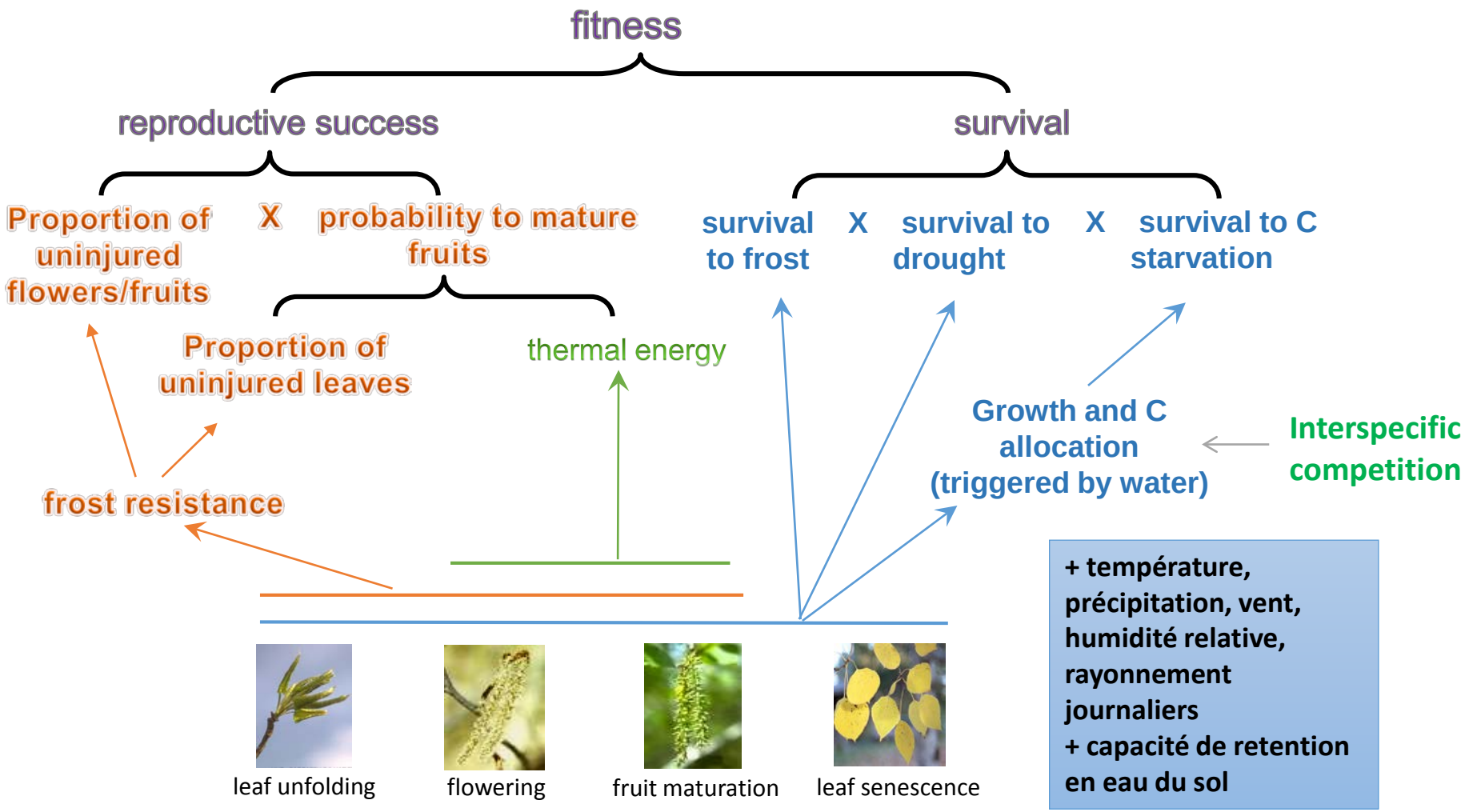
- Conflict between selection for early budburst (C-survival, growth, reproductive output) versus late budburst (hydraulic survival)
- Interest/limit of the biophysical and ecophysiological model CASTANEA to simulate fitness
- Tipping point : none fitness component is optimized anymore ?



Thank you for your attention !

- Many thanks to :
- UEFM Avignon : Frédéric Jean, Olivier Gilg, Jean Thevenet, Frank Rei, Norbert Turion…
- URFM Avignon
- MeCC team : Julie Gaüzere, Isabelle Chuine, Ophélie Ronce …

PHENOFIT
nouvelle version



Chuine & Beaubien Ecol. Let. 2001