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Local adaptation to climatic gradients: application of a Physio-Demo-Genetics simulation model to European Beech populations

Sylvie Oddou-Muratorio

Hadrien Lalagüe

Hendrik Davi

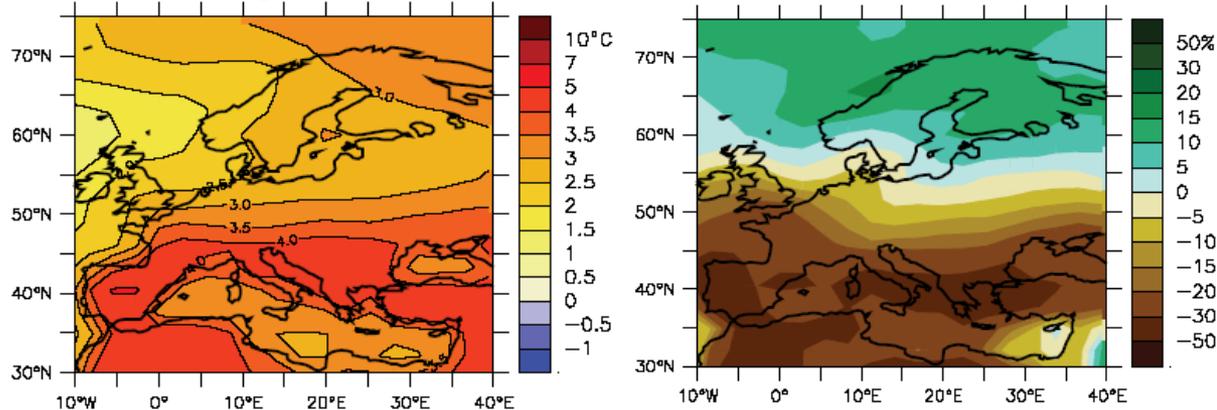
Ecologie des Forêts Méditerranéennes

INRA Avignon, FRANCE



Accounting for genetic adaptation in the response of tree populations to Climate Change (CC)

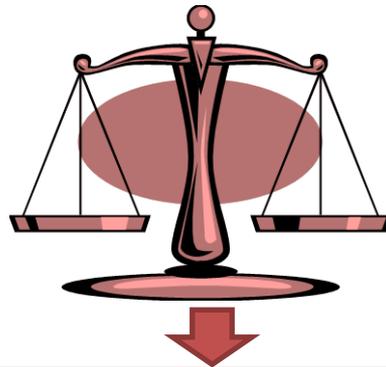
Predicted change in summer (JJA) temperatures/rainfall (IPCC 2007)



Migration ?
Plasticity ?
Genetic adaptation ?

Capacities of genetic adaptation of tree populations over few generations ???

- + High levels of genetic diversity
- + High levels of gene flow



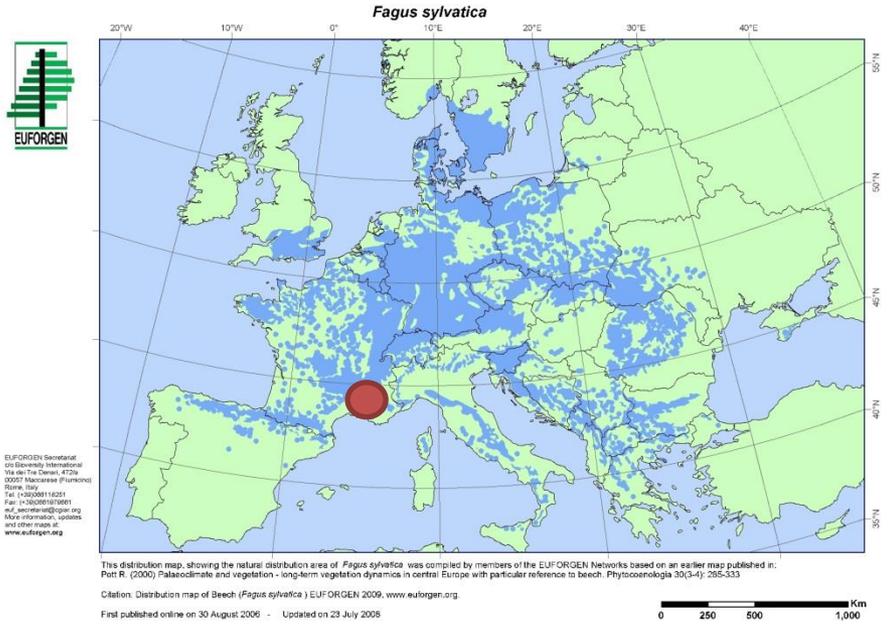
- Long generation time
- Low mortality of established trees
- Genetic and environmental constraints on adaptive traits

ECO-GENETIC MODEL incorporating these characteristics

- 1) Accounting for intra-specific genetic variability in Species Distribution Model (Benito-Garzon et al. 2011): both genetic variability and phenotypic plasticity reduce the decrease of area occupancy under CC
- 2) Accounting for adaptive processes in forest dynamic model : High mortality (Kuparinen et al 2010) or dynamic silviculture (Kramer et al. 2008) can favor rapid adaptation to a warming climate

Objectives

2. Application to the study case of *Fagus sylvatica* (European Beech) on Mont Ventoux



Beech populations occur between :

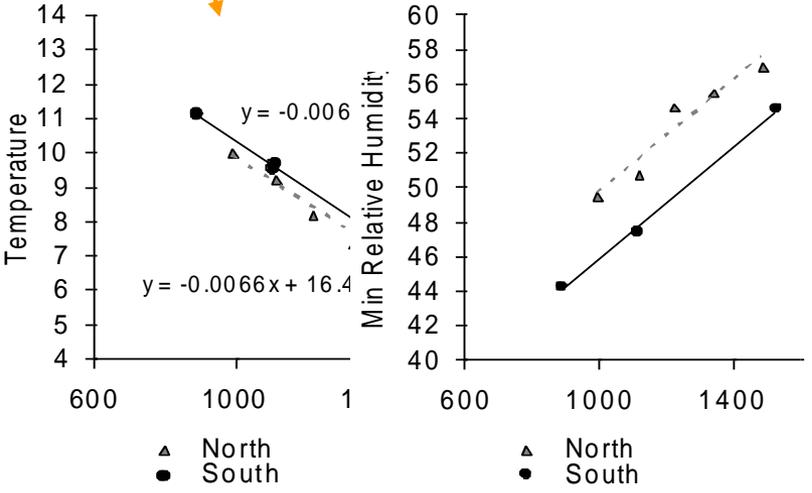
- 750 and 1700 m on North face
- 840 and 1615 m on the South face



Ecological data (growth, fructification, dispersal, phenotypic and genetic diversity)

How adaptive genetic variation and phenotypic plasticity respectively contribute to the variation of functional traits along environmental gradient?

How fast can genetic adaptation develop ?



PDG, a new hybrid model



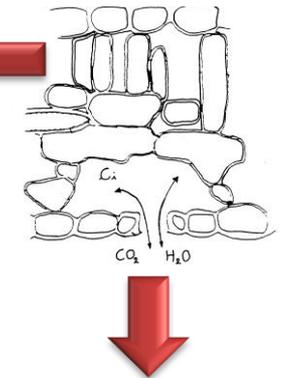
$Fecundity = f(reserves)$



ADULTS

CASTANEA

Dufrêne et al. 2005
Tree level

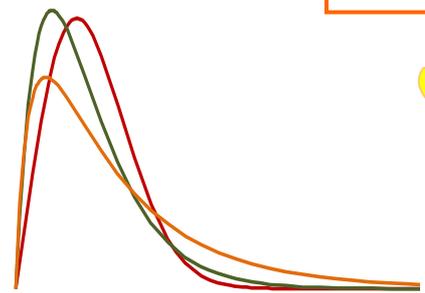


Growth/ mortality

ADULTS

Date of Budburst

Mating system
(2% selfing)



SEEDS

Dispersal
-pollen dispersal kernel



GENETICS

Rate of empty seed,
germination, survival

Density-dependence
mortality

SEEDLINGS

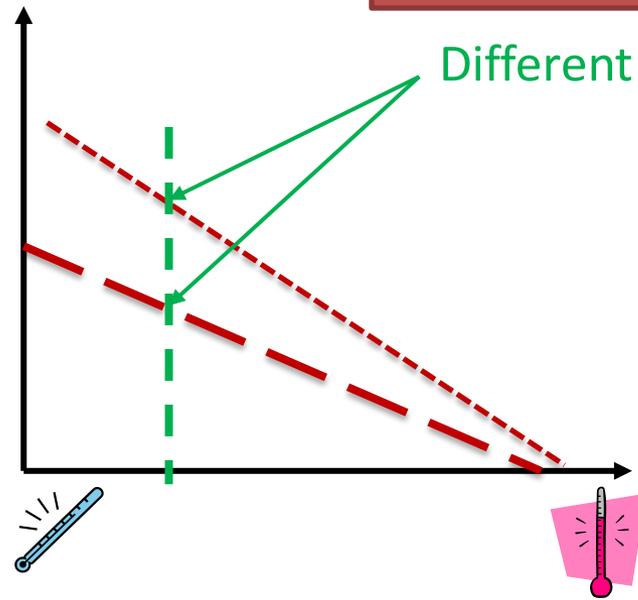
Dispersal

Plastic/genetic variation of date of budburst



Date of budburst (BBD)

lower BBD → longer growth season
→ higher risk of late frost



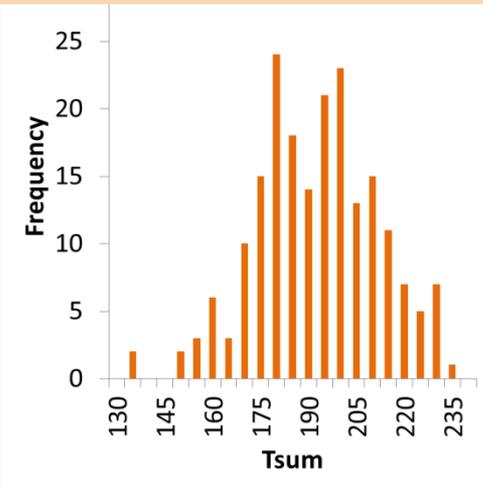
Different Sum of temperatures required for budburst,
 $T_{sum}(late) > T_{sum}(early)$

Trait: $P = f(Env + Gen + Gen \times Env)$

BBD = $f(T^\circ + T_{sum} + T_{sum} \times T^\circ)$

Environment = Temperature

The parameter Tsum of the biophysical model is genetically based and variable :



- 10 unlinked genes, 2 alleles /gene (=10 SNPs)
- Effect of each gene <- Gaussian distribution at initiation
- First step $h^2=1$
- + 400 neutral SNPs

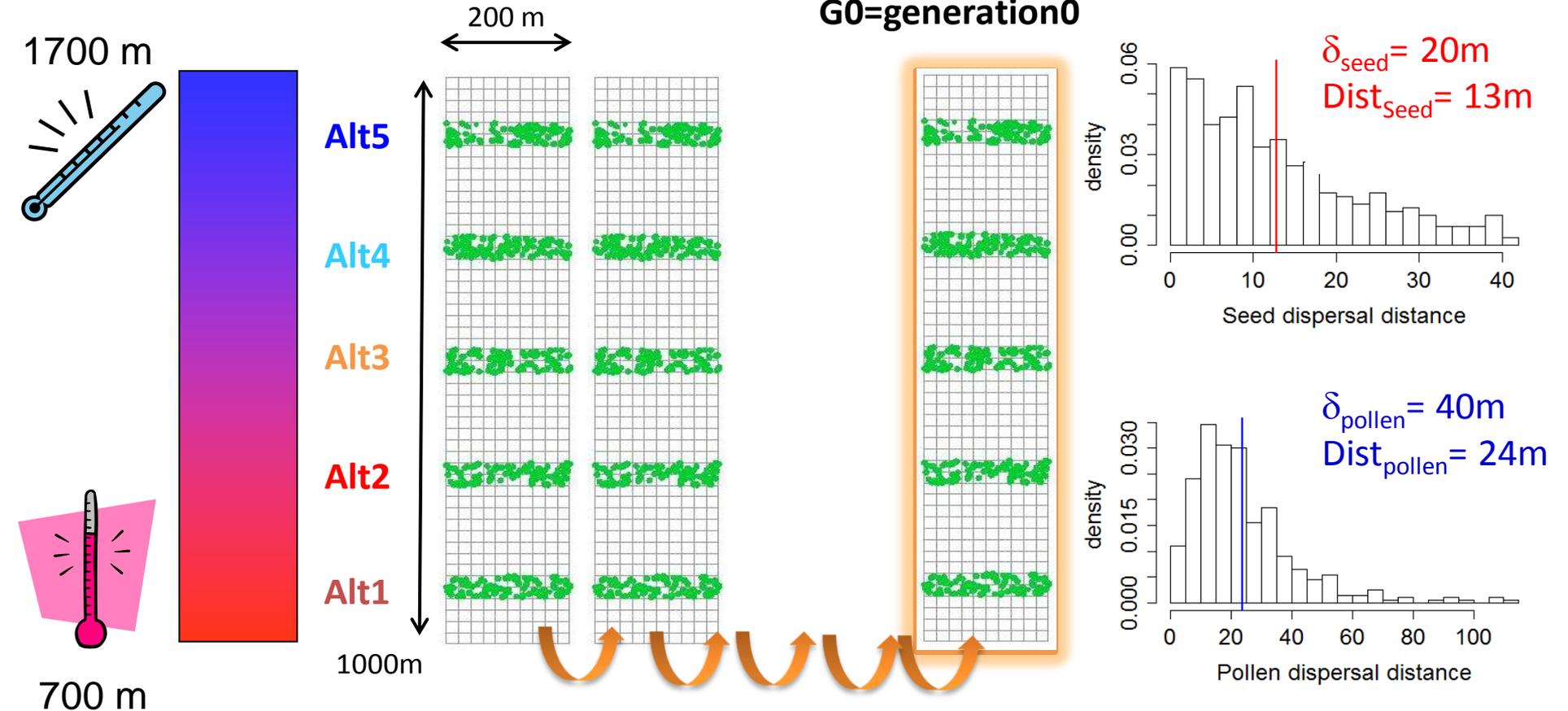
Mean Tsum = 190

Simulation design : Initial state

- N=500 adult trees, age 40
- 100 trees at each elevation
- Plot size = 200m×1000m



- Genetic equilibrium
- No adaptive differentiation for Tsum and for the underlying genes

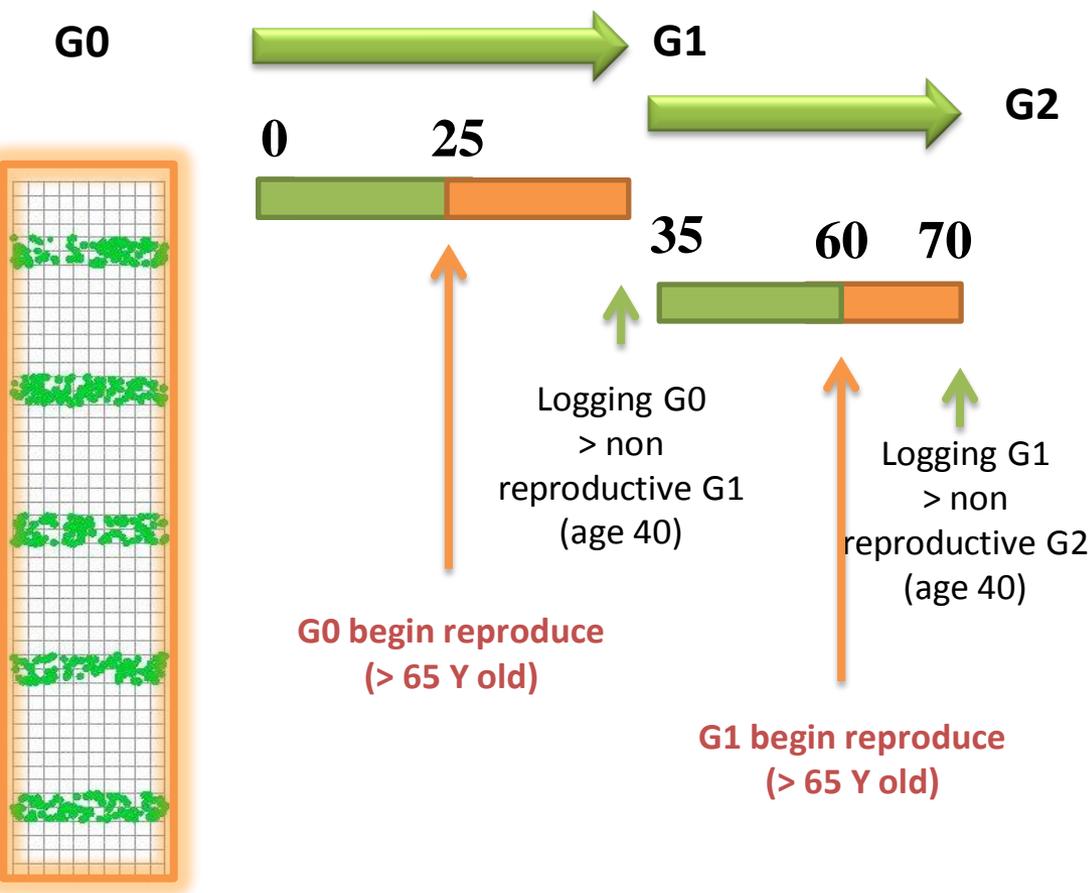


**Neutral pre-evolution = genetic drift + dispersal
at constant population size**

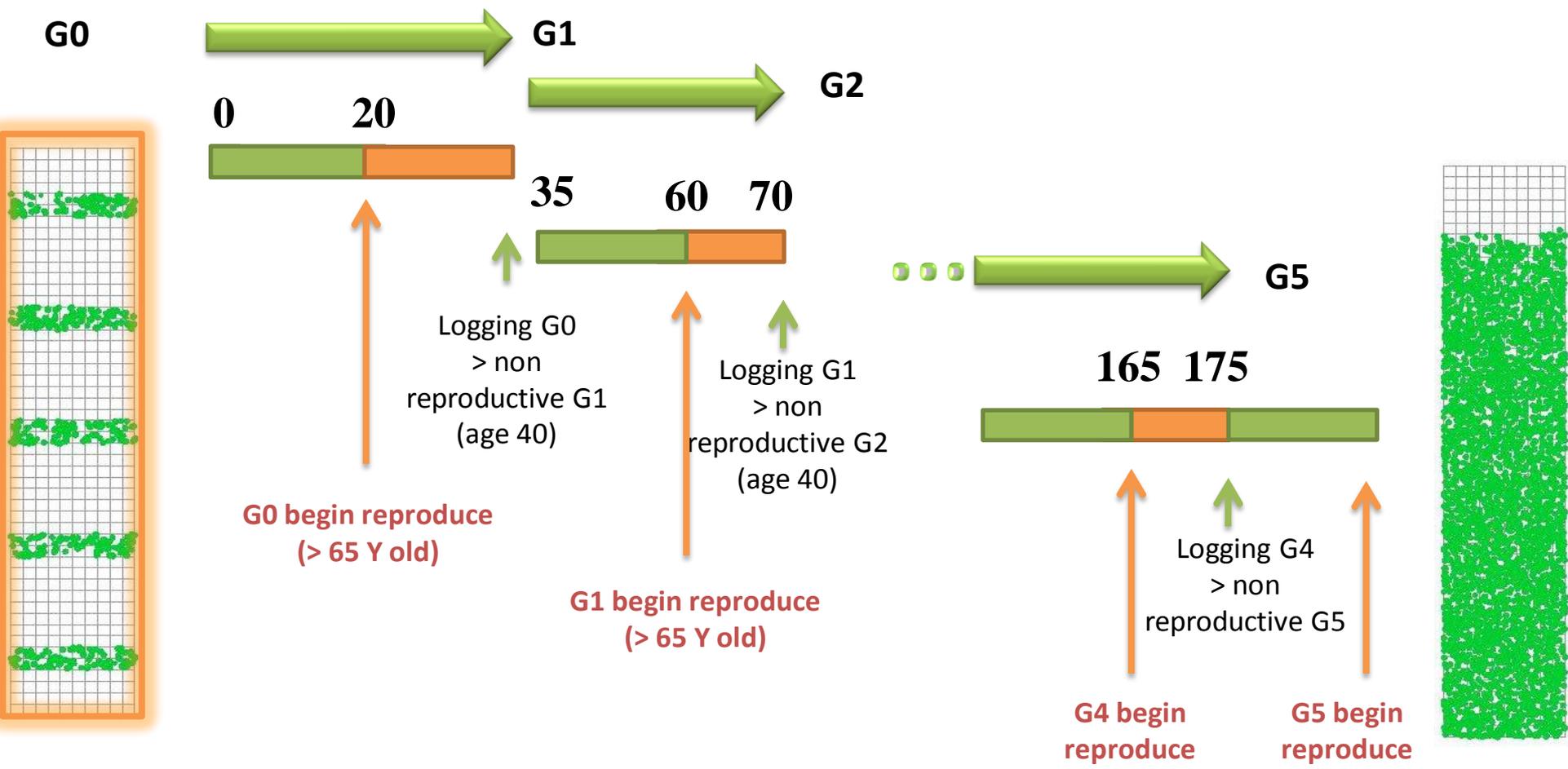
Simulation design : Evolution with selection while colonization



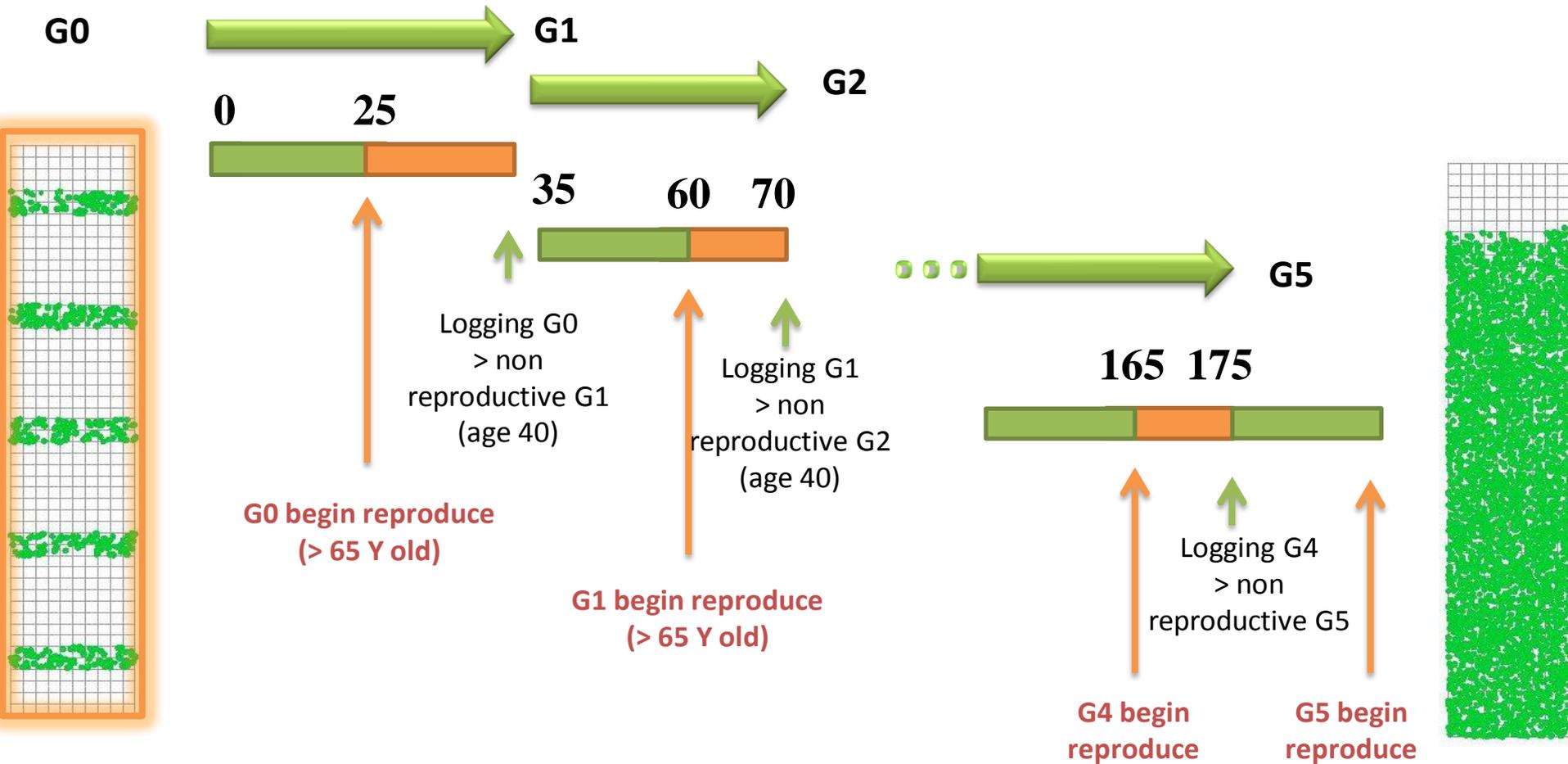
Simulation design : Evolution with selection while colonization



Simulation design : Evolution with selection while colonization



Simulation design : Evolution with selection while colonization

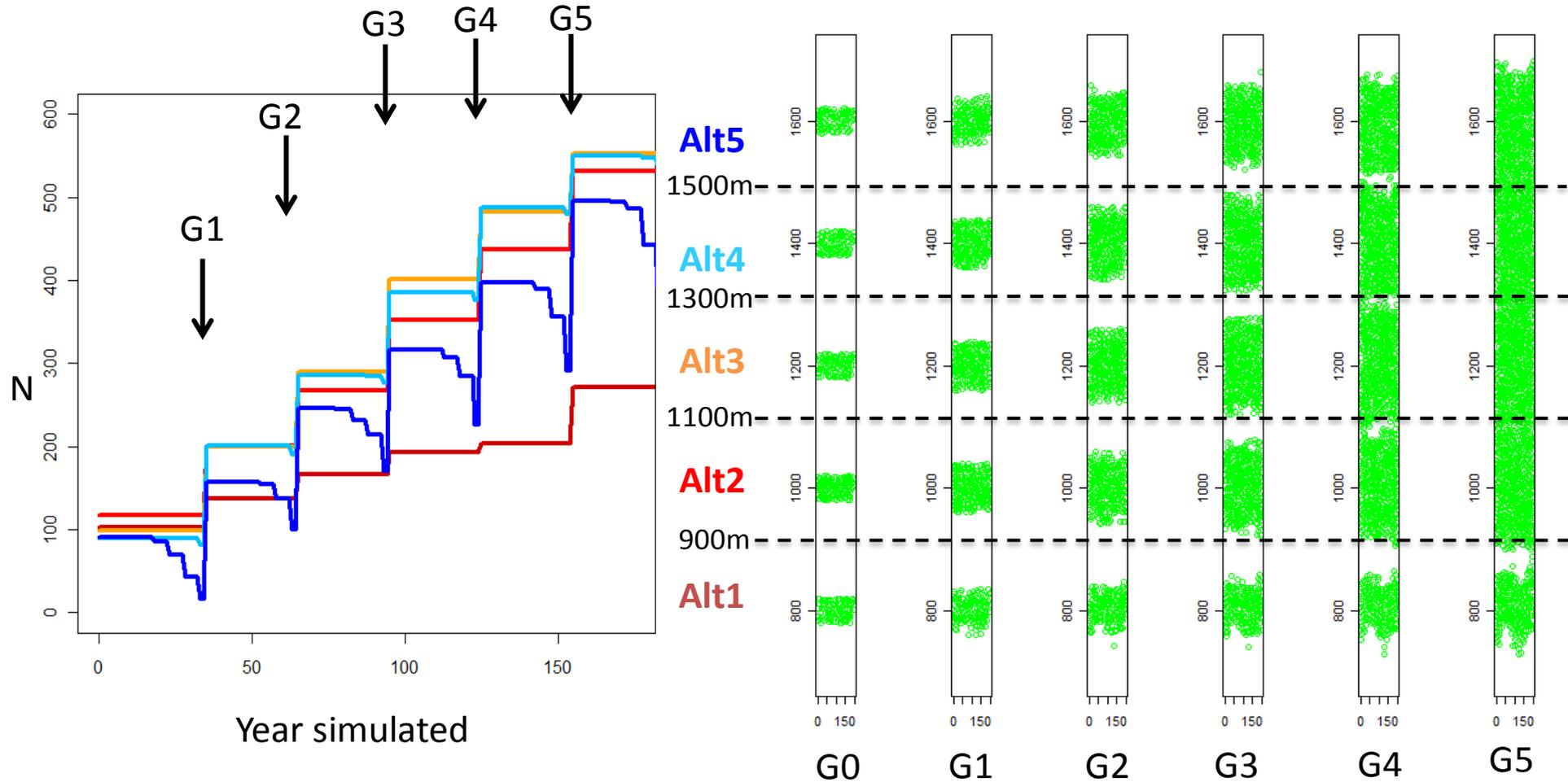


Working hypothesis for the studied case

- No overlapping generations (sequential logging of reproductive trees)
- No selection on date of budburst during the regeneration step
- No mutation (only standing genetic variation + recombination)
- No competition for light among adults
- Climate (2002-2006 repeated) with elevation effect on T, Rainfall, and relative humidity

Results: population dynamics

Frost effect on LAI = 0

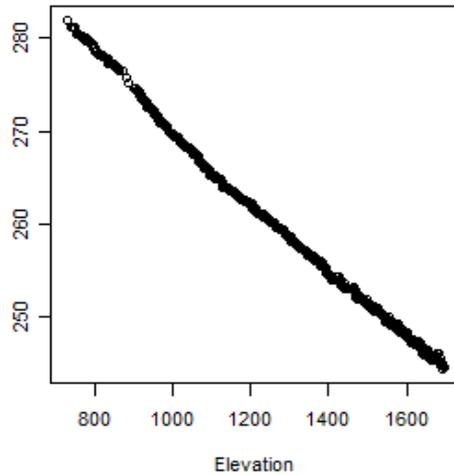


- Colonization without mortality at Alt2 → Alt4
- Expansion slower at Alt1
- Colonization with mortality at Alt5; Treeline at 1620 m (versus observed =1700 m)

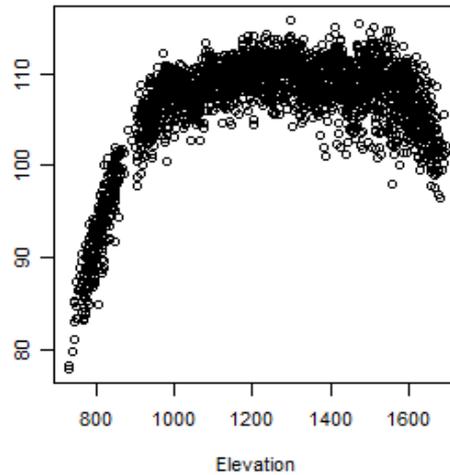
Results : validation

Frost effect on LAI = 0

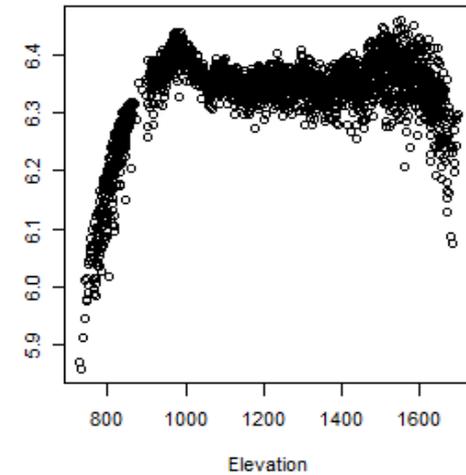
End of wood production period (Julian Day)



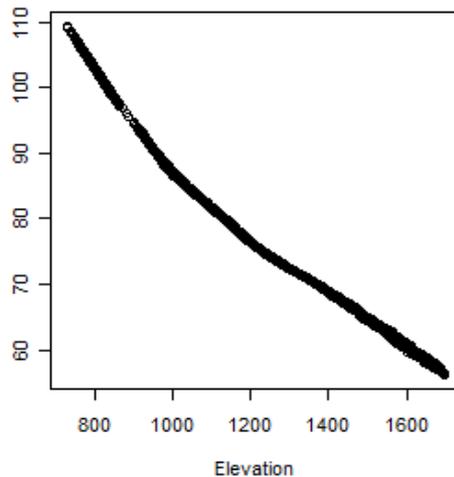
Carbohydrate reserves



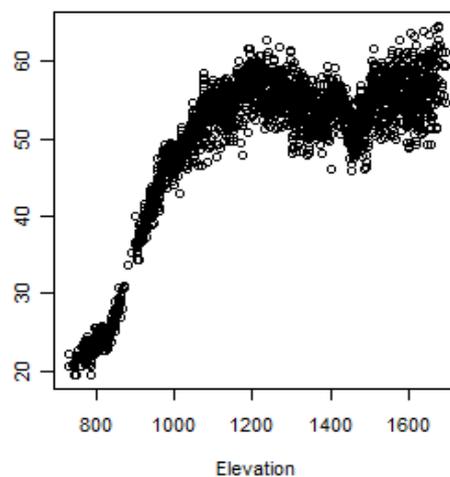
LAI



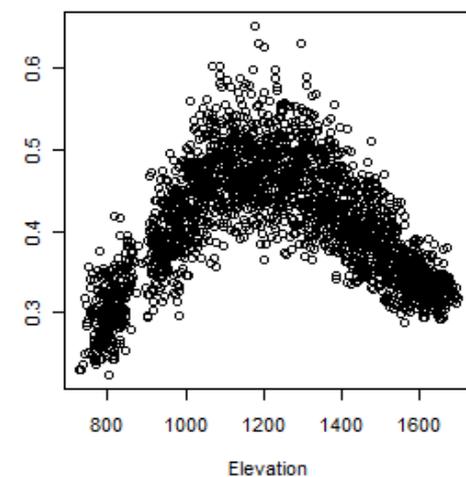
StressLevel



Number of seed produced



Annual ring width (mm)

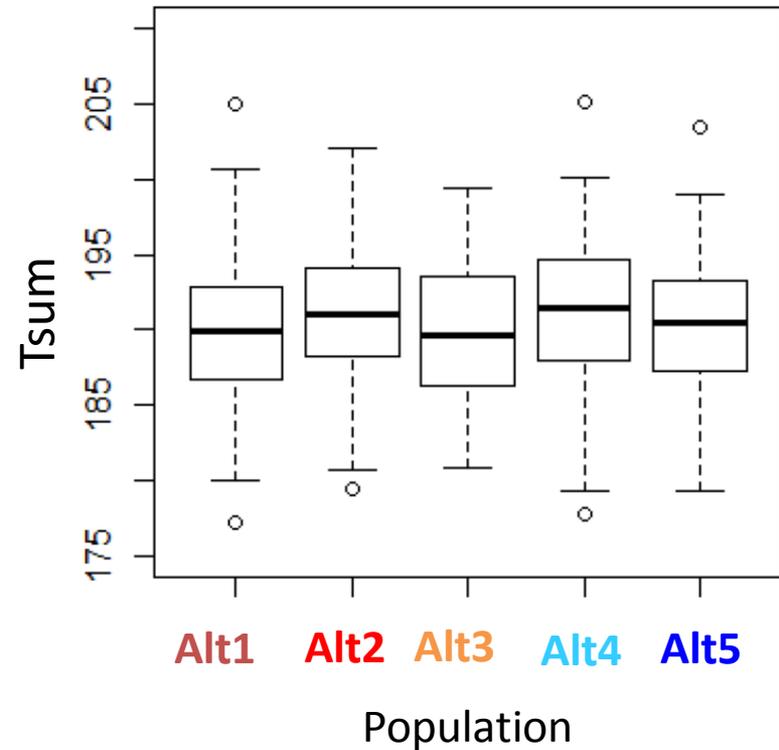
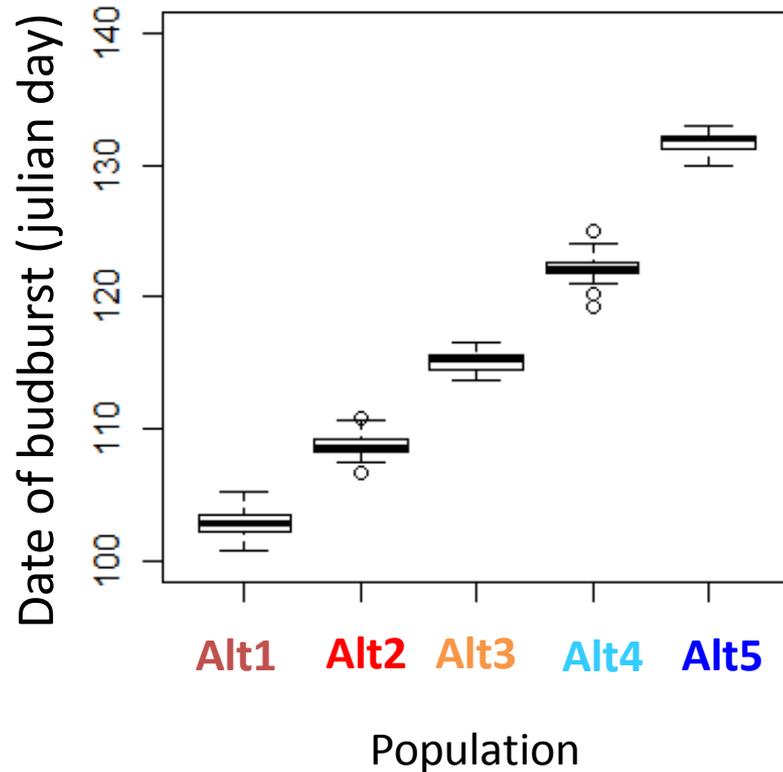


- The model reproduces well patterns of variation of physiological and ecological variables with elevation.

Results : spatial patterns of budburst

Frost effect on LAI = 0

At generation G0



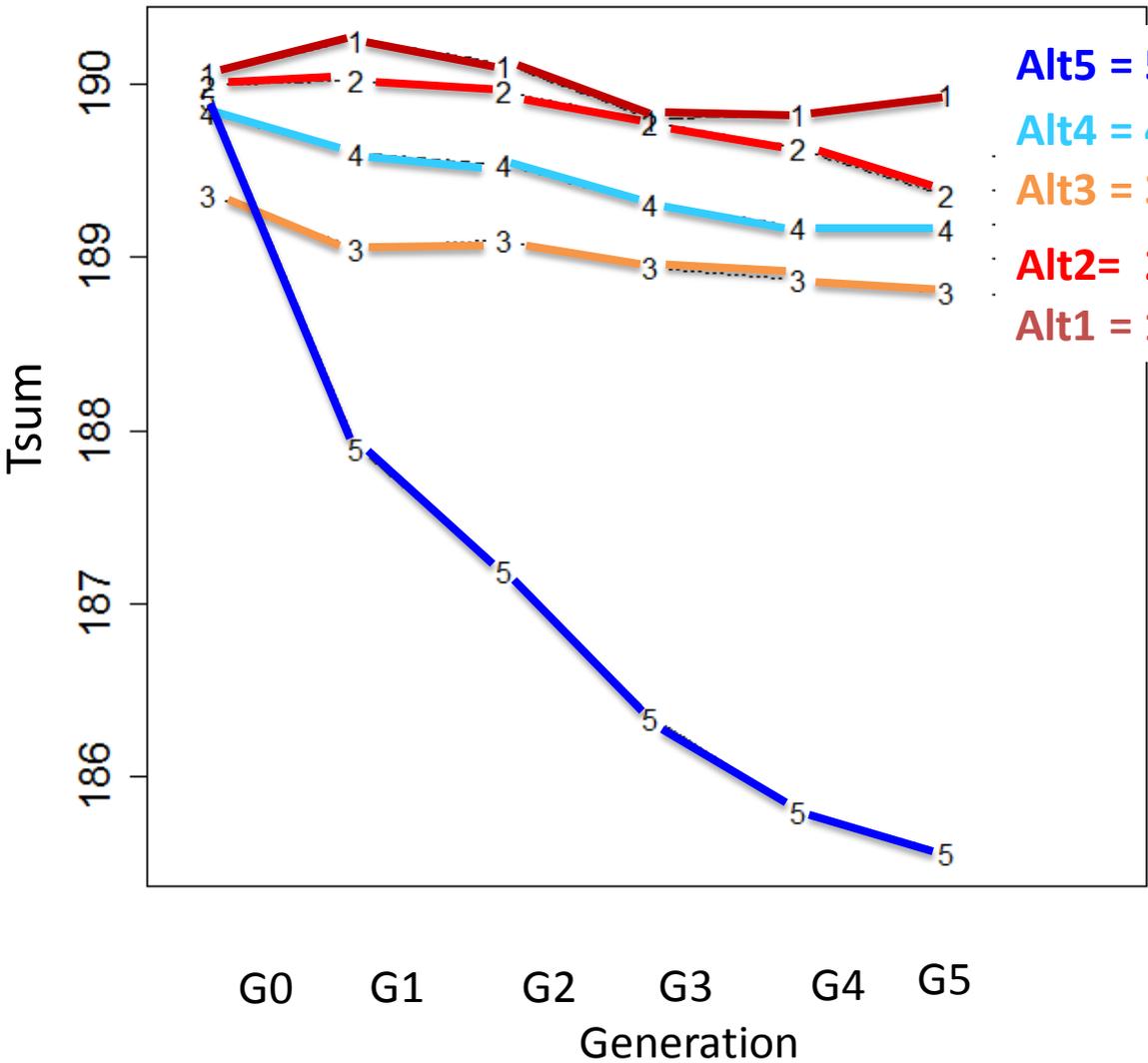
Temperature decreases with elevation
→ later budburst

Genetic differentiation for BBD at
initiation ← genetic drift

Results : temporal evolution of Tsum/BBD

Frost effect on LAI = 0

$$Tsum_{ij} = Population_i + Generation_j + \epsilon_i (+ interaction(Population_i, Generation_j))$$



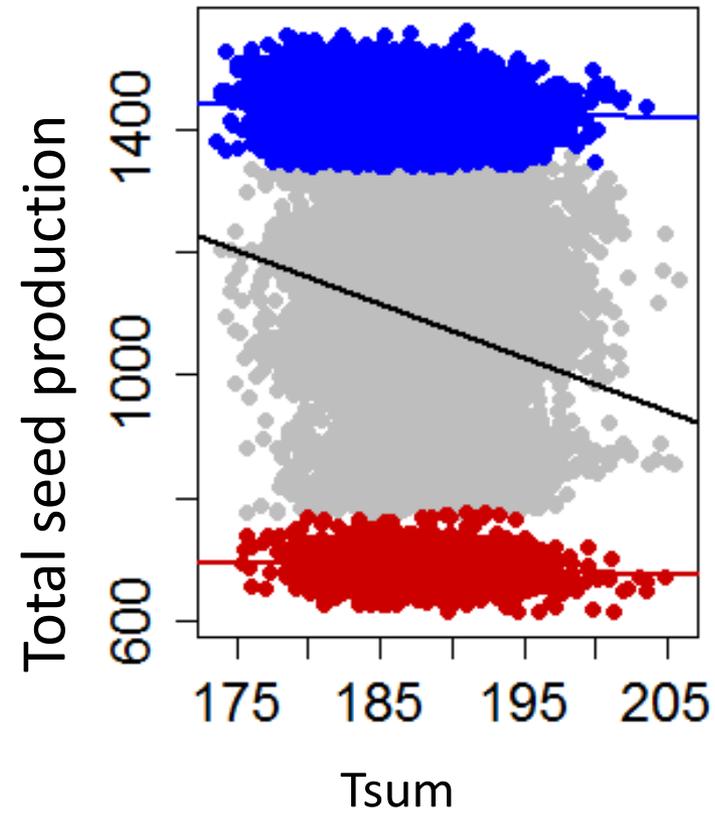
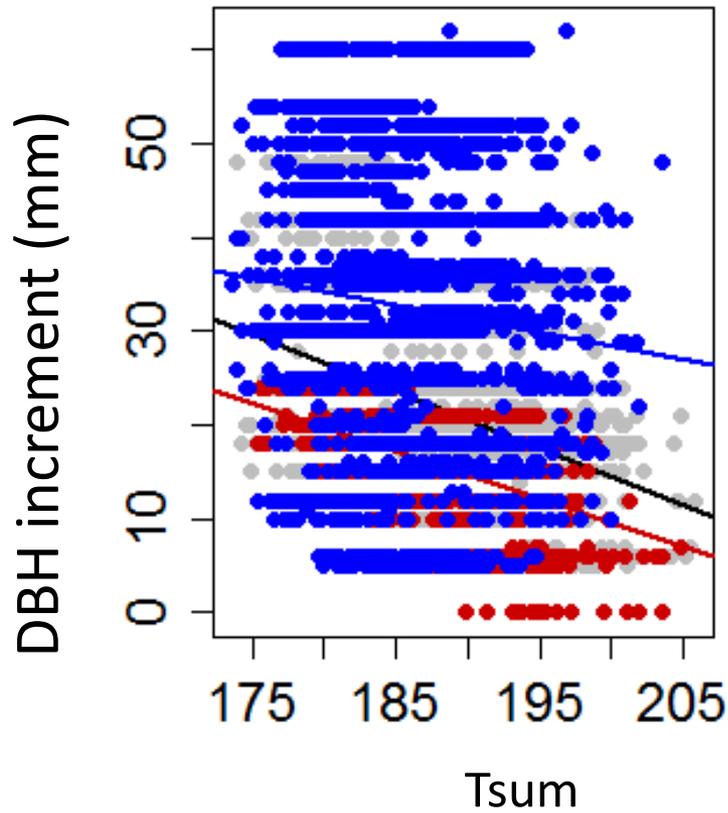
- Overall pattern of evolution towards lower Tsum
- In pop Alt5, where Tsum advanced from 188-190 to 184-188 in 5 generations

Results : strength of selection on *tsum*

All populations

Population Alt 1

Population Alt5



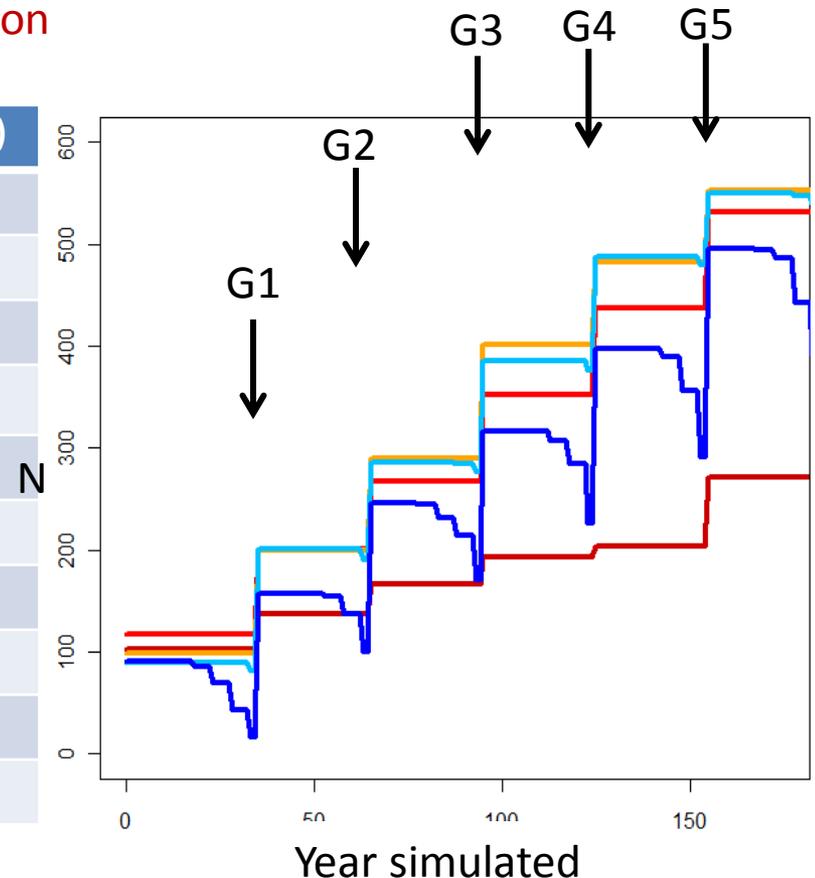
— Both components of fitness decreased with increasing Tsum

Results : strength of selection on *tsum*

linear model: $\text{Fitness} = \text{Tsum} + \text{pop} + \text{pop} * \text{Tsum}$

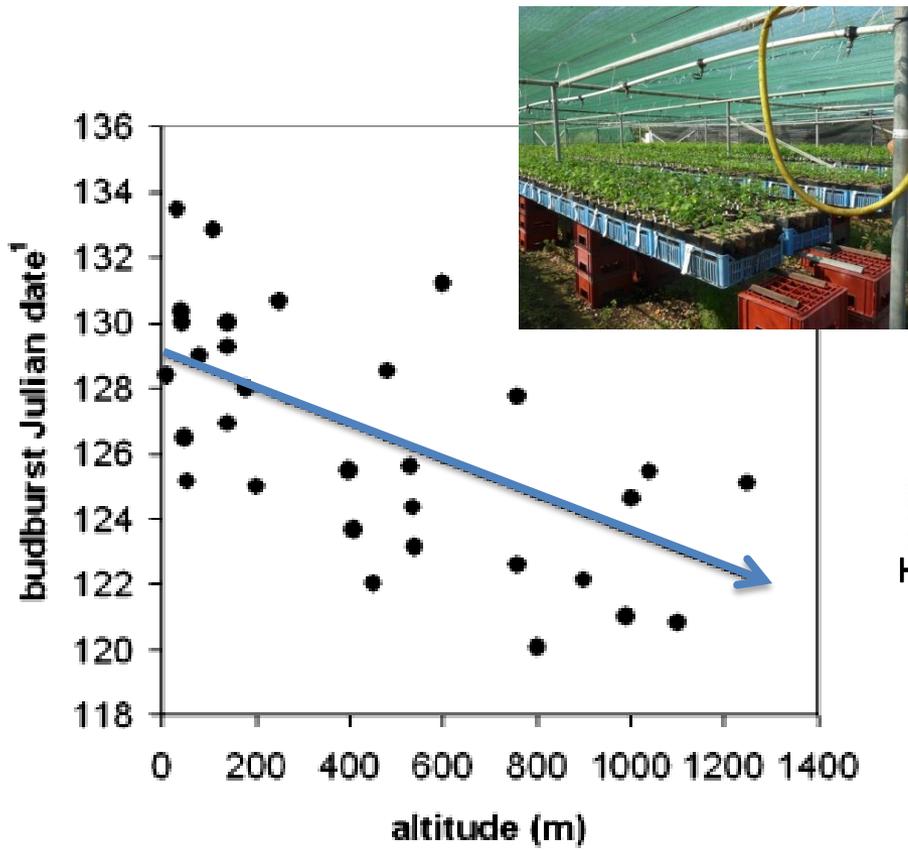
Number of reproducing offspring at next generation

	Estimate	Std error	t-value	Pr(t-value)
(Intercept)	3.407	1.091	3.122	0.00
TSUM	-0.006	0.006	-0.963	0.34
PopAlt2	1.394	1.422	0.981	0.33
PopAlt3	-0.329	1.376	-0.239	0.81
PopAlt4	1.930	1.400	1.379	0.17
PopAlt5	11.747	1.423	8.257	<2e-16
TSUM:PopAlt2	-0.006	0.007	-0.859	0.39
TSUM:PopAlt3	0.003	0.007	0.384	0.70
TSUM:PopAlt4	-0.009	0.007	-1.239	0.22
TSUM:PopAlt5	-0.062	0.008	-8.252	<2e-16



- Higher individual fitness in population Alt5 due to mortality combined with density-dependent selection
- Strong selection gradient on *Tsum* in population Alt5

Back to the real world...



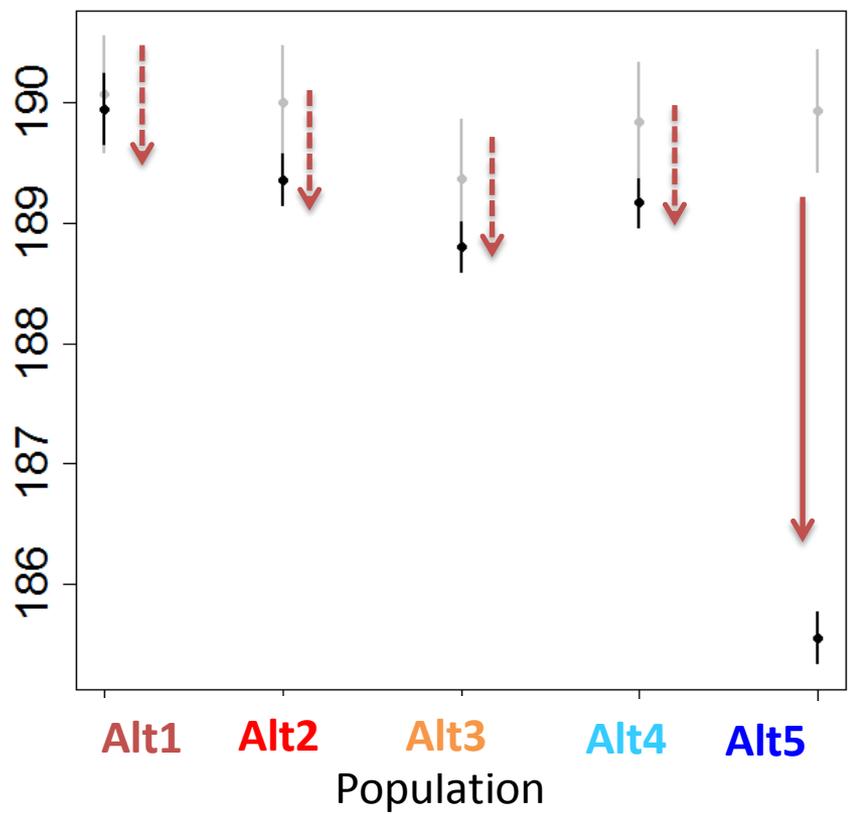
Gömöry & Paule, ASF 2012

— In the case of beech, genetic cline shows counter-gradient variation (Tsum is lower for populations of high elevation)

~~Frost effect on LAI = 0~~

Frost effect on LAI = 20%

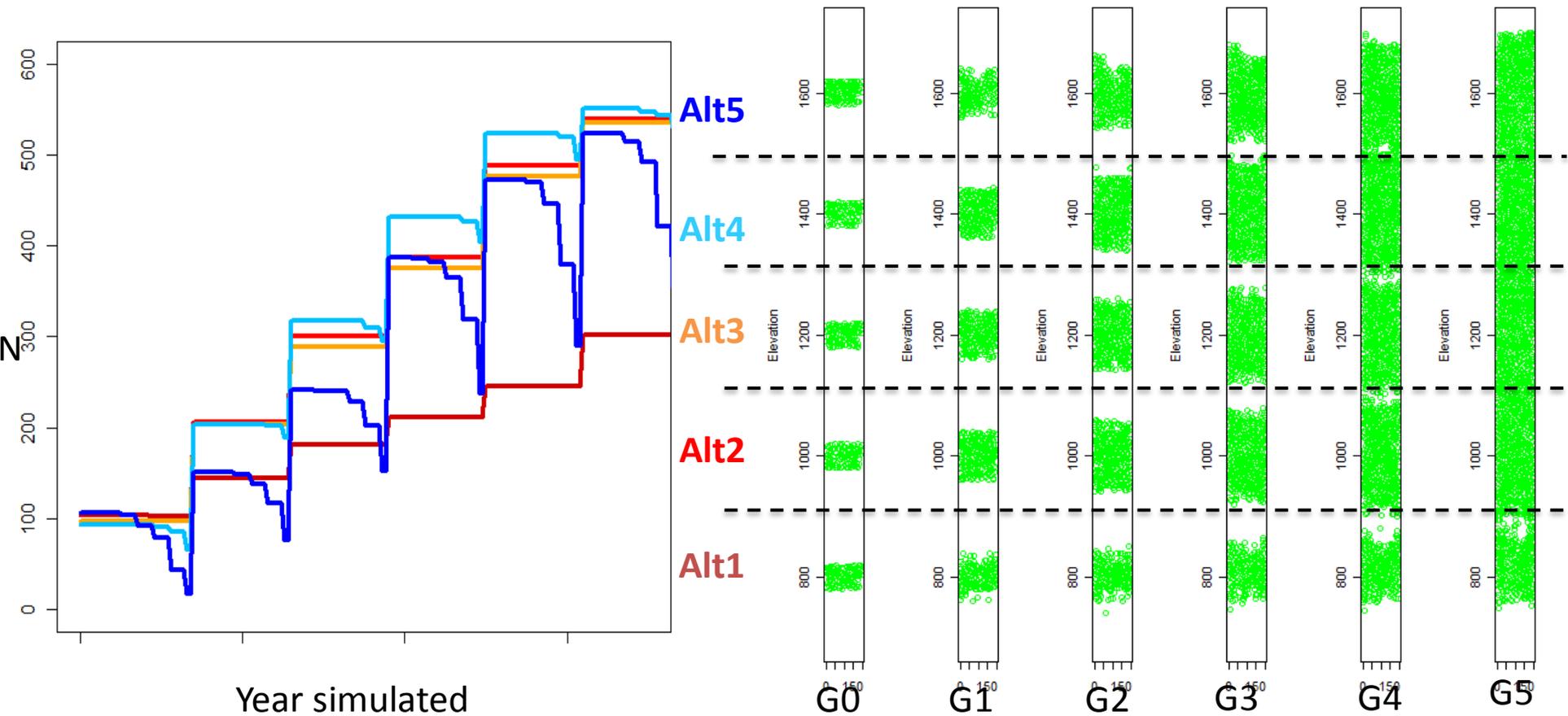
From G0 to G5



— In the simulations, consistent because of Alt5

Results: population dynamics

Frost effect on LAI = 20%

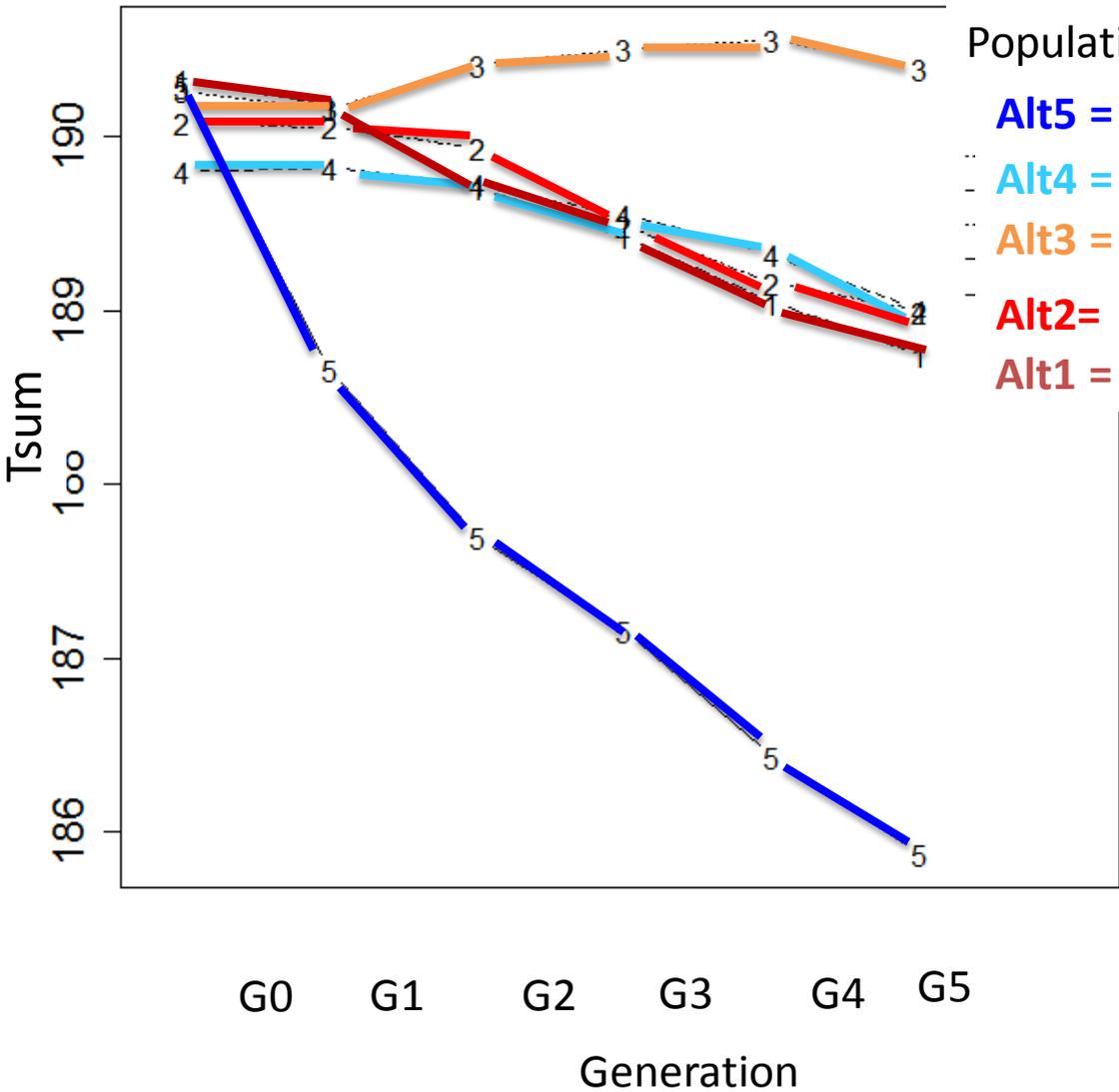


- Colonization without mortality at Alt2 → Alt4
- Expansion slower at Alt1
- Colonization with mortality at Alt5; Treeline at 1620 m (versus observed =1700 m)

Results : temporal evolution for Tsum

Frost effect on LAI = 20%

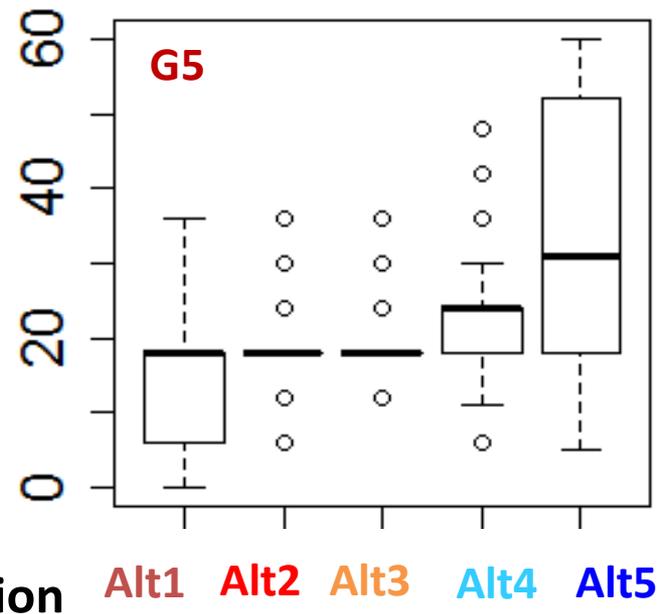
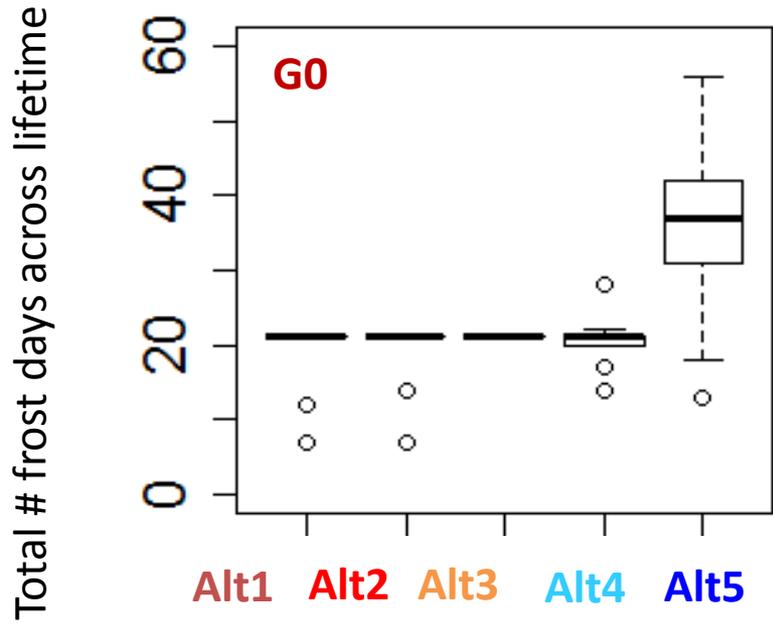
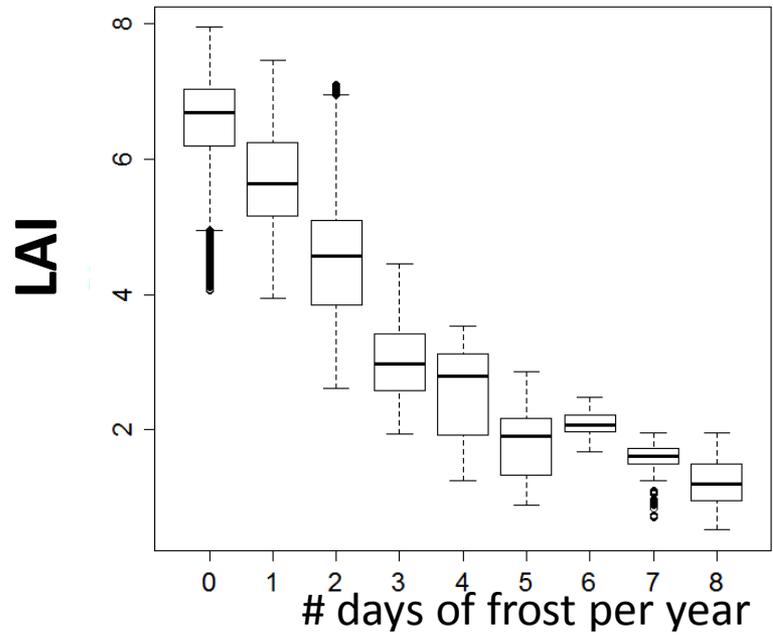
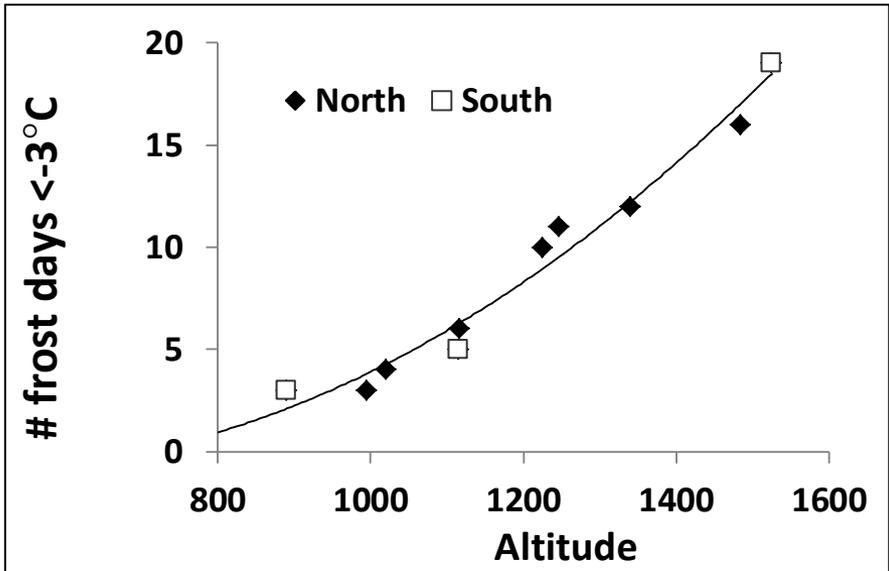
$$Tsum_{ij} = Population_i + Generation_j + \epsilon_i (+ interaction(Population_i, Generation_j))$$



- Overall pattern of evolution towards lower Tsum, particularly in Alt 5 where Tsum decreased by 4.4
- In Alt3, no evolution

Results: variation of frost risk with elevation

Frost effect on LAI = 20%

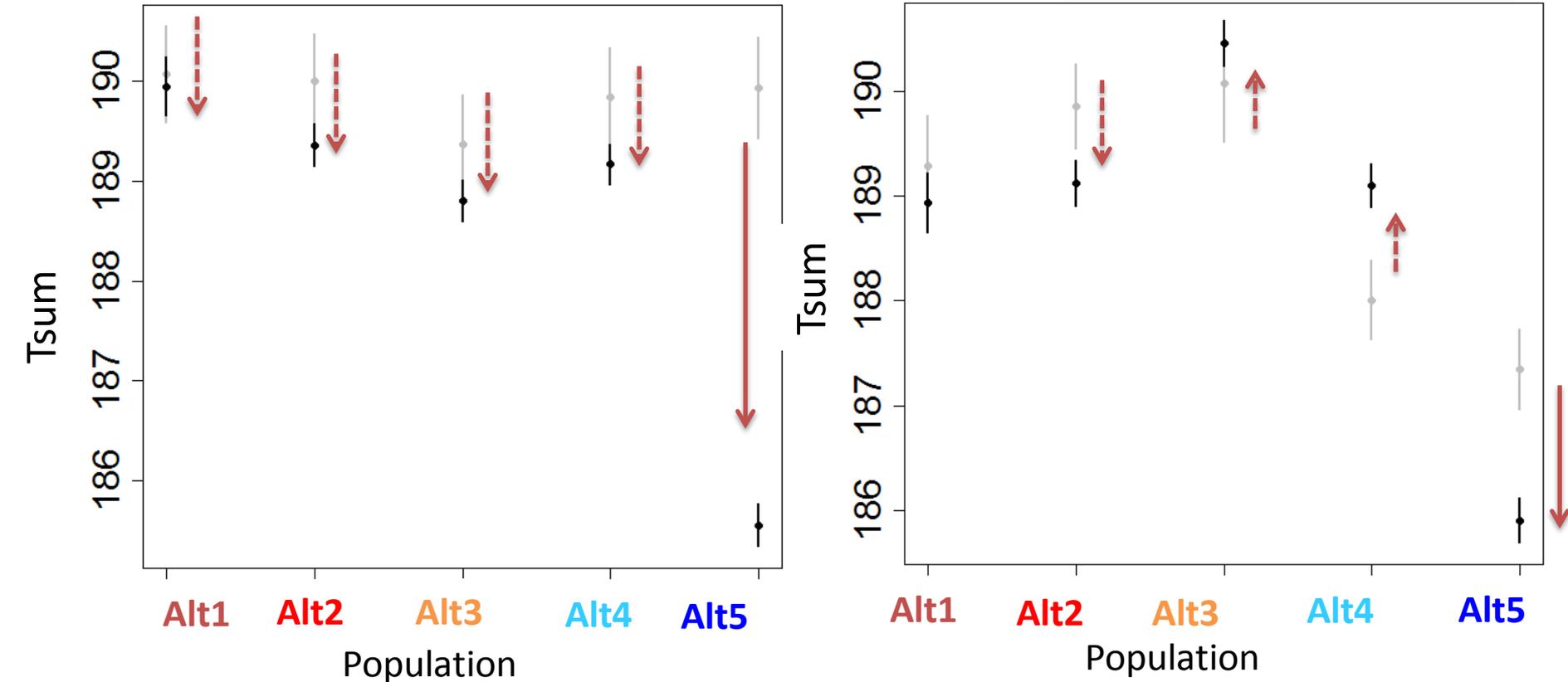


Summary: Patterns of evolution of *Tsum*

From *G0* to *G5*

Frost effect on LAI = 0

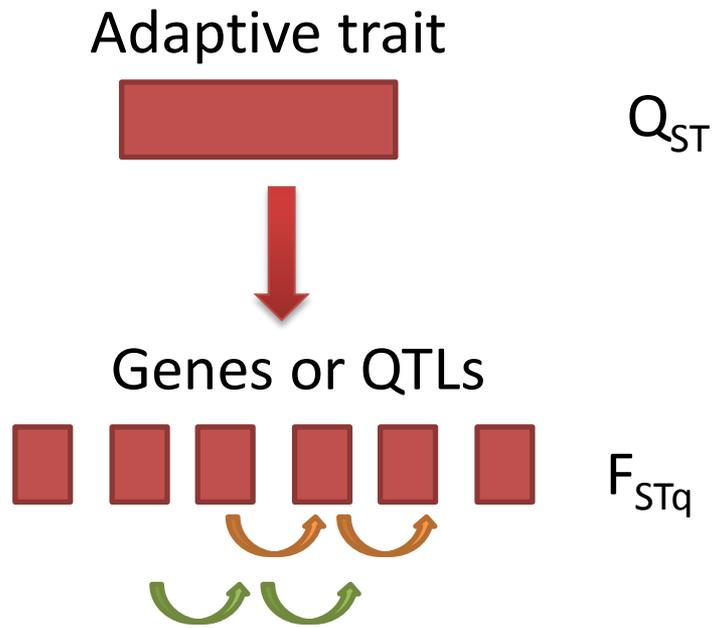
Frost effect on LAI = 20%



- At high elevation (Alt5) early genotypes were not more affected by late frost than late genotypes → early genotypes were still selected
- At middle elevation (Alt 3-4) risks of late frost were maximum → early genotypes were counter-selected
- At low elevation, risks of late frost are lower → early genotypes are still selected

Objectives

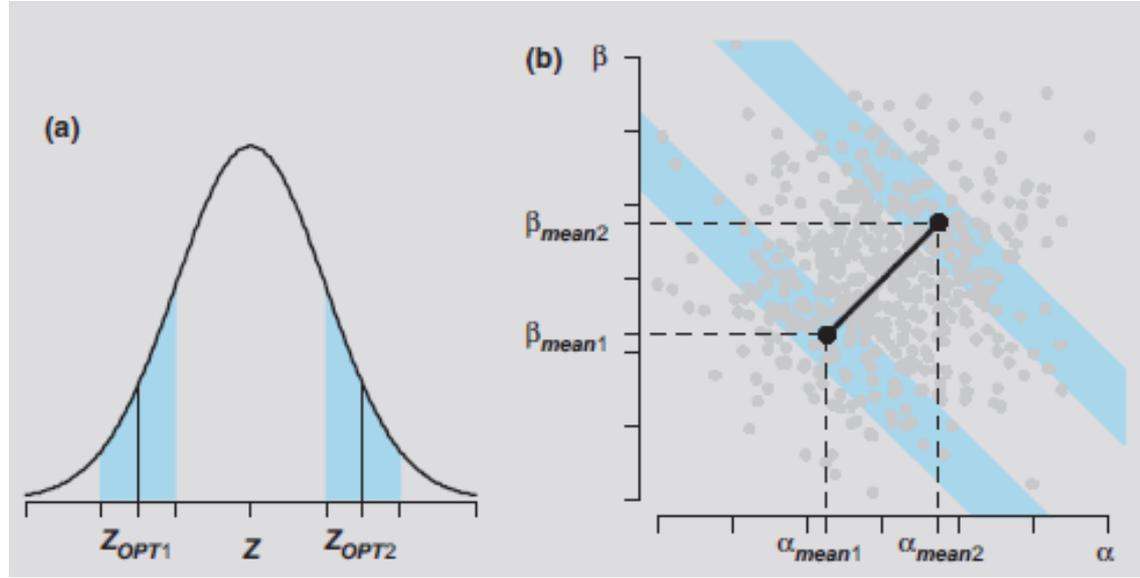
3. Signature of diversifying selection on genetic diversity and differentiation at QTLs ?



Θ_w = Covariation of gene effects within pop

Θ_b = Covariation of gene effects between pop

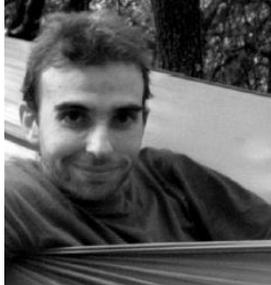
Le Corre et Kremer 2003, 2012



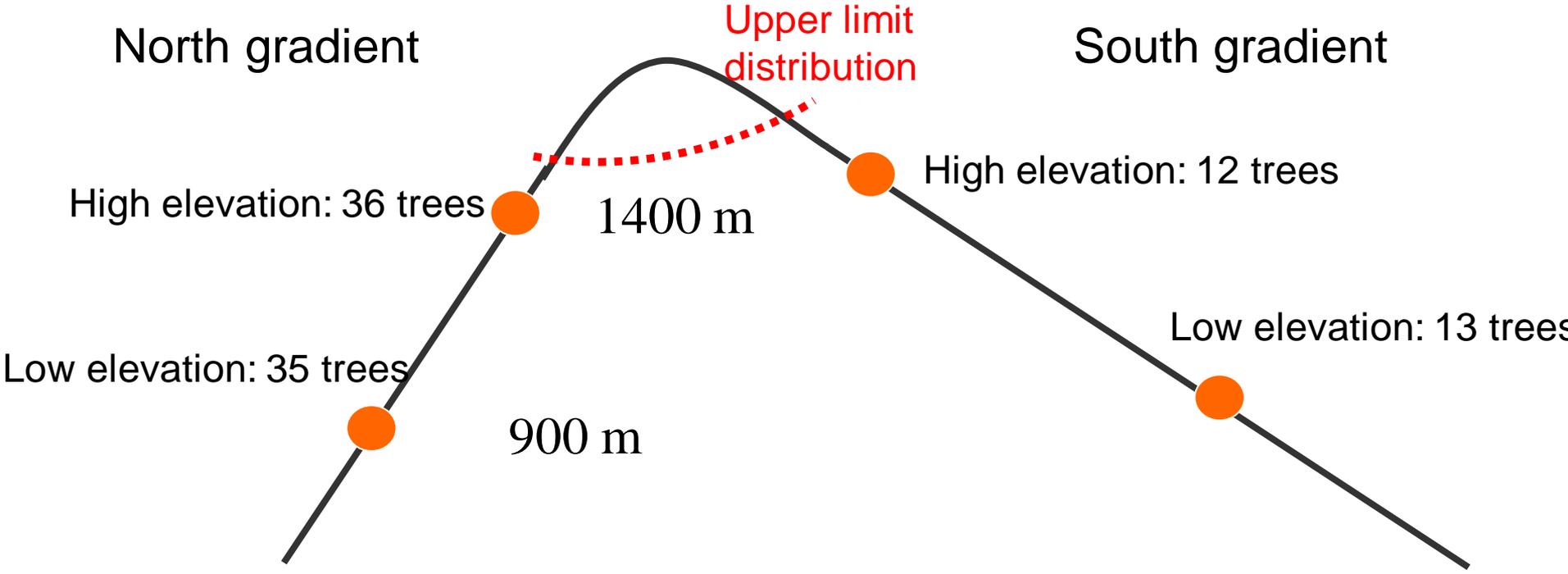
In case of high gene flow, diversifying selection is capturing first beneficial allelic associations (θB) distributed among the loci contributing to the trait, prior to modifying allele frequencies \rightarrow decoupling of Q_{ST} and F_{STq}

*Investigation of this prediction with PDG model
What is the power of F_{ST} -based methods (outlier approaches) to detect selection in such cases ?*

Experimental results : outlier approaches



57 candidate genes - 485 SNPs
(phenology- abiotic stress response)

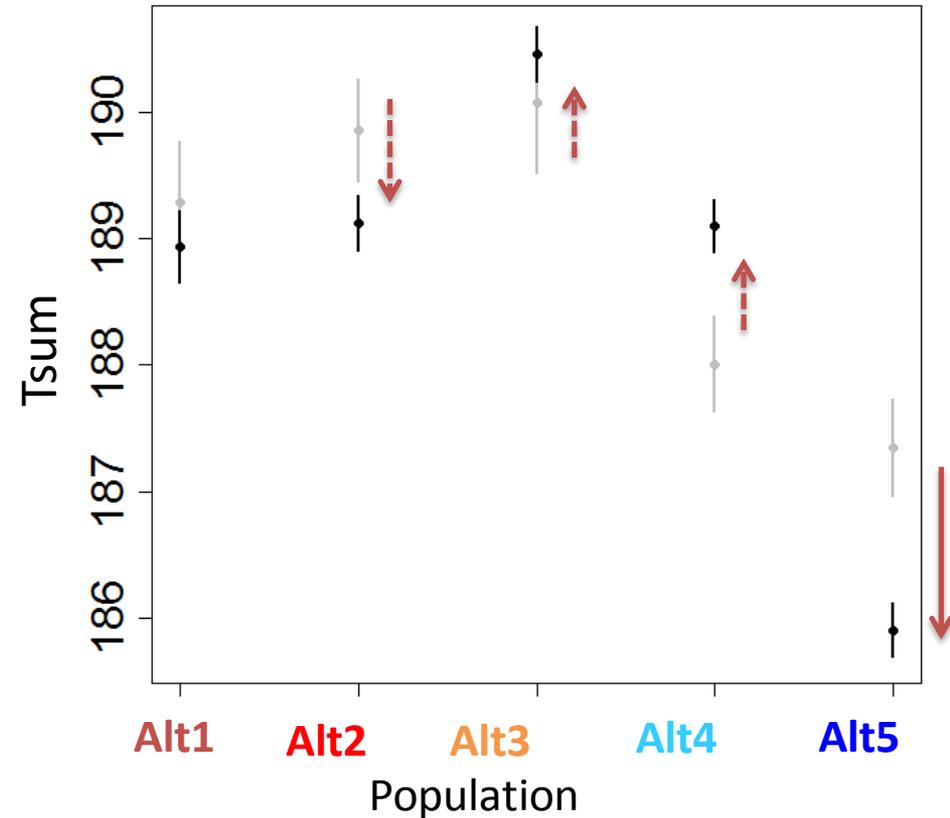


9 outlier SNPs at 5% level

4-7 outlier SNPs at 5% level

Simulation results : outlier approaches

Frost effect on LAI = 20%

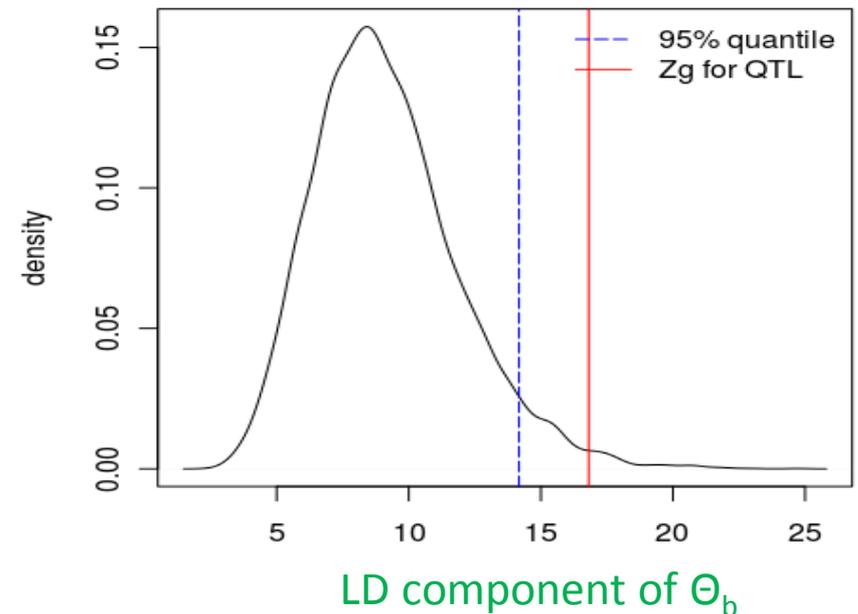


10 QTLs

400 neutral SNPs

→ ~3 % of outliers with the classical FDIST approach

Distribution of LD in neutral SNP versus QTL



Conclusions

1. A new tool to understand selection ← climate

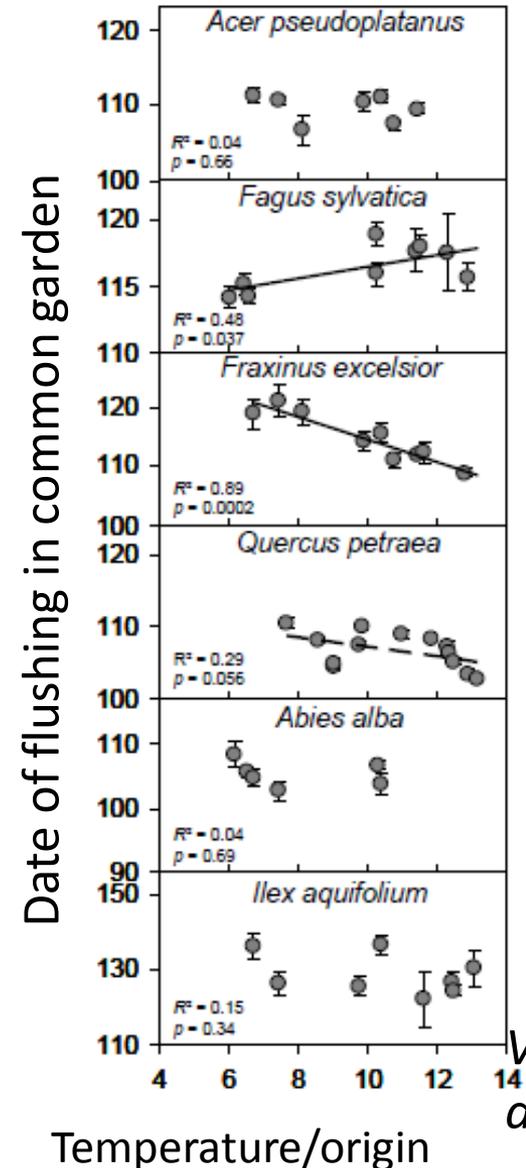
- ✓ Mechanistic biophysical models → valid for other environment conditions
- ✓ Modularity → adapted to other species

2. Evolution can be quick and strong

- ✓ At high elevation Tsum decreased by 4° in 5 generations (mortality)

3. Climatic effects and phenotypic optimum variation across elevation are non monotonic

- ✓ Increasing effect of frost on LAI → either early or late genotypes are selected for depending on elevation
- ✓ Highlights patterns in common garden →

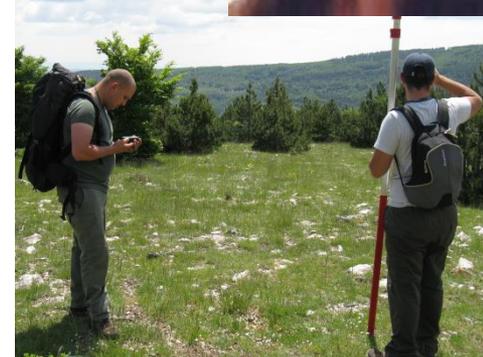


Vitasse et al. 2009



Special Thanks :

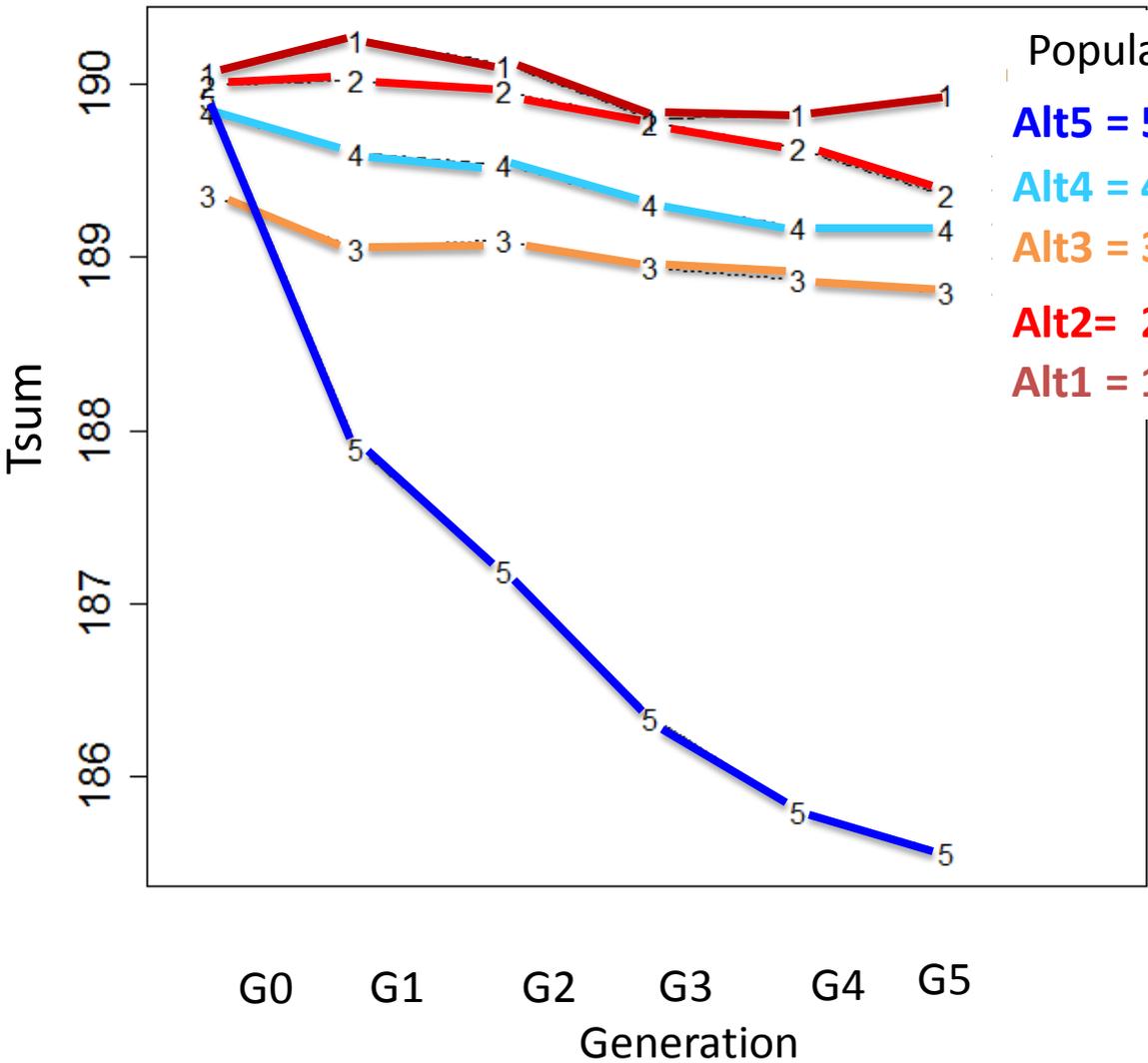
- *François de Coligny*
- *Christian Pichot, Philippe Dreyfus, Marianne Alleaume-Benharira & Francois Lefèvre*
- *Aurore Bontemps, Maxime Cailleret, Julie Gaüzere*
- *The field team of URFM (Nicolas, William) and UEFM (Norbert, Olivier, Frank)*



Results : temporal evolution for Tsum

Frost effect on LAI = 0

Linear model: $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \epsilon_i$

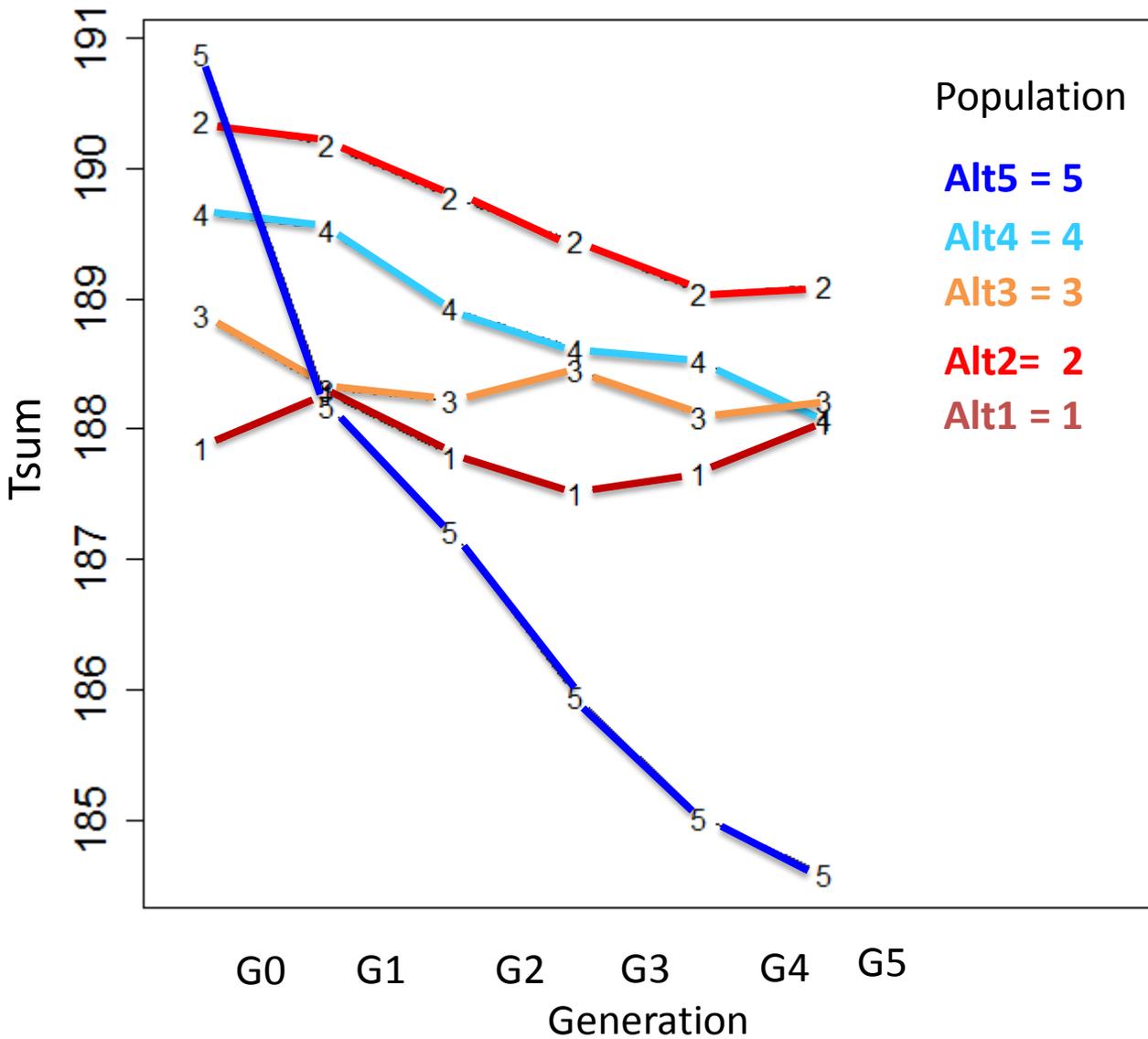


- At all elevation but Alt 5, no significant pattern of evolution for Tsum
- In popAlt5, date of budburst advanced from 188-190 to 184-188 in 5 generations

Results : temporal evolution of T_{sum}/BBD

Frost effect on LAI = 0

Linear model: $T_{sum}_{ij} = Population_i + Generation_j + \epsilon_i$

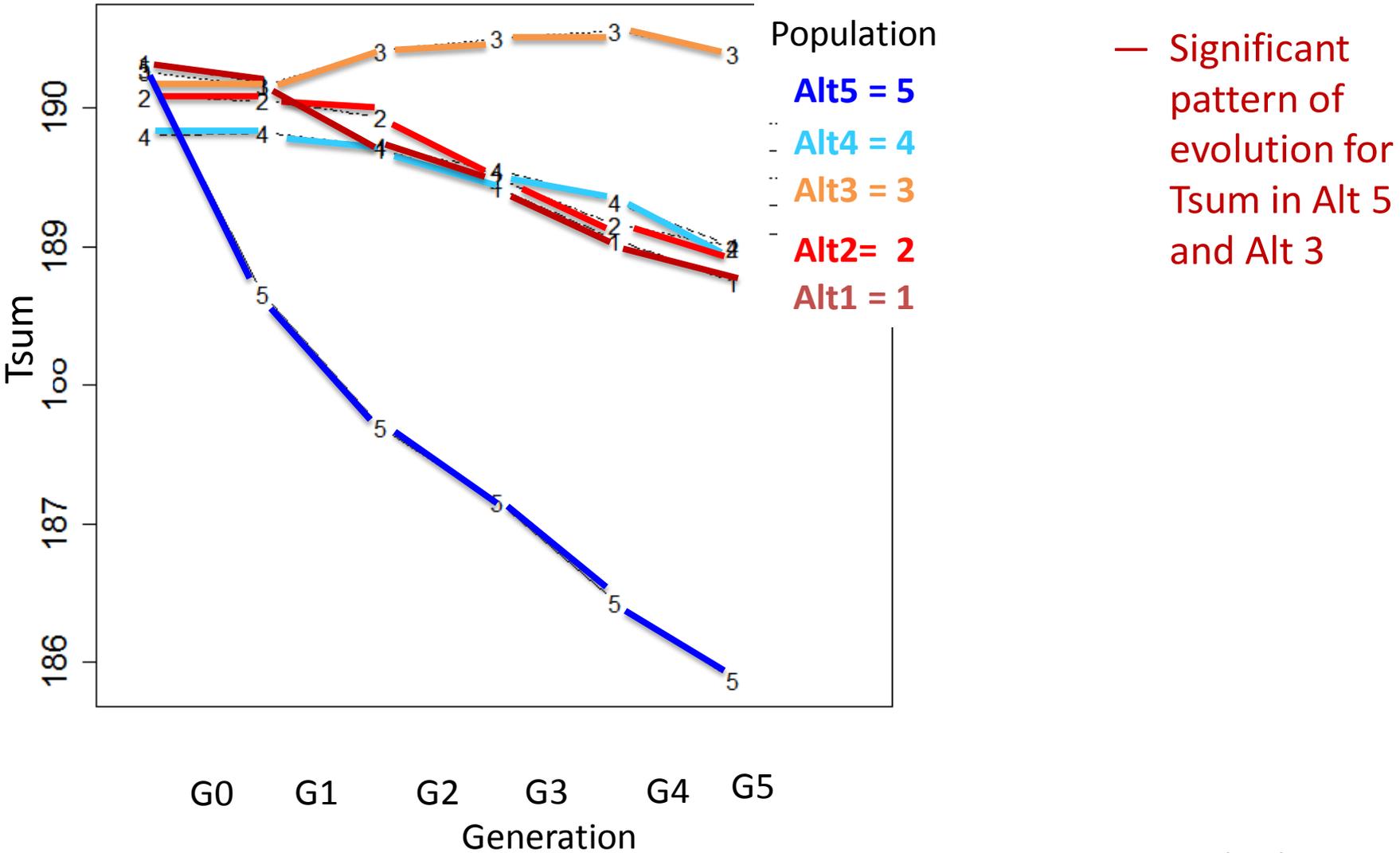


- Overall pattern of evolution towards lower Tsum
- In pop Alt5, the date of budburst advanced from 188-190 to 184-188 in 5 generations

Results : temporal evolution for Tsum

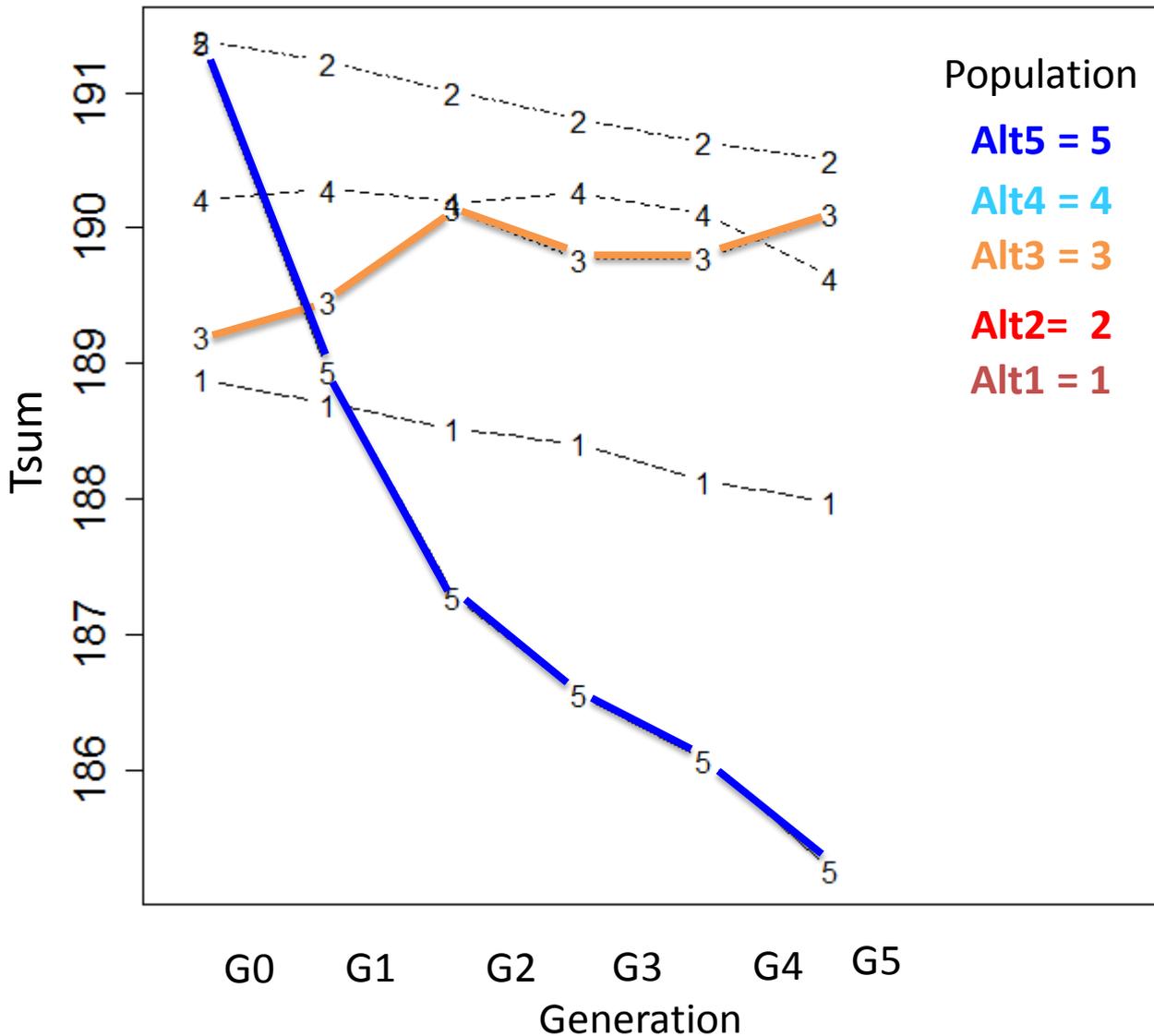
Frost effect on LAI = 20%

Linear model: $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \epsilon_i$



Results : temporal evolution for Tsum

Linear model: $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \epsilon_i$



Significant pattern of evolution for Tsum in Alt 5 and Alt 3:

- BBDAY advanced by 4.4 days in Alt 5
- BBDAY moved back by 0.7 days in Alt 3