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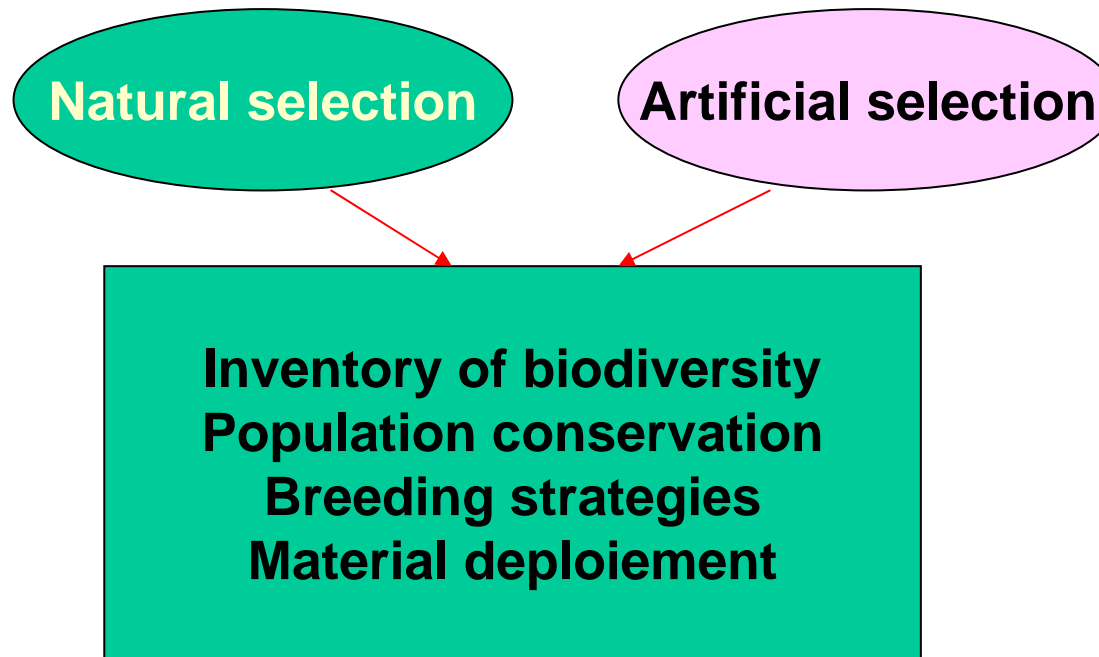
# What might be useful measures of genetic variability for adaptive traits in Scots pine natural populations?

*Catherine Bastien  
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**PROFOREST Workshop, Warsaw, 24-27 August 2004**

# “Adaptive variation” in forest trees

- **common interest** for evolutionary ecology and forestry



- **Survival, growth, resistance and tolerance to biotic and abiotic constraints, and *reproductive behaviour*,...**  
the expression of **multiple genes**, influenced by **multiple environmental factors**

Definition

# “Adaptive variation” in forest trees

- The **idea of compensation** for change in environmental conditions :
  - short-term adaptation is **physiological**
  - long-term adaptation is **genetic**

*“The amount of heritable genetic variation is the ultimate determinant of populations’ potential to respond and adapt to environmental changes”*
- Quest of **individual fitness** or/and most probably of **population fitness**

# “Adaptive variation” in forest trees

## Quantitative genetics

fundamental discipline in plant and animal breeding with  
extended application to evolutionary biology

(Roff 1997, Lynch and Walsh 1998)

- description of **genetic** and **environmental** components of phenotypic variation of quantitative traits

$$P = \mu + G + E + G \times E$$

*Fisher 1918*

- knowledge on **structure** and **location of specific genes**  
**non needed**
- phenotypic resemblance between **relatives**

*Roff D.A. 1997. Evolutionary quantitative genetics. Chapman & hall, New York*

*Lynch M., Walsh B. 1998. Genetics and analysis of quantitative traits. Sinauer Assoc., Sunderland, MA.*

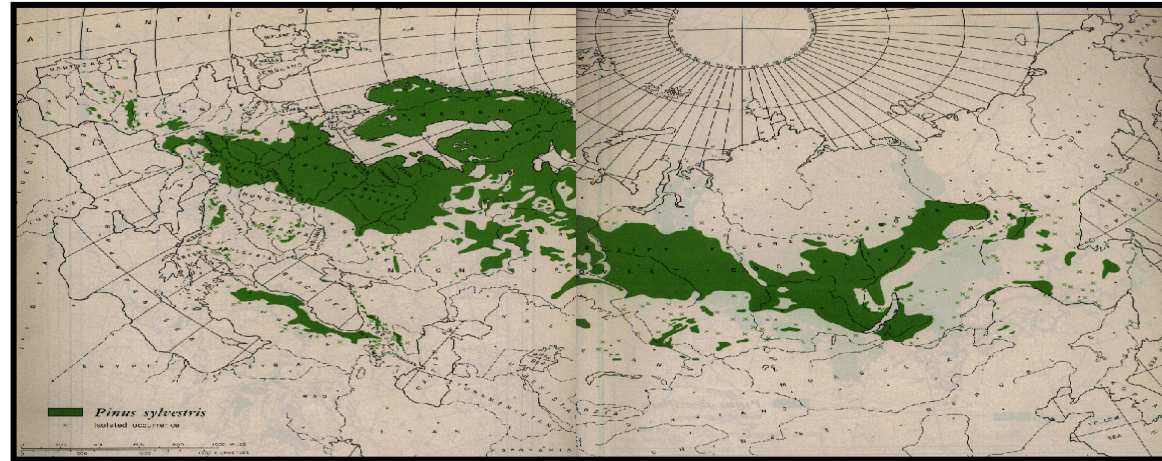
# “Adaptive variation” in forest genetic experiments

## Scots pine Provenance tests

Ogiyevskii series 1910-1916

IUFRO international series 1937-1939, 1982

VNILM series 1974-1976



W.B. Critchfield & E.L. Little, 1966.



**Geographical** structuration for **adaptive variation** in Scots pine  
effects of migration history or/and natural selection ?

Tools : genetic variation in the natural range

# Differentiation of Scots pine populations for adaptive traits

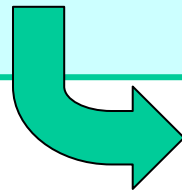
In provenance tests :

$$F_{\text{prov-test}} \text{ from ANOVA } t = V_{\text{Between}} / (V_{\text{Between}} + V_{\text{Within}})$$

$$t' = t / (2 - t) = V_{\text{Between}} / (V_{\text{Between}} + 2 * V_{\text{Within}}) = G_{\text{ST}} = Q_{\text{ST}}$$

(Kremer, 1994, 1997) (Spitze, 1993)

Specific adaptation to abiotic factors	Specific adaptation to biotic factors	Growth potential	Reproductive potential
frost resistance (4 ref in Sweden)	resistance to pathogens (9 ref in Sw, Ge, Pl, Fr)	opt. growth rhythm (3 ref in Sw)	Flowering ability (2 ref in Ru, Fr)
drought resistance (1 ref in Es)	resistance to insects (4 ref in Sw, Pl, Ge, Fr)	competition ability	Seed maturation
pollution resistance (O <sub>3</sub> , SO <sub>2</sub> , NO <sub>x</sub> ) (10 ref in Pl, Ge, Fi)	resistance to herbivores (3 ref in Fi)	nutrient efficiency	



$$Q_{\text{ST}} \cong 0.25 - 0.55$$

# “Scots pine differentiation for adaptive traits”

Tools : indirect prediction with marker loci

```
GACACTGTGCCTTCGCAAATTAAGTGAACCTCATNTTTTTTATTATTCGAG
GACACTGTGCCTTCGCAAATTAAGTGAACCTCATNTTTTTTATTATTCGAG
GACACTGTGCCTTCGCAAATTAAGTGAACCTCATNTTTTTTATTATTCGAG
GACACTGTGCCTTCGCAAATTAAGTGAACCTCATNTTTTTTATTATTCGAG
```

genotype

allozymes

RFLP

microsat

RAPDs

rDNA

SNP



Qualitative information per locus

$A$  = nb alleles in the population or **coefficient of allelic richness**

$H_e = 1 - \sum p_i^2$ , **Nei genetic diversity** or expected **Heterozygosity** within population

$N_e = 1 / (1 - H_e)$ , **mean effective number of alleles per locus** in the population

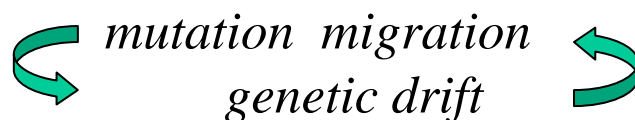
$G_{ST} = 1 - H_S / H_T$ , **Genetic Differentiation Coefficient** between populations (Nei 1986)



# Differentiation of Scots pine populations at marker loci

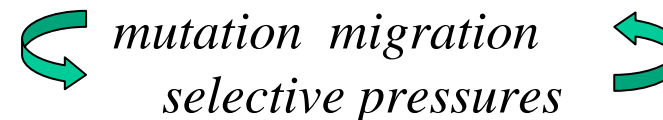
Geographical area	Nb pop.	Nb. loci	N <sub>A</sub>	He	Gst	References
Sweden	9	11 isoz.	4.36	-	0.008	Gullberg et al. 1985
Finland	4	10 isoz.	-	0.34	0.002	Karhu et al. 1996
	5	3 RFLP	3.0	0.49	0.02	Karhu et al. 1996
	4	8 rDNA	-	-	0.14	Karvonen and Savolainen 1993
	2	2 microsat	8.5	0.77	0.014	Karhu et al. 1996
	4	SNP 2phyto	-	-	no diff	Garcia-Gil et al. 2003
Scotland	14	16 isoz.	2.60	0.309	0.028	Kinloch et al 1986
East and Central Europe	16	7 isoz.	2.74	0.363	0.025	Prus-Glowacki and Stephan 1994
	30	3 RAPD	-	0.1-0.25	0.215	Nowakowska 2003
Latvia, Ukraine, Russia	18	21 isoz.	4.00	0.282	0.030	Goncharenko et al 1994
Ukraine, Western Siberia, Turkey	13	8 isoz.	3.50	0.357	0.076	Prus-Glowacki and Bernard 1994
Spain	7	7 isoz.	2.86	0.325	0.040	Agundez et al 1990
Spain+France	14	11 isoz.	2.44	0.311	0.042	Prus-Glowacki et al. 2003

## Genetic diversity



**low population differentiation  
high within population diversity**

## Genetic variability



**high population differentiation for  
some adaptive traits  
still between 45% and 75% of  
genetic variability within  
population**

**Neutral markers can't substitute direct measures of  
quantitative variation for adaptive traits in Scots pine**  
(*Karhu et al. 1996*)

**Direct assessment of adaptive variation is still needed for  
Scots pine and many other forest species**

# “Adaptive variation” within population

What could we learn from provenance tests ?

based on phenotypical approximation

$V_w$  = within provenance variance of design-adjusted individual performances

$CV_{wp} = 100 * \text{sqrt}(V_w) / X$ , corresponding coefficient of variation

$R_w = t_{90} - t_{10}$ , range of design-adjusted individual performances

$r_p$  = phenotypical matrix of correlations between traits if more than 50 to 80 unrelated individuals per population

**Caution = overestimation of genetic adaptive variability !**

# “Adaptive variation” within population

How to measure (easily) usable genetic variation under sexual reproduction ?

*Fisher 1918*

$$G = A + D + I$$

One of Fisher's key insights was that the genotypic value consists of a fraction that can be passed from parent to offspring and a fraction that cannot.

$$A = \text{Breeding Value} = \sum (a_i^k + a_j^k) \quad k=1 \text{ to } n \text{ loci}$$

*Average effects of alleles i and j at locus k*

We can thus estimate the Breeding Value A for a parent by twice the deviation of his offspring from the pop mean

$$A = \text{Breeding Value} = 2 (\mu_{\text{pop}} - \mu_G)$$

# “Adaptive variation” within population

## How to measure (easily) usable genetic variation under sexual reproduction ?

*Fisher 1918*

$$G = A + D + I$$

$$V_G = V_A + V_D + V_I$$

Estimates of  $V_A$  require known collections of relatives

- The amount of phenotypic resemblance among relatives for the trait provides an indication of the amount of genetic variation for the trait.
- If trait variation has a significant genetic basis, the closer the relatives, the more similar their appearance
- Easiest available collections of relatives for forest tree species:
  - open pollinated progenies : half-sib, parent-offspring
  - controlled crosses : full-sib, half-sib (polymix, nested /factorial design)
  - vegetative copies : clones
- Two key statistical ANOVA identities
  - Total variance = between-group variance ( $V_{Fam}$ ) + within-group variance ( $V_W$ )
  - Variance(between groups) = covariance (within groups)

# “Adaptive variation” within population

## How to measure (easily) usable genetic variation under sexual reproduction ?

- Two key statistical ANOVA identities
  - Total variance = between-group variance ( $V_{Fam}$ ) + within-group variance ( $V_W$ )
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### Half-sib progenies

$$V_{Fam} = Cov(HS)$$

$$V_{Fam} = V_A / 4$$



4  $V_{Fam}$  gives an estimation of  $V_A$

### Full-sib progenies

$$V_{Fam} = Cov(FS)$$

$$V_{Fam} = V_A / 2 + V_D / 4$$



2  $V_{Fam}$  is an upper bound for  $V_A$

### Coefficient of additive genetic variation

$$CV_A = 100 * \sqrt{V_A} / \text{mean},$$

# “Adaptive variation” within population

## Narrow sense heritability

$$h^2 = V_A / V_P$$

- **heritability** determines the degree of **resemblance between parents and offsprings** and thus determines the **response to selection**
- **Heritabilities** are **functions of populations**  
h<sup>2</sup> values only make sense in the content of the populations for which it was measured
- **Heritabilities** are also **functions of the distribution of environmental values**  
h<sup>2</sup> values measured in one environment may not be valid under another  
→ interest of multisite evaluation to predict response to different selection pressures
- **Heritability** is a good to excellent **predictor of short-term response to selection** **BUT** is completely unreliable **for long-term response** (over 5 to 10 generations)

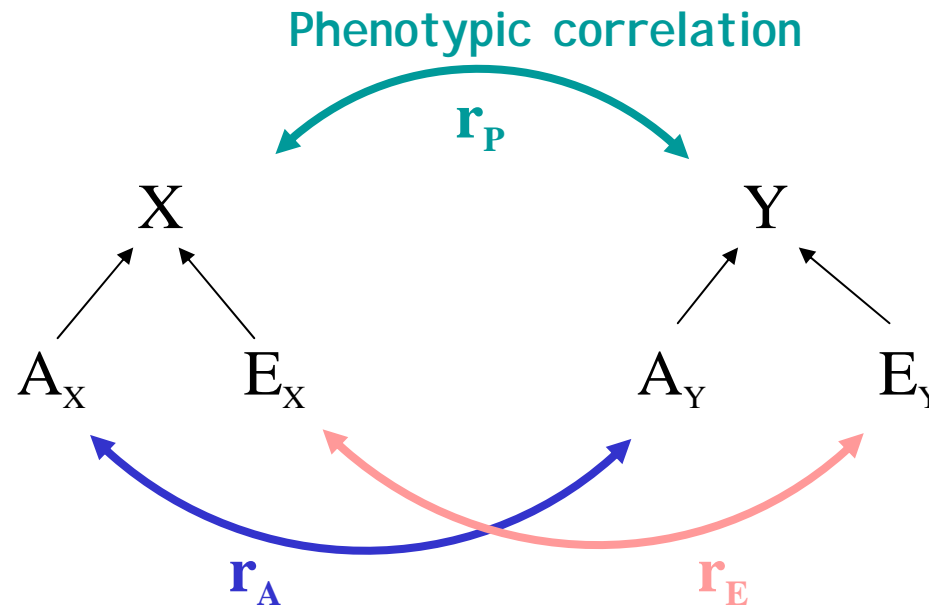
# Estimations of genetic variability measures in Scots pine progeny tests : Data

<b>Adaptive and production Traits</b>	<b>Age</b>	<b>Population Progenies</b>	<b>h<sup>2</sup></b>	<b>References</b>
<b>Frost resistance</b>	1	"+" trees Full-Sib progenies	?	Nilsson and Andersson 1987
<b>Frost hardiness</b>	1	"+" trees Full-Sib progenies	?	Norell et al 1986
<b>Bud-set phenology</b>	1-3	"+" trees Full-Sib progenies	<b>0.51</b>	Mikola 1982
<b>Twisting rust resist</b>	3	"+" trees OP progenies	<b>0.70</b>	Quencez et Bastien 2000
<b>Height growth</b>	6-11	"+" trees OP progenies	<b>0.24-0.38</b>	Krusche et al 1980
	13	random trees OP progenies		Poykko 1982
	16	random trees OP progenies	<b>0.33</b>	Bastien 1998, non publ.
	30	random trees OP progenies.	<b>0.21-0.42</b>	Eriksson et al 1987
<b>Diameter growth</b>	11	"+" trees OP progeniesP	<b>0.15</b>	Krusche et al 1980
	16	random trees OP progenies	<b>0.26</b>	Quencez et Bastien 2000
	140	random trees OP progenies	<b>0.27</b>	Bastien et Kowalczyk 2003
	30	random trees OP progenies	<b>0.10-0.35</b>	Eriksson et al 1987
<b>Branch angle</b>	13	random trees OP progenies	<b>0.12</b>	Poykko 1982
	16	"+" trees Full-Sib progenies	<b>0.20</b>	Velling and Tigerstedt 1984
	140	random trees OP progenies	<b>0.35</b>	Bastien et Kowalczyk 2003
<b>Stem straightness</b>	30	random trees OP progenies	<b>0.13-0.23</b>	Eriksson et al 1987
<b>Wood density</b>	33	"+" trees Full-Sib progenies	<b>0.50</b>	Hannrup and al 1998



# “Adaptive variation” within population

## Genetic and environmental correlations



$r_A$  = correlation of breeding values arises from two sources

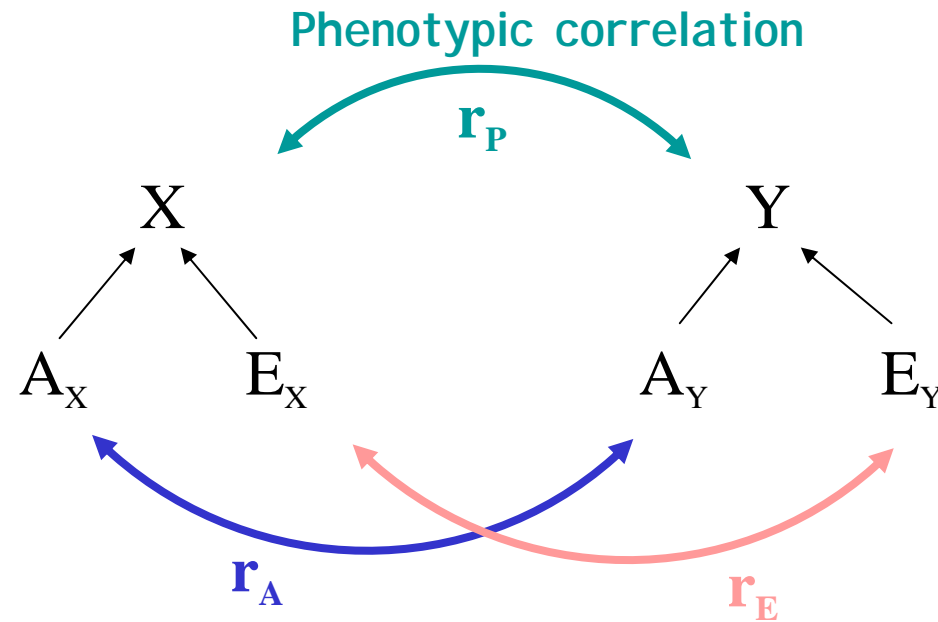
- Pleiotropic effects of loci on both traits
- Linkage disequilibrium which will decay over time

$r_E$  = correlation of environmental deviations

- Includes non-additive genetic effects
- Arises from exposure of the two traits to the same individual environment

# “Adaptive variation” within population

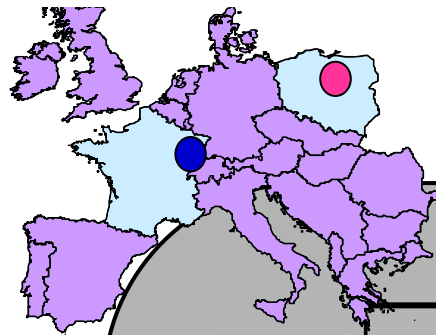
## Genetic and environmental correlations



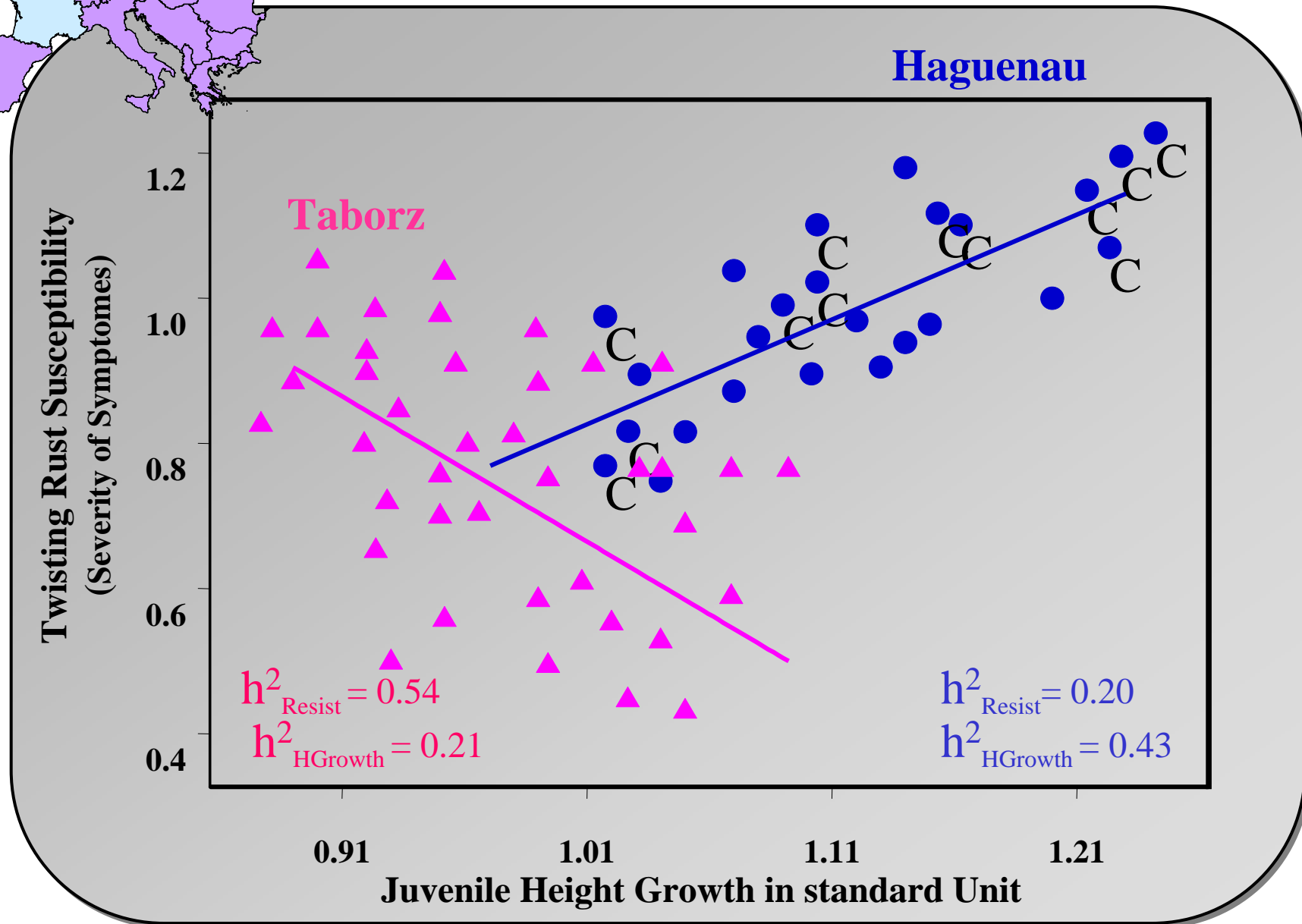
$$r_P = r_A h_X h_Y + r_E \sqrt{(1-h_X^2)(1-h_Y^2)}$$

Phenotypic (observed correlation) is a function of the heritabilities of the traits and the genetic and environmental correlations

- If  $h^2$  are high,  $r_A$  is more important
- If  $h^2$  are low,  $r_E$  is more important



# “Adaptive variation” within Scots pine populations

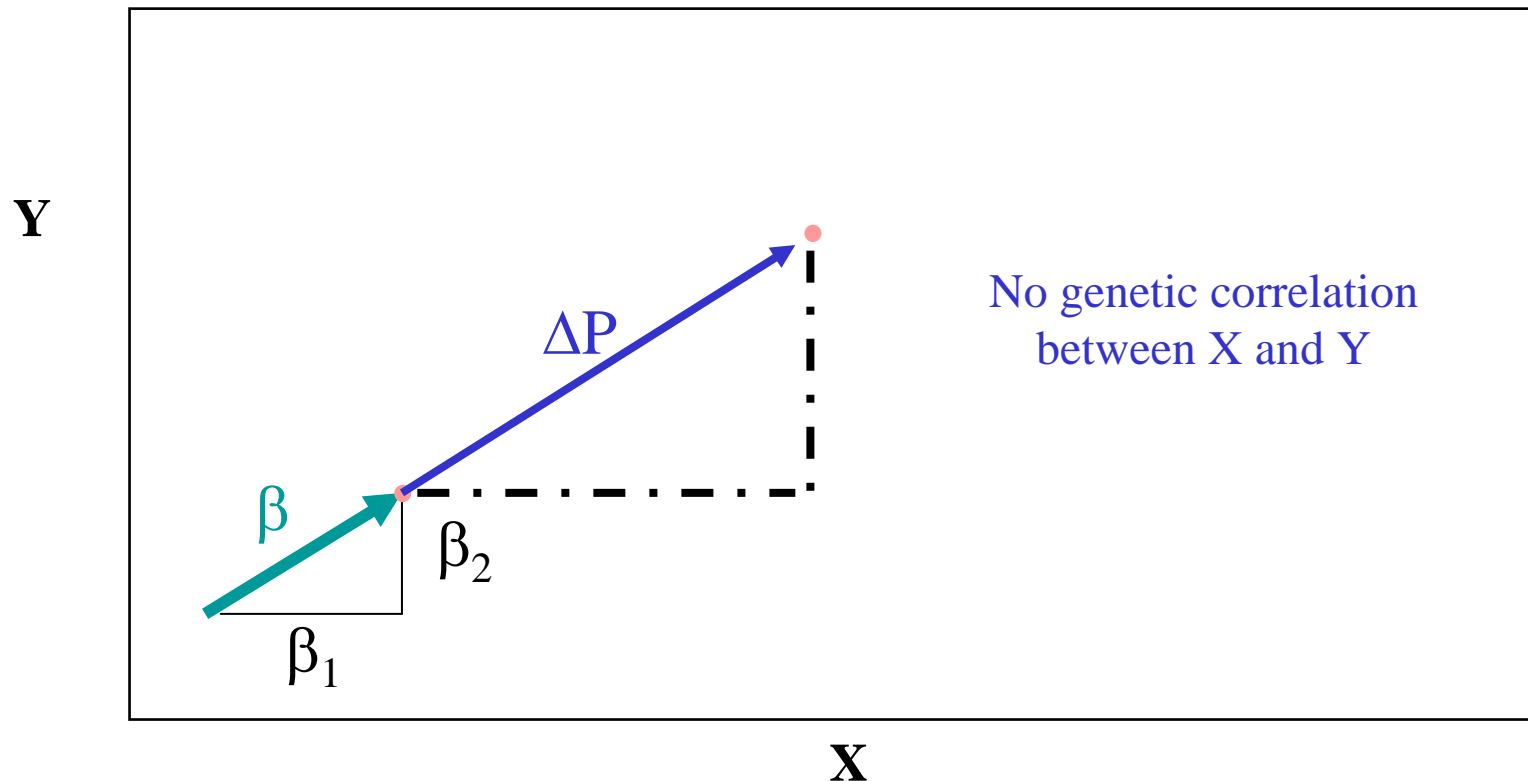


# “Adaptive variation” within population

## Prediction of response to natural/artificial selection in the whole phenotype

Informations needed :

- genetic variance of each trait  $V_A$
- genetic correlation or covariance of each set of traits  $r_A$
- selection on each trait: vector of selection gradients  $\beta$

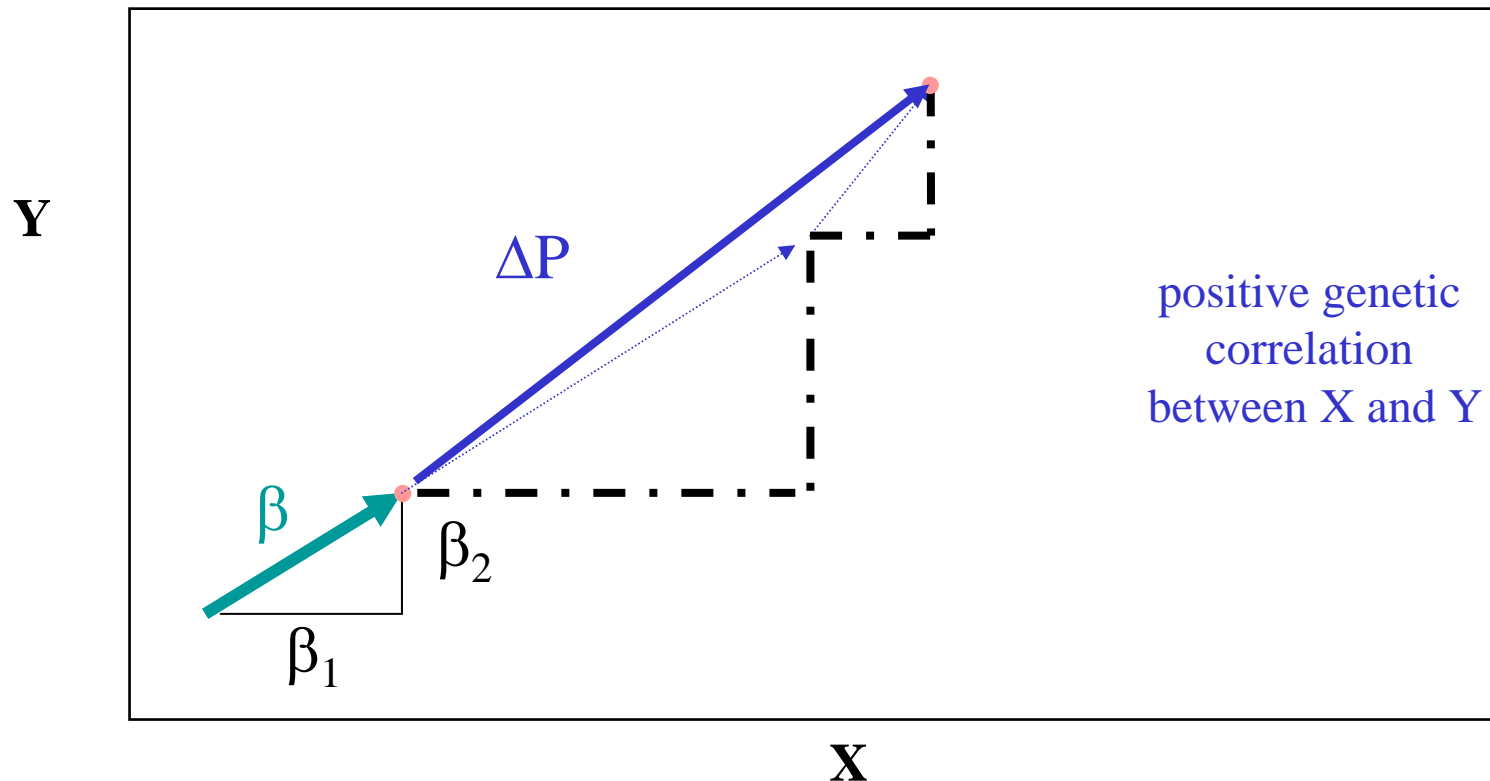


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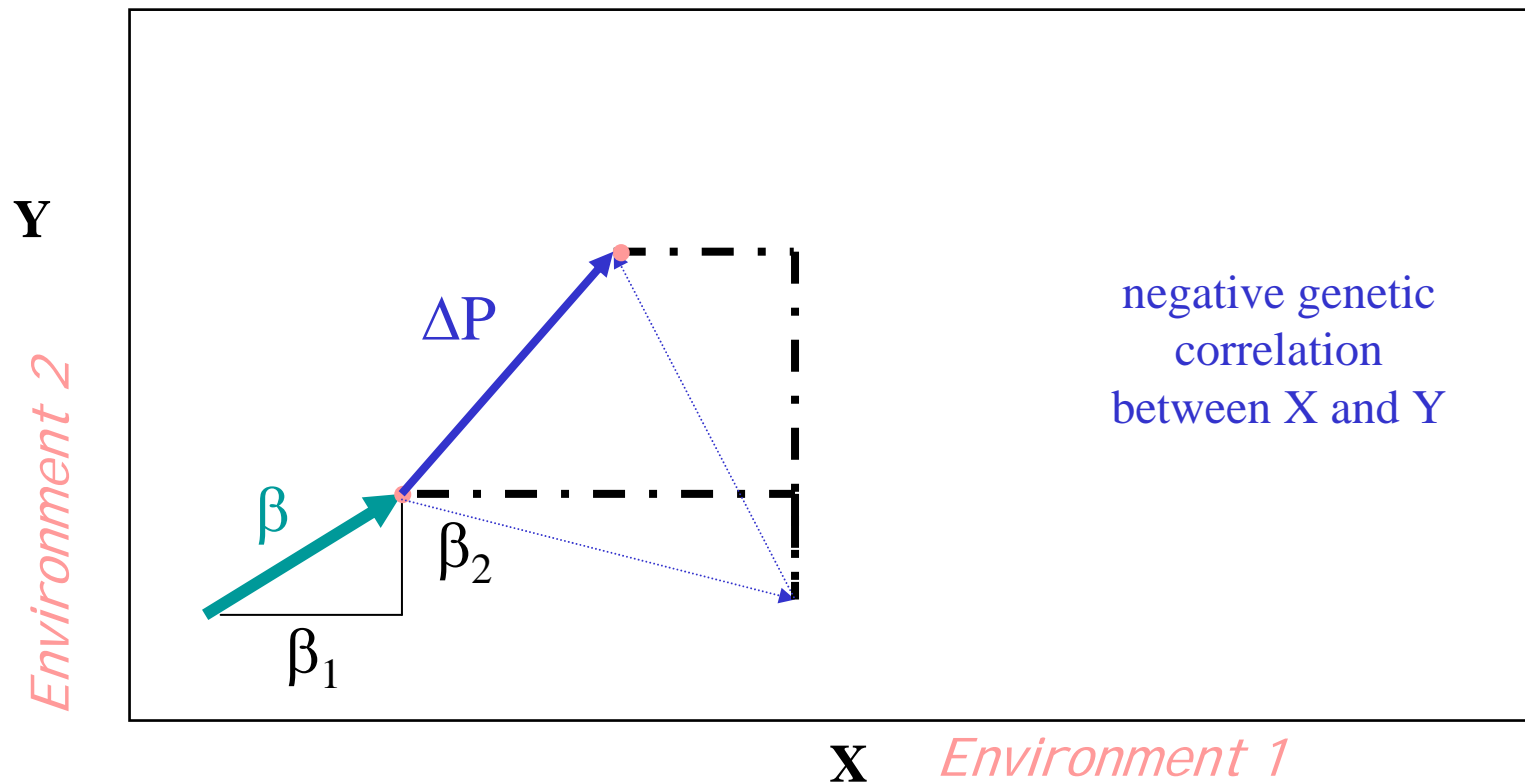


# “Adaptive variation” within population

Prediction of response to natural/artificial selection in the whole phenotype

Informations needed :

- genetic variance of each trait  $V_A$
- genetic correlation or covariance of each set of traits  $r_A$
- selection on each trait: vector of selection gradients  $\beta$



## Estimations of genetic variability measures in Scots pine progeny tests : lessons and gaps

- Genetic variability measures are available mostly for **Scots pine populations from the continuous range** covered by ice during last glaciation.
- **Few differences between these populations** are observed for the amount of genetic variability for adaptive, morphological and wood production traits.
- **High level of within population genetic variability** can be observed for complex traits such as *volume growth* or for *pest resistance*
- Most studies are based on “+” tree progenies : estimates of genetic variability of unselected populations are probably **underestimates**
- Few data are available on genetic variability for **reproductive behaviour** of Scots pine which is directly linked to fitness.
- Few multi-environmental evaluation of genetic variability within populations

# “Adaptive variation” within population

## Genetic basis of phenotypic plasticity ?

Option 1 : phenotypic plasticity evolves in response to selection for plasticity genes per se



Option 2 : phenotypic plasticity is simply a by-product of selection favoring the expression of specific phenotypes in different environments



How phenotypic plasticity could be measured in multisite experiments



# “Adaptive variation” within population

Informations collected on multisite experiments

$$E(G_{ij}) = \mu + G_i + E_j + (GE)_{ij}$$

Mean value  
over the range  
of sites

Site  
effect

Genotype. x Site  
interaction

General adaptation  
to the range of sites  
tested

Specific adaptation  
to a particular  
environment

*Of interest only if GxE is limited*

Tools : partitioning of GxE interaction

# Potential measures of genetic variability within populations of Scots pine

## Stability parameters experiment-dependent

$S_i^2$  , Shukla variance stability (1972)

$W_i$  , Wricke ecovalence (1962)

$S_i^4$  , Hühn rank coefficient (1979)

$\gamma^1, \gamma^2, \dots, \gamma^r$  , r multiplicative terms of  
AMMI model (Gauch and Zobel 1988)  
(*eq. PCA of GE terms*)

## Stability parameters and predictive models

$b_j$  , regression coefficient of Finlay  
and Wilkinson joint regression  
(1963)

*limit of linear model of interaction*

$\lambda_i^1, \lambda_i^2, \dots, \lambda_i^r$  , regression coefficients of  
factorial regression with sites  
covariates (Denis 1988)

*interest of environmental constraints covariates  
(drought index, site index, mean t°)*

# Scots Pine Genetic variability for adaptability to different environments

**Scots pine provenance flexibility:** a seed transfer guide for scandinavian populations (Eiche 1966, Eriksson et al 1980, Raymond and Lindgren 1990)

$$E(Y) = A / (1 - ((X-B)/C)^2)$$

**X** = site index reflecting the relative site severity for volume production (described by latitude adjusted to a constant altitude)

**A** = maximal performance of the provenance over the range of sites

**B** = optimal site index for the given provenance

**C** = change in the environment from the optimum which cause a 50% reduction in performance

**Scots pine within population general adaptability :** GxE interactions limited to scale effects over sites but not clearly explained by genetic variability for nutrient efficiency (Gullberg and Vegerfors 1987, Jiang 1988, Jonsson et al. 1992)

## Scots Pine genetic variability for adaptability: lessons and gaps

- Most studies concern **general adaptation** to a given range of environments and not **specific adaptation** to climatic, edaphic or silvicultural constraints.
- Environmental conditions of the European range of Scots pine forests must be described by **pertinent covariates** : latitude, altitude, longitude but also covariates describing selective pressures (frost, drought, wind, biotic aggressors, competition,...)
- Is Scots pine adaptability a matter of **genotypic buffering** (nb and variability of genetic components) or a matter of **heterozygosity** per se ? No real data available



**More analyses of reaction norms or response curves is needed**

*(Debat and David 2002, Sultan 2003)*

# What might be useful measures of genetic variability for adaptive traits in Scots pine populations?

## OBJECTIVES FOR THE FUTURE

### Molecular biology

Saturated genetic maps  
Comparative mapping in Pinaceae

### Phenotypical evaluation

Phenotypical performances  
in artificial and multisite genetic tests

### Genetic basis of phenotypic plasticity

Identification of molecular markers linked to adaptive traits  
And candidate loci involved in adaptive traits  
(ATL)

**ATL diversity analysis over Scots pine natural range**  
*(spatial structuration according to selection pressures)*

**Recommendations for management of  
genetic resources**



**Thank you very much for your attention**

**PROFOREST Workshop, Warsaw, 24-27 August 2004**

*Catherine Bastien  
INRA, UAGPF Orléans*