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

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BIOADAPT 2013 - projet MeCC

Ecologie des Forêts Méditerranéennes (URFM)
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

Frost hardiness

Budburst

~ End April

Forcing

~ Mid February

Ecodormancy

Vegetative period
170-180 days

Dormancy period

Endodormancy

Paradormancy

Fruit maturation

~ October

Senescence

Chilling

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Forcing:
~ End April
~ Mid February
~ October

Frost hardiness

Pictures: O Gilg, F Bonne & F Jean

Paradormancy

Endodormancy

Ecodormancy

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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)
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)?

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Schéma de O Ronce
What is the adaptive value of BBday?

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

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

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Genetic differentiation of phenological traits along an altitudinal gradient

Common garden, Aix en Provence

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

CAQSIS 2019
Genetic differentiation of phenological traits along an altitudinal gradient

J. Gaüzère PhD thesis (2014)

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

- « SPECIES » prm
- « TREE » prm
- « SOIL » prm
- Climate

**Module CastaneaOnly**

**Process-based “library” CASTANEA**

**FITNESS**
Methods

Phenological model: UNICHIll
(<Phenofit)

Variable parameter = sum of forcing temperatures (Fcrit)

Range of $F_{\text{crit}} = [11 - 60] \rightarrow$ computation of mean(Bbday) over x years

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

Adaptive landscape

Optimum

Fecundity (or survival)

BBday

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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 3rd of May to the 21th of May → 19-days range
Reproductive output: sum of seeds produced \([\text{SumSeed}]\)

Growth/Biomass: sum of wood ring area \([\text{SumWoodArea}]\)

Safety margin from carbon starvation: minimal level of carbon storage \([\text{MinStorage}]\)

Risk of hydraulic failure: max percentage of loss of conductance \([\text{maxPLC}]\)

Methods

CASTANEA

FITNESS

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Trend to overestimate ring width
Species parameter related to frost hardiness [IFROST]

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

AGE: \{\text{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

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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

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IFROST3; Age: 90; SWC = 60 mm; Current climate
I. Altitude effect on adaptive landscapes

- 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
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
I. Altitude effect on adaptive landscapes

- Weak mean PLC as compared to lethal values (88%)
- PLC increases as altitude decreases
I. Altitude effect on adaptive landscapes

- maxPLC get closer from lethal values (88%)
- Later budburst increases the safety margin to hydraulic failure
I. Effect of frost hardness on adaptive landscapes

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

Age : 90 ; SWC= 60 mm; Current climate
Conclusions I. : shape of adaptive landscapes

The shape of adaptive landscapes 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 ($\sigma^2_{BBday} = 5$)
Resampling of 100 individuals within $\mathcal{N}(\mu_{BBday}, \sigma^2_{BBday})$

Estimation of direct ($\beta$) and quadratic ($\gamma$) gradients (Lande & Arnold 1983):

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

with $\text{RelatFitness} = \frac{\text{Fitness}}{\mu_{\text{fitness}}}$ and $BBday_{sd} = BBday / \sigma_{BBday}$
II. Selection gradients on growth and reproductive output

- Negative $\beta$-values ↔ selection towards early budburst
- Selection intensity increases with altitude for growth, reverse for reproductive output?
II. Selection gradients on growth and reproductive output

- $\beta_{\text{SumWoodArea}}$
  
- $\beta_{\text{SumSeeds}}$

SWC = 60 mm

SWC = 145 mm
II. Selection gradients on survival components

• Positive $\beta$-values ↔ selection towards late budburst

• Weaker $\beta$-values
II. Selection gradients vary with SWC

Selection is more intense at low SWC

Selection change direction depending on SWC
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?

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

**Current climate**

- $\beta_{\text{SumWoodArea}}$
- $\beta_{\text{SumSeeds}}$

**Future climate (RCP8.5)**

- $\beta_{\text{SumWoodArea}}$
- $\beta_{\text{SumSeeds}}$

Altitude

IFROST3; Age: 90; SWC= 60 mm
III. Selection gradients on survival components

**Current climate**

- β-MinStorage
- β-% conserved conductance

**Future climate (RCP8.5)**

- β-MinStorage
- β-% conserved conductance

Altitude: 995, 1117, 1225, 1340, 1485

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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!

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PHENOFIT
nouvelle version

fitness

reproductive success

survival

Proportion of uninjured flowers/fruits × probability to mature fruits

survival to frost × survival to drought × survival to C starvation

Proportion of uninjured leaves

frost resistance

thermal energy

Growth and C allocation (triggered by water)

Interspecific competition

+ température, précipitation, vent, humidité relative, rayonnement journaliers + capacité de retention en eau du sol

leaf unfolding
flowering
fruit maturation
leaf senescence

Chuine & Beaubien Ecol. Let. 2001