



**HAL**  
open science

## Micro-evolutionary patterns of juvenile wood density in a pine species

Jean-Baptiste J.-B. Lamy, Frédéric F. Lagane, Christophe Plomion, Hervé H.  
Cochard, Sylvain S. Delzon

► **To cite this version:**

Jean-Baptiste J.-B. Lamy, Frédéric F. Lagane, Christophe Plomion, Hervé H. Cochard, Sylvain S. Delzon. Micro-evolutionary patterns of juvenile wood density in a pine species. *Plant Ecology*, 2012, 213 (11), pp.1781-1792. 10.1007/s11258-012-0133-2. hal-02649653

**HAL Id: hal-02649653**

**<https://hal.inrae.fr/hal-02649653v1>**

Submitted on 29 May 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# *Micro-evolutionary patterns of juvenile wood density in a pine species*

**Jean-Baptiste Lamy, Frédéric Lagane,  
Christophe Plomion, Hervé Cochard &  
Sylvain Delzon**

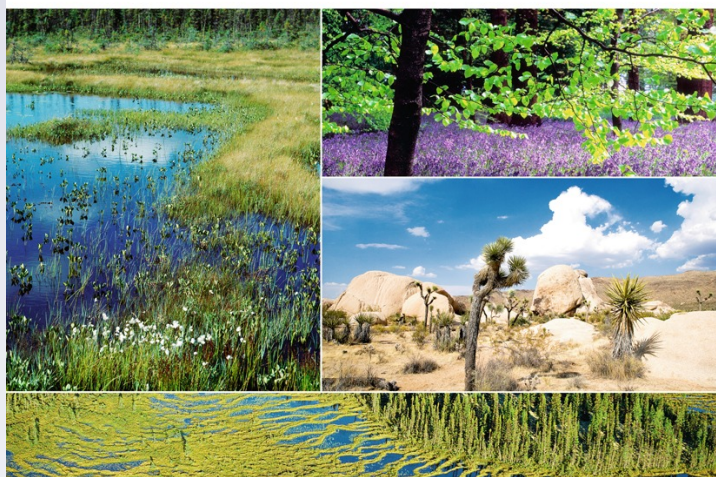
**Plant Ecology**  
An International Journal

ISSN 1385-0237  
Volume 213  
Number 11

Plant Ecol (2012) 213:1781-1792  
DOI 10.1007/s11258-012-0133-2

**Plant  
Ecology**

VOLUME 213 NUMBER 11 NOVEMBER 2012  
ISSN 1385-0237  
AN INTERNATIONAL JOURNAL



 Springer

 Springer

**Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media Dordrecht. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

# Micro-evolutionary patterns of juvenile wood density in a pine species

Jean-Baptiste Lamy · Frédéric Lagane ·  
Christophe Plomion · Hervé Cochard ·  
Sylvain Delzon

Received: 13 February 2012 / Accepted: 26 September 2012 / Published online: 5 October 2012  
© Springer Science+Business Media Dordrecht 2012

**Abstract** Wood density can be considered an adaptive trait, because it ensures the safe and efficient transport of water from the roots to the leaves, mechanical support for the body of the plant and the storage of biological chemicals. Its variability has been extensively described in narrow genetic backgrounds and in wide ranges of forest tree species, but little is known about the extent of natural genetic and phenotypic variability within species. This information is essential to our understanding of the evolutionary forces that have shaped this trait, and for the evaluation of its inclusion in breeding programs. We assessed juvenile wood density, leaf area, total aboveground biomass, and growth in six *Pinus pinaster* populations of different geographic origins

(France, Spain, and Morocco) growing in a provenance-progeny trial. No genetic differentiation was found for wood density, whereas all other traits significantly differed between populations. Heritability of this trait was moderate, with a low additive genetic variance. For retrospective identification of the evolutionary forces acting on juvenile wood density, we compared the distribution of neutral markers ( $F_{ST}$ ) and quantitative genetic differentiation ( $Q_{ST}$ ). We found that  $Q_{ST}$  was significantly lower than  $F_{ST}$ , suggesting evolutionary stasis. Furthermore, we did not detect any relationship between juvenile wood density and drought tolerance (resistance to cavitation), suggesting that this trait could not be used as a proxy for drought tolerance at the intraspecific level.

**Keywords** Canalization · Heritability ·  $Q_{ST}/F_{ST}$  comparison · Pine · Evolutionary stasis · Juvenile wood density

J.-B. Lamy · F. Lagane · C. Plomion · S. Delzon  
INRA, UMR 1202 BIOGECO, 33610 Cestas, France

J.-B. Lamy · F. Lagane · C. Plomion · S. Delzon (✉)  
Université de Bordeaux, UMR 1202 BIOGECO, Avenue  
des Facultés, 33405 Talence, France  
e-mail: sylvain.delzon@u-bordeaux1.fr

J.-B. Lamy · H. Cochard  
INRA, UMR 547 PIAF, University of Blaise Pascal,  
63100 Clermont-Ferrand, France

*Present Address:*  
S. Delzon  
Department of Agriculture, Food & Natural Resources,  
University of Sydney, 1 Central Avenue, Australian  
Technology Park, Eveleigh, NSW 2015, Australia

## Introduction

Recent ecological theories have included wood density (mass of wood per unit volume) as key dimension of the variation between woody plant strategies (Westoby et al. 2002; Westoby and Wright 2006; Chave et al. 2009; Zanne et al. 2010). Wood density describes the proportion of cell walls in a given woody tissue. This proportion reflects three functions: the safe

and efficient transport of water from the roots to the leaves, mechanical support for the body of the plant, and the storage of biological chemicals. Wood density is strongly constrained by a trade-off between these functions (Chave et al. 2009) that has influenced the evolution of woody plants over millions of years. It is possible to extrapolate some of the features of the tree, such as growth rate and hydraulic strategy, from the wood density of the species concerned (McCulloh et al. 2011). Species with high wood density are expected to grow more slowly and to have a lower hydraulic efficiency and a higher resistance to embolism than species with a lower wood density (Poorter et al. 2010; Markesteijn et al. 2011). Wood density is also thought to be a good proxy for drought tolerance (i.e., survival of extreme drought events) (Hacke and Sperry 2001; Brodribb and Cochard 2009). For example, after the 2003 heatwave in Europe, *Pseudotsuga menziesii* trees with denser wood and a higher proportion of late wood had higher survival rates than trees with a lower wood density (Martinez-Meier et al. 2008). In *Pseudotsuga menziesii* and *Picea abies* clones, Rosner et al. (2008) and Dalla-Salda et al. (2011) found that wood density was negatively correlated with resistance to cavitation.

Chave et al. (2006) countered the widespread belief that wood density is determined principally by environmental conditions, by suggesting that there is a strong phylogenetic signal controlling interspecific wood density variation. However, in temperate region, wood density may vary considerably in the environment of an individual plant (increasing from the early to the late wood), but the variation between individuals of a given species remains limited and, more importantly, the mean wood density for a given species is generally highly conserved. Many studies have investigated the intraspecific variability of wood density, dissecting the phenotypic variation of wood density into genetic and environmental components (and their interaction) for most commercial forest tree species (Aguiar et al. 2003; Bouffier et al. 2008; Martinez-Meier et al. 2011; Apiolaza 2011). The phenotypic coefficient of variation for wood density is generally low, as is the genetic additive coefficient of variation (these conclusions do not apply to interspecific crosses, such as *Eucalyptus* sp.) (Apiolaza 2011). However, these quantitative estimators have often been measured in narrow genetic backgrounds (or hybrids), without reference to the natural variation of

wood density within the species concerned. Even in studies in which wood density was measured in several populations, efforts were rarely made to determine whether the observed variation between populations was caused by genetic drift or past selective events, even though knowledge about the mechanisms shaping the variability of this trait would be useful if this trait was to be incorporated into a breeding program. Some traits are known to be robust to genetic alterations (e.g., wing shape in *Drosophila* sp., mammalian body temperature), such as mutation, drift, or recombination events, and these traits generally have a low variability (phenotypic and/or genetic) (Gilchrist and Partridge 2001; Hansen and Houle 2004). In a breeding context, it is difficult to manipulate these traits: genetic gains at each generation are limited by the low additive genetic variance. However, such “canalized” traits provide a guarantee of a certain level of trait constancy in diverse environmental conditions (Knap 2005; Mormede et al. 2011).

Most of the previous studies dealt with wood density measured on mature trees and very little work has been devoted to juvenile wood density from an evolutionary ecology point of view. The seedling stage is the woody plant life stage with the greatest mortality (the strongest selection pressure) (Petit and Hampe 2006). Young seedling performance may be more important than mature individual performance in determining species distributions and evolution (Figuroa and Lusk 2001). This study had three main objectives: (i) to assess between- and within-population variation of juvenile wood density, using genetic material originating from contrasting climatic environments, (ii) to determine the main evolutionary forces responsible for shaping the genetic variability of juvenile wood density between populations (i.e., contributing to population differentiation), and (iii) to assess the strength of the correlation between juvenile wood density and drought tolerance (resistance to cavitation). We carried out a case study in maritime pine (*Pinus pinaster* Ait.), a species with a fragmented distribution in the western part of the Mediterranean region. The scattered distribution of this species may have prevented or limited gene flow between different groups of populations, promoting high levels of genetic divergence between ecotypes, due to genetic drift (Ribeiro et al. 2002) and/or natural selection (Quezel and Barbero 1998 in Richardson 1998).

## Materials and methods

### Plant material

We used the same material described in a recent paper by Lamy et al. (2011). Briefly, a provenance-progeny trial was established in December 2003 at the INRA forestry station (Cestas, France, 44°44'N, 00°46'W), with 1-year-old seedlings from open-pollinated seeds collected from 24 natural populations (or ecotypes) in France, Spain, Morocco, and Tunisia, to cover the fragmented distribution of *Pinus pinaster* (see Lamy et al. 2011). Each population was represented by 20–30 half-sib families. The trial was arranged in a randomized block design (15 blocks in total) with single-tree plots. Each block contained at least one tree from each half-sib family. A selective sampling of 6-year-old saplings was carried out as described by Lamy et al. (2011), leading to the selection of six populations representative of the maritime pine climatic envelope. Climate and location of the studied population are presented in Table 1. We sampled eight families with one half-sib in each block (6 populations/8 families/5 blocks = 240 genotypes) at random for further analysis.

### Assessment of wood density

Wood density ( $D$ ,  $\text{g cm}^{-3}$ ) was measured on a section of dry branch. The samples corresponded to the 2007 and 2008 growth units on the 2007 whorl when possible. Sampled branches were fully exposed to the sun, more than 40 cm long and had a diameter of 0.3–1 cm. The number of trees for which wood density data were available per cambial year was as follows:

10 for 2 years old, 151 for 3 years old, 76 for 4 years old, and nine for 5 years old. No difference of branch age was found between populations ( $F_{1/221} = 0.07$  and  $P = 0.79$ ), reducing the risk of sampling procedure bias. Mean wood density was measured for 240 genotypes. For each sample, we used a double-bladed saw to cut a transverse section with a constant thickness of 2 mm. Wood density was measured with an indirect-reading X-ray densitometer (Polge 1966). Two orthogonal (longest and shortest axes) radial density profiles were obtained by analyzing the scanned images with WinDENDRO software (Guay et al. 1992). Ring limits were determined automatically, checked manually, and then corrected with this software. For each genotype, we derived three parameters from the distribution of wood density values (after removing the values corresponding to the pith), the mean value ( $D_{\text{mean}}$ ), the 10th percentile ( $D_{\text{min}}$ ) and the 90th percentile ( $D_{\text{max}}$ ).  $D_{\text{min}}$  was strongly correlated with the mean density of earlywood, whereas  $D_{\text{max}}$  was correlated with the mean density of latewood (data not shown,  $r > 0.8$ ). We carried out the analysis on both radial density profiles separately to check the impact of compression and normal wood on the variance estimation. Similar patterns were observed for both profiles (not in absolute values, but in terms of significance) because the sampled branches were orthotropic, so we pooled the data.

### Biomass, collar diameter, leaf area, and cavitation resistance measurement

At the age of 3 years, all the saplings in six blocks (blocks 1–6) were cut at the collar position. Total

**Table 1** Climatic data, location, and elevation of the studied maritime pine populations

Sampling location	Longitude (°)	Latitude (°)	$n$	Elevation (m)	$P_i$ (mm)	$T_m$ (°C)	VPD <sub>max</sub> (hPa)	ETP (mm)
Bayubas de Abajo (Central Spain)	−2.87	41.52	39	955	561	10.5	11.42	882.9
Coca (Central Spain)	−4.08	41.37	40	788	452	11.9	14.23	718.7
Mimizan (South-western France)	−1.30	44.13	40	37	1176	13.2	7.26	751.59
Oria (South-eastern Spain)	−2.62	37.87	40	1232	451	13.4	14.29	922.59
San Cipriano de Ribarteme (Northern Spain)	−8.70	42.13	40	310	1625	13.8	8.54	721.91
Tamrabta (Southern Morocco)	−5.02	33.66	40	1760	550	15.1	18.56	976.54

$n$  number of sampled individuals for wood density measurements,  $P_i$  mean annual precipitation,  $T_m$ , mean annual air temperature, VPD<sub>max</sub> maximum water vapor pressure deficit (in July for all provenances), ETP annual sum of potential evapotranspiration

above-ground biomass ( $W_a$ , g), including the main stem, branches, and needles, was determined by weighing after the material had been dried in an oven at 55 °C for 72 h (Eveno 2008). Needle biomass ( $W_{\text{needle}}$ , g) was also determined separately. For this study, we used a subset of data corresponding to the selected populations.

On the other blocks (blocks 7–12), collar diameter ( $\phi$ , mm) was measured on the selected populations and families only at the age of 6 years, in 2007. Specific leaf area (SLA, in  $\text{m}^2 \text{kg}^{-1}$ ) was also determined for 20 needles per genotype. Total leaf area ( $A_{\text{Leaf}}$  in  $\text{m}^2$ ) was estimated retrospectively, by multiplying total  $W_{\text{needle}}$  (blocks 1–6) by family mean of SLA (blocks 7–12). Resistance to cavitation was determined in a previous study (Lamy et al. 2011).

### Quantitative genetic analysis

Genetic analysis was conducted with the following mixed model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{pop} + \mathbf{Z}_2\mathbf{f} + \boldsymbol{\varepsilon}, \quad (1)$$

where  $\mathbf{y}$  is the vector of observation for a trait,  $\mathbf{b}$  is the vector (number of blocks) of fixed block effects,  $\mathbf{pop}$  is the vector (number of populations) of random population effects,  $\mathbf{f}$  is the vector (number of mother trees) of the random genetic effects of mother tree within the population,  $\boldsymbol{\varepsilon}$  is the vector (number of individuals  $\times$  1) of residuals,  $\mathbf{X}$  is called the design matrix,  $\mathbf{Z}_1$  and  $\mathbf{Z}_2$  are the incidence matrices linking the observations to the effects. A variance was fitted for each random effect:  $\sigma_{\text{pop}}^2$  is the genetic variance between populations,  $\sigma_{f(\text{pop})}^2$  is the genetic variance between mother trees nested within a population and  $\sigma_{\varepsilon}^2$  is the residual variance for repeated analyses. As the density record for each year constitutes a new measurement for the same tree (Littell et al. 2000; Apiolaza and Garrick 2001), there is an autocorrelation between measurements, which was taken into account using a special variance–covariance  $\mathbf{R}$  matrix structure for repeated analysis. Several covariance structures were considered for specification of the  $\mathbf{R}$  matrix in the mixed model (autoregressive, heterogeneous autoregressive, first-order autoregressive moving-average, toeplitz, banded correlation). On the basis of Akaike's information criterion and Bayes' information criterion, a banded correlation structure for additive genetic

effects was found to be the most appropriate (data not shown). We also ran the analysis with the seed mass as covariate to control potential maternal effect, but it did not change the observed patterns.

Variance and covariance components were estimated by the restricted maximum likelihood (REML) method, assuming a normal distribution of the random effects. The significance of variance components was assessed in log-likelihood ratio tests. We included population as a random effect, for inference at the species level and to obtain an unbiased estimate of heritability and genetic population differentiation (Wilson 2008). The normality, identity, and independence of the residuals of each trait were checked graphically by plotting studentized marginal and conditional residuals. These plots confirmed that the data conformed to the assumptions of the mixed model. We estimated narrow-sense heritability as follows:  $h_{\text{ns}}^2 = 4\sigma_{f(\text{pop})}^2 / (\sigma_{\varepsilon}^2 + \sigma_{f(\text{pop})}^2)$ . In our study,  $\sigma_A^2$  was estimated as  $\sigma_A^2 = 4\sigma_{f(\text{pop})}^2$  because trees from the same family were presumed to be half-sibs (open-pollinated seeds). We did not include the population effect in the heritability calculation, because natural selection appeared to occur within each population (Visscher et al. 2008). The standard deviation of heritability was calculated with the delta method (Lynch and Walsh 1998). Phenotypic differentiation between populations,  $Q_{\text{ST}}$  (Spitze 1993), was estimated as  $Q_{\text{ST}} = \sigma_{\text{pop}}^2 / (\sigma_{\text{pop}}^2 + 2\sigma_A^2)$ . Variance components were standardized with the trait mean (Houle 1992) as follows:  $\text{CV} = \frac{\sqrt{\sigma_{\text{trait}}^2}}{\bar{X}_{\text{trait}}} 100$ , where CV is the coefficient of variation. Each variance component was expressed with a CV (CV<sub>A</sub>: additive coefficient of variation; CV<sub>BP</sub> (V<sub>BP</sub> =  $\sigma_{\text{pop}}^2$ ): between-population coefficient of variation; CV<sub>P</sub>: phenotypic coefficient of variation; CV<sub>R</sub>: residual coefficient of variation). The variance of each component was extracted from the asymptotic covariance matrix. The significance of mean population differences was estimated with model (#1), with the GLM procedure and Student–Newman–Keuls post hoc tests.

### Correlation between traits and climatic variable

Genetic correlations between traits were evaluated by calculating Pearson's coefficients for the family best

linear unbiased predictor (BLUP) estimate. These correlations are referred to hereafter as genetic correlations. Phenotypic correlations were evaluated by calculating Pearson's coefficients for the family BLUP plus the population BLUP and the grand-mean. Data from a previous study (Lamy et al. 2011) were also included, to assess the correlation between density parameters and cavitation resistance (estimated from  $P_{50}$ , the xylem pressure at which a sample lost 50 % of its conductance).

We also explore relationships between climatic variables from population origin and the population performance in the provenance-progeny trial. The first PCA axis was used as an aridity index because soil water deficit and evapotranspiration are the main contributors.

### $Q_{ST}$ and $F_{ST}$ comparison

We investigated the contribution of selection to the differentiation of phenotypic traits, as previously described (Lamy et al. 2011) by comparing the distribution of phenotypic differentiation ( $Q_{ST}$ ) with the distribution of genetic differentiation ( $F_{ST}$ ) assessed with molecular markers assumed to be neutral. Briefly, the  $F_{ST}$  distribution ( $F_{ST}^*$ ) was constructed from a dataset for eight neutral nuclear microsatellites previously genotyped in the populations studied (Eveno et al. 2008). Neutral expectations were simulated by randomly resampling  $10^3$  times with replacement between loci, to estimate the sampling variance of  $F_{ST}$ . Each  $F_{ST}$  replicate value was multiplied by a random number drawn from the (Lewontin and Krakauer 1973) distribution, which accounts for demographic deviations from the neutral model (Whitlock 2008; Whitlock and Guillaume 2009).  $Q_{ST}$  distributions ( $Q_{ST}^*$ ) were constructed by performing a parametric bootstrap resampling procedure  $10^3$  times (O'Hara and Merilä 2005), making it possible to estimate the distribution of each variance component ( $\sigma_A^2$ ,  $\sigma_{pop}^2$ ) by Satterthwaite's approximation (Satterthwaite 1946). Finally, the two resulting distributions were compared in a non-parametric test on the 2.5 and 97.5 quantiles (Kosorok 1999). A more classical Whitlock test was also performed. All analyses were performed with SAS software (2008, version 9.2 SAS Institute, Cary, NC, USA). Codes are available on request.

## Results

### Between-population variation

No significant difference between populations ( $V_{BP}$ ) was detected for wood density ( $D_{mean}$ ,  $D_{min}$ , and  $D_{max}$ ), whereas significant differences were found for  $W_a$ ,  $A_{Leaf}$ , and  $\phi$  (Fig. 1; Table 2). Wood density-related traits had much lower coefficients of variation than  $W_a$  (Table 2), particularly at the between-population level ( $CV_{BP} = 1\%$  and  $19\%$  for  $D_{mean}$  and  $W_a$ , respectively). The fixed block effect was significant for all the traits studied; indicating that environmental variations were significant and taken into account by the model.

The populations from the wettest areas (Mimizan and San Cipriano) had the highest  $A_{Leaf}$  and  $\phi$  values (Fig. 1), whereas the Tamrabta population (from Morocco) had the lowest values. Iberian populations from the central and southern part of Spain (Coca, Bayubas, Oria) had intermediate values, with no detectable trend in terms of environmental aridity.

### Within-population variation

Heritabilities and normalized measurements of trait dispersion (i.e., CVs) were estimated to evaluate within-population additive variance (through the analysis of  $CV_A$ ) and micro-environmental sensitivity (through the analysis of  $CV_R$ ) (Table 2). The values of narrow-sense heritability ( $h_{ns}^2$ ) for  $D_{mean}$  ( $0.38 \pm 0.20$ ) and  $D_{max}$  ( $0.51 \pm 0.20$ ) indicated that wood density was moderately genetically determined, although the standard error was high, due to the small number of progenies per mother tree analyzed for this trait. The CVs of wood density and growth traits presented contrasting patterns, with a lower coefficient of additive variation ( $CV_A \leq 7\%$ ) for wood density than for other traits ( $CV_A > 20\%$ ), suggesting that evolvability is limited for wood density.

### Evolutionary forces driving population differentiation

Comparisons of  $Q_{ST}$  and  $F_{ST}$  may have three possible outcomes (Spitze 1993): (i) if  $Q_{ST} > F_{ST}$ , the degree of differentiation for quantitative traits exceeds that attainable by genetic drift alone, (ii) if  $Q_{ST}$  and  $F_{ST}$  are not significantly different, the observed degree of



**Table 2** Variance components ( $V_P$ ,  $V_{BP}$ ,  $V_A$ ,  $V_R$ ), narrow-sense heritability ( $h_{ns}^2 \pm SE$ ), coefficient of variation ( $CV_P$ ,  $CV_A$ ,  $CV_{BP}$ ,  $CV_R$ ) and population differentiation ( $Q_{ST}$ )

Traits	$V_P$	$V_{BP}$	$V_A$	$V_R$	$h_{ns}^2$	$CV_P$	$CV_A$	$CV_{BP}$	$CV_R$	$Q_{ST}^a$
$D_{mean}$	0.001	$1.9 \cdot 10^{-5}$ ns	$0.5 \cdot 10^{-3}$ *	0.001	$0.38 \pm 0.20$	11	7	1	10	0.02*/**
$D_{max}$	0.001	$1.7 \cdot 10^{-5}$ ns	$0.7 \cdot 10^{-3}$ *	0.001	$0.49 \pm 0.20$	10	7	1	9	0.01 */**
$D_{min}$	0.001	$1.6 \cdot 10^{-5}$ ns	$0.2 \cdot 10^{-3}$ ns	0.001	$0.22 \pm 0.21$	12	5	1	11	0.03 */**
$\phi_{2007}$	50.63	31.92***	17.55*	46.24	$0.34 \pm 0.12$	37	22	29	36	0.47 ***/****
$B_{tot}$	16124	3246***	9207***	13822	$0.57 \pm 0.08$	43	32	19	40	0.14 ns/ns
$A_{Leaf}$	0.427	0.104***	0.1817**	0.382	$0.425 \pm 0.14$	37	24	35	35	0.22 */ns

$h_{ns}^2$  narrow-sense heritability and SE is the standard error of heritability,  $V_P$  phenotypic variance,  $V_A$  additive genetic variance,  $V_{BP}$  between-population variance,  $V_R$  residual variance,  $CV_A$  additive variation coefficient after adjustment for the block effect,  $CV_P$  phenotypic variation coefficient after adjustment for the block effect,  $CV_R$  residual coefficient of variation,  $CV_{BP}$  between-population coefficient of variation,  $Q_{ST}$  quantitative genetic variation between populations (Spitze 1993)

<sup>a</sup> We provide  $P$  value for  $Q_{ST}$  and  $F_{ST}$  comparison based on Whitlock's method and our method based on Kosorok test

The significance of random effects is indicated after each variance estimator: ns  $P > 0.05$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

differentiation for quantitative traits could have been reached by genetic drift alone, and (iii) if  $Q_{ST} < F_{ST}$ , the observed degree of differentiation is lower than expected from genetic drift alone. Consistent with previous reports (Waldmann et al. 2005; O'Hara and Merilä 2005), we found that  $F_{ST}^*$  and  $Q_{ST}^*$  had skewed distributions (Fig. 2). Only  $\phi$  and  $D_{mean}$  (together with  $D_{min}$ ,  $D_{max}$ , data not shown) had a  $Q_{ST}^*$  distribution that differed from the  $F_{ST}^*$  distribution ( $P < 0.0001$  and  $P = 0.0008$ , respectively). For,  $A_{Leaf}$  (and  $W_a$ , data not shown), the difference between  $Q_{ST}^*$  and  $F_{ST}^*$  values was centered on 0 (see Fig. 2c, right panel), and it was, therefore, not possible to distinguish between drift and selection ( $P = 0.23$ ). Conversely, differences between the  $Q_{ST}^*$  and  $F_{ST}^*$  distributions for  $D_{mean}$  were centered on  $-0.13$ , suggesting that the studied populations were less differentiated than would be expected in the presence of drift alone (Fig. 2a). Thus, natural selection favors the same phenotypic mean in different populations. For  $\phi$ , the difference between  $Q_{ST}^*$  and  $F_{ST}^*$  distributions was centered on 0.34, suggesting that the studied populations displayed more differentiation than would be expected with drift alone (Fig. 2b). The population sampling protocol lead us to select population bearing different mitotypes and chlorotypes reflecting different evolutionary histories (Vendramin et al. 1998; Burban and Petit 2003). It is worth noticing that this procedure did not bias the population genetic differentiation upward because our  $F_{ST}$  estimation (0.10) was close to the lower bound of  $F_{ST}$  estimated for this species (0.10–0.14, Bucci et al. 2007).

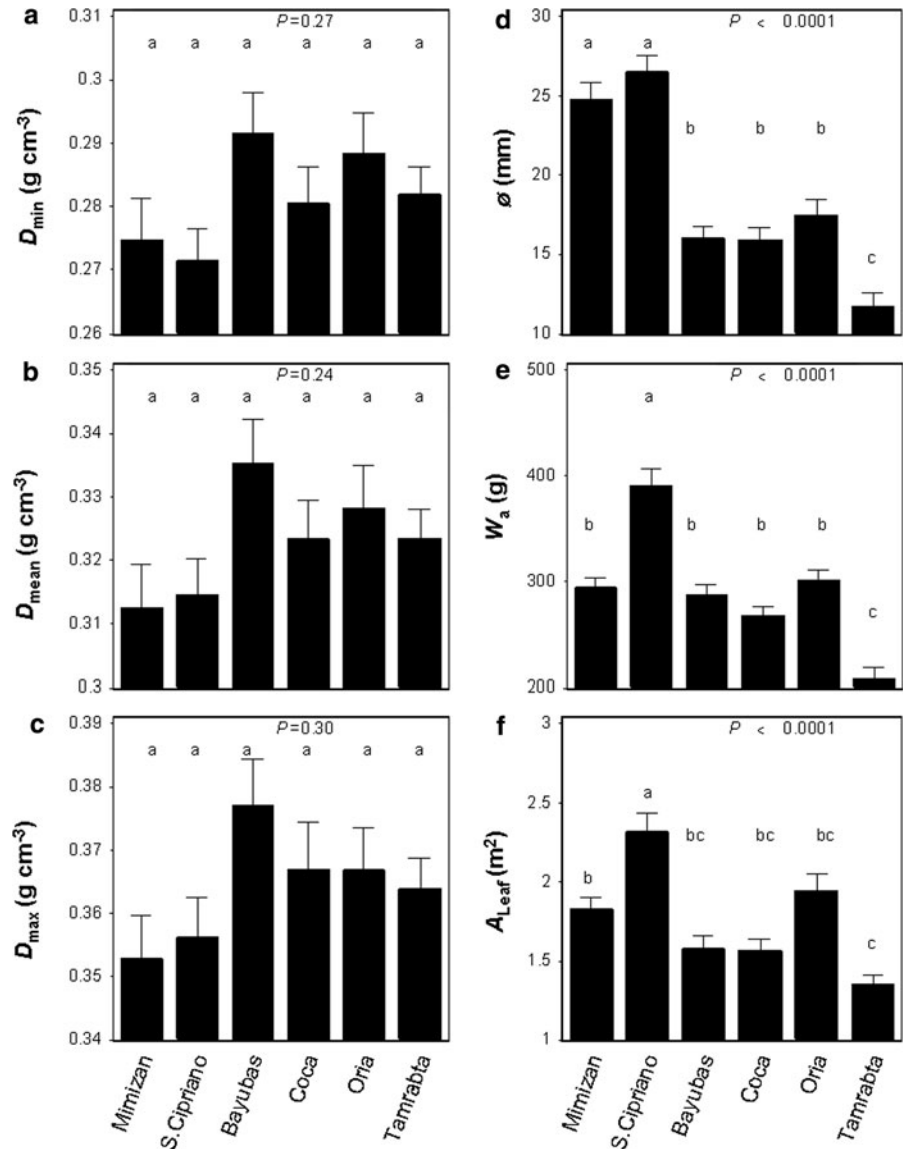
### Correlation between traits and climate

We found a significant negative phenotypic correlation between  $D_{mean}$  and  $\phi$  ( $r = -0.33$ ,  $P = 0.02$ ), indicating that individuals with denser wood tended to have a smaller stem diameter. However, the genetic correlation was not significant ( $r = -0.20$ ,  $P = 0.16$ ). We observed no significant phenotypic correlation between  $D_{mean}$  (or  $D_{max}$  and  $D_{min}$ ) and cavitation resistance ( $P_{50}$ ) (Fig. 3). No significant correlations were found between  $D_{mean}$  and  $W_a$ ,  $A_{Leaf}$ . Soil water deficit and evapotranspiration are the main contributors to the first axis of the PCA of climatic variable at population origin (see “Plant material” section). Therefore, this axis represents an index of aridity for each provenance site. No significant relationships were found between population's traits and aridity, except for  $\phi$  ( $P = 0.02$ , data not shown).

### Discussion

We here evidenced that juvenile wood density ( $D_{min}$ ,  $D_{mean}$ , and  $D_{max}$ ) had a low additive variance and moderate heritability. Although the studied populations originated from contrasting climates and presented different evolutionary histories, no significant difference between populations was detected and the variability between populations was smaller than expected under genetic drift alone ( $Q_{ST} < F_{ST}$ ). In other words, these populations from different climates

**Fig. 1** Histogram showing, for each population, the 10th percentile of wood density distribution ( $D_{\min}$  **a**), mean values of mean wood density ( $D_{\text{mean}}$  **b**), 90th percentile of wood density distribution ( $D_{\max}$  **c**), stem diameter in 2007 ( $\phi$  **d**), total above-ground tree dry biomass in 2005 ( $W_a$  **e**), total tree leaf (needle) area ( $A_{\text{Leaf}}$  **f**), for each studied population ( $n = 40$  per population). Error bars standard errors. The  $P$  value is that for the mixed model and indicates whether the population effect is significant. Different letters indicate significant differences between populations at the  $\alpha = 0.05$  level (from a fixed effect model)

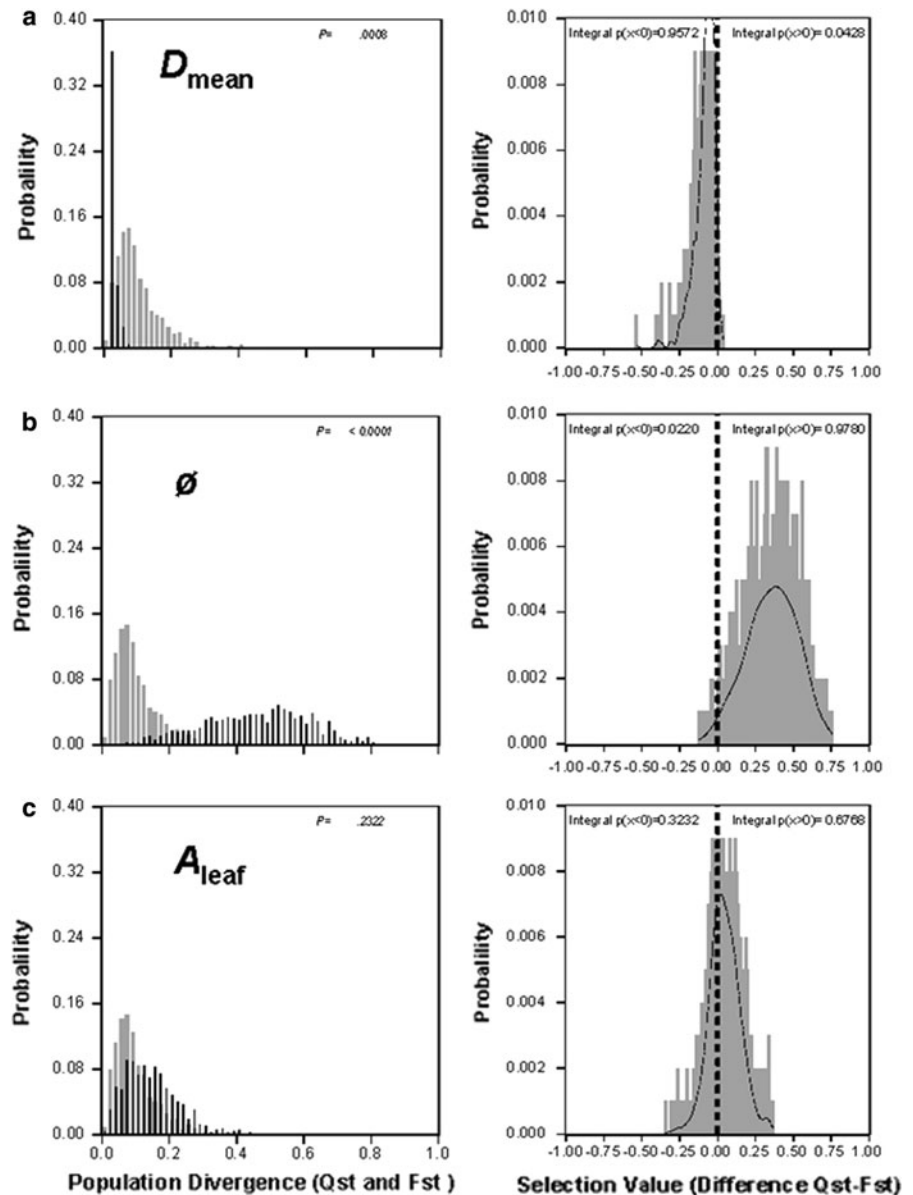


and with different evolutionary histories shared the same trait value, suggesting an evolutionary process had driven the trait variability. Conversely, growth (collar diameter) presented a higher additive genetic variance and differentiation between populations, consistent with the action of diversifying selection on the studied populations. Concerning other biomass estimates ( $W_a$ ,  $A_{\text{Leaf}}$ ), we were unable to disentangle the effects of genetic drift and natural selection. We discuss below the possible evolutionary mechanisms underlying the low degree of variability of juvenile wood density between populations.

#### Juvenile wood density variability

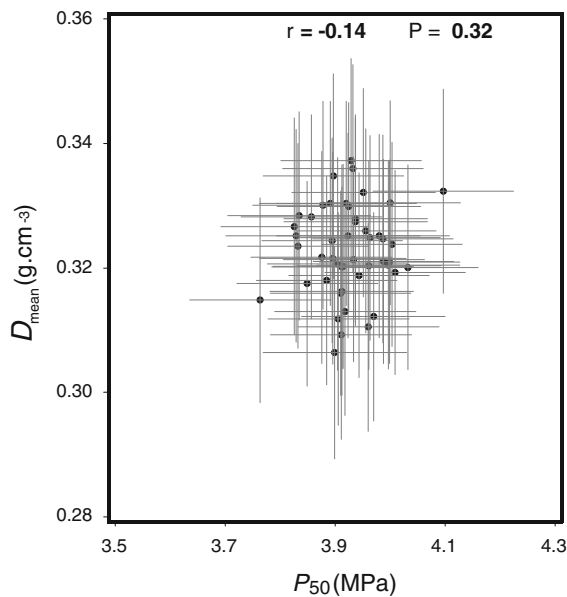
Our results showed that mean juvenile wood density did not change between *Pinus pinaster* ecotypes. Wood density variability has been thoroughly dissected in previous studies (Gapare et al. 2009), but generally in mature tree with a narrow genetic backgrounds (elite trees, crossing between local populations) or mature interspecific hybrids. Conversely, few studies have considered the between-population variability of wood density because this information is usually not required for classical

**Fig. 2** Comparison between  $F_{ST}$  (histogram in gray) and  $Q_{ST}$  (histogram in black) distributions for mean wood density ( $D_{mean}$  a), stem diameter ( $\phi$  b), total tree leaf (needle) area in 2006 ( $A_{leaf}$  c), in the left panel. The observed distribution (gray histogram) and kernel density (black curves) of the  $Q_{ST} - F_{ST}$  difference are represented on the right panel for each trait. On the right panel, we also show the integral probability of the distribution (using the kernel density estimator) above (see “Integral  $p(x > 0)$ ” on the right panel) and below (see “Integral  $p(x < 0)$ ” on the right panel) zero (marked with the dashed and dotted lines)



breeding programs. In some instance, evolutionary biologists have compared between-population variability and expectations under genetic drift for wood density as for *Picea glauca*, *Eucalyptus globulus*, and *Pinus contorta* (Yang et al. 1996; Jaramillo-Correa et al. 2001; Steane et al. 2006). In some studies, between-population variation was detected, but comparisons with ours remain difficult because: (i) these previous studies were not designed to assess the level and structure of variation across a wide range of ecotypes. Population sampling was usually restricted

to a subset of the distribution area. The results were, therefore, biased toward low  $F_{ST}$  values ( $< 0.1$ ). For instance, Jaramillo-Correa et al. (2001) obtained an  $F_{ST}$  of 0.02, much lower than that found by Tremblay and Simon (1989) ( $F_{ST} = 0.11$ ) for broader sampling in *Picea Glauca*, (ii) the protocols for assessing wood density differ between studies: with the use of pilodyn (Steane et al. 2006) or the water displacement method to estimate wood-specific gravity (Yang et al. 1996), (iii) the age at which wood density was measured also differed considerably between studies. Apiolaza



**Fig. 3** Adjusted mean values of wood density ( $D_{\text{mean}}$ ) versus cavitation resistance ( $P_{50}$ , xylem pressure inducing 50 % loss of hydraulic conductance). Dots correspond to the composite BLUP estimate and the error bar to the associated standard error ( $n = 48$ ). The BLUP estimate for each family is calculated as the sum of population BLUP, family BLUP and the grand mean

(2011) and Zamudio et al. (2002) showed that genetic variability in *Pinus radiata* increases with age for wood density, and mature wood and juvenile wood are known to be the subject of different genetic controls (Plomion et al. 2001). The ring's age in our studies is much more younger compare to Jaramillo-Correa et al. (2001) and Yang et al. (1996), who worked on 22-year-old and 10-year-old trees, respectively. Our conclusions could, therefore, not be extrapolated to mature wood (and mature tree) even for *Pinus pinaster*. Low variability within population for juvenile wood density and the lack of genetic differentiation between populations may have different consequences; (i) breeding different ecotypes will not bring much more genetic variation for this trait; (ii) it may be more valuable to select for a better diameter growth and/or for a greater proportion of the latewood in the juvenile wood. It is important to keep in mind that all the above-mentioned studies, including our own, have sample size (<1,000 individuals) still far from the standard required by quantitative genetics theory ( $\gg 1000$  individuals), more studies are needed to draw robust conclusions.

### Impact of environment variation on wood density

Comparing  $CV_R$  between traits, it seems that wood density is less sensitive to environmental variance compare to growth-related traits. Wood density should exhibit some phenotypic plasticity but in a less extent compare to growth trait, and it may be possible that such phenotypic plasticity is stereotyped. To specifically study the reaction norm of mean wood density, multi-site approach would be valuable to draw robust conclusion about the environmental sensitivity of such trait (Vitasse et al. 2010). Another alternative to explore phenotypic plasticity is to study reaction norm of wood density along the whole profile (Martinez-Meier et al. 2011). It was not possible to investigate more deeply the reaction norm of wood density in this study because of the low number of wood rings (3-year-old branches). In addition, the extraction of phenotypic plasticity out of the total wood density signal is still a conceptual (no mechanistic model of wood density genesis) and statistical challenge (non-linearity with time). However, there are some pertinent approaches at the intra-annual level (Martinez-Meier et al. 2011).

### Evolutionary significance of trait conservatism and underlying mechanisms

In our study, variance between populations ( $Q_{ST}$ ) was lower than expected under a hypothesis of genetic drift ( $F_{ST}$ , from neutral markers), suggesting an evolutionary stasis for wood density. Such a pattern of variability was recently described for cavitation resistance-related traits in a study based on the same experiment (Lamy et al. 2011). Here, we demonstrated, using another complex trait (wood density), that functional traits are not always labile and prone to diversifying selection or homoplasy. Explaining trait conservatism (the extreme form of conservatism lead to stasis) is one of the most challenging questions in evolutionary biology (Bradshaw 1991). Uniform selection is often proposed as a classical explanation of narrow between-population trait variation resulting in evolutionary stasis. According to this model, independent stabilizing selection events act within each population, with the same selection optimum. However, this model provides no clues as to why the selection optimum should be the same. Genetic constraints (such as canalization) could also represent alternative explanations, particularly for

traits still displaying some degree of variability within populations (Gould and Lewontin 1979; Bradshaw 1991; Lamy et al. 2011). Simulations have also shown that the  $Q_{ST} < F_{ST}$  pattern can be obtained for traits that are non additively genetically controlled (Goudet and Buchi 2006; Lopez-Fanjul et al. 2007). Deciphering uniform selection from canalization hypotheses is a difficult task. Across 21 *Pinus* species, Creese et al. (2011) have shown that wood density presented the lowest coefficient of variation among plant mass, hydraulic conductivity, and transpiring surface on the conductive surface ratio, and they found no relation with climatic variables despite a large range of mean annual precipitation (500–2,000 mm). If closely related species living in different climate have the same value of trait (i.e., evolutionary stasis), it is difficult to conceive that all the populations of each species share the same value of selective optima as it is assumed in the uniform selection hypothesis. Therefore, the alternative hypothesis that evolutionary stasis is due to a robust genetic architecture that narrows trait variability (i.e., canalization) should be considered with more attention.

#### Wood density and other adaptive traits

Juvenile wood density is negatively correlated with growth trait as diameter and/or height in mature tree (Bouffier et al. 2008). Between water use efficiency and wood density, the relationships are difficult to predict as a ring could be build up with the carbon from the previous years. Indeed, theoretically, the correlation is very loose between these two processes. For hydraulic safety traits (drought tolerance), at the interspecific level, Hacke and Sperry (2001) showed that cavitation resistance is correlated with wood density, species with higher wood density being more resistant to cavitation. In *Pseudotsuga menziesii* and *Picea abies* clones, a negative correlation was found between wood density and cavitation resistance (Rosner et al. 2008; Dalla-Salda et al. 2011). Even with considerable statistical power compared to these previous studies, we found no relationship between wood density and cavitation resistance within species (Fig. 3). In provenance tests, Corcuera et al. (2011) and Wortemann (2011) also found no relationship between wood density and cavitation resistance. In *Pinus sylvestris*, Martinez-Vilalta et al. (2009) did not detect any correlation between these traits in situ in

natural populations. We propose two hypotheses to account for these discrepancies: (i) despite the greater statistical power of our design, the relationship between cavitation resistance and wood density does not seem to be robust to environmental variation and genetic variation and (ii) from a physiological point of view, this lack of correlation is unsurprising, because there is no direct causal link between wood density and cavitation resistance (Delzon et al. 2010; Jansen et al. 2012) in *Pinus* genera. For instance, Delzon et al. (2010) showed that bordered pit dimensions are much more important for cavitation resistance than total tracheid lumen area. However, even if these two traits are not correlated, they have other features in common: they both have a low  $CV_A$  (<7 %) and display extremely low levels of variation between populations ( $CV_{BP} \leq 1$  %), suggesting that this trend follows a general rule for wood anatomy-related traits. These findings indicate that additional, more detailed investigations of the naturally occurring variability of wood anatomy-related traits (e.g., cell wall thickness, aperture pit dimensions, torus diameter, margo pore diameter, etc.) are required to gain greater insight into canalization. However, it should be pointed out that our study focused on juvenile wood, and trait values at the start of ontogeny are known to be canalized (Milton et al. 2003; Sangster et al. 2008). Further studies are required to confirm that conservatism for mean wood density is also conserved in mature trees.

**Acknowledgments** SD and JBL received funding from INRA-EFPA (innovative project Grant) and a PhD Grant from INRA Région Auvergne, respectively. This trial was set up by the experimental unit of INRA Pierroton within the Treesnips EC-funded project (QLK3-CT-2002-01973). Cavitation resistance, wood density and leaf area were measured with fundings from the European Union (Noveltree project, FP7-21868). We thank Emmanuelle Eveno and Pauline Garnier-Géré for sharing biomass data.

#### References

- Aguiar A, Almeida MH, Borralho N (2003) Genetic control of growth, wood density and stem characteristics of *Pinus pinaster* in Portugal. *Genetica* 11:131–139
- Apiolaza LA (2011) Basic density of radiata pine in New Zealand: genetic and environmental factors. *Tree Genet. Genomes*. doi:10.1007/s11295-011-0423-1
- Apiolaza LA, Garrick DJ (2001) Analysis of longitudinal data from progeny tests: some multivariate approaches. *For Sci* 47:129–140

- Bouffier L, Rozenberg P, Raffin A, Kremer A (2008) Wood density variability in successive breeding populations of maritime pine. *Can J For Res* 38:2148–2158
- Bradshaw AD (1991) The Croonian Lecture, 1991. Genostasis and the limits to evolution. *Philos Trans R Soc Lond B* 333:289–305
- Brodribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol* 149:575–584
- Burban C, Petit RJ (2003) Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Mol Ecol* 12:1487–1495
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, Ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol Appl* 16:2356–2367
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366
- Corcuera L, Cochard H, Gil-Pelegrin E, Nativol E (2011) Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism ( $P_{50}$ ) under severe drought. *Trees*. doi:10.1007/s00468-011-0578-2
- Creese C, Benscoter A, Maherali H (2011) Xylem function and climate adaptation in *Pinus*. *Am J Bot* 98(9):1437–1445
- Dalla-Salda G, Martinez-Meier A, Cochard H, Rozenberg P (2011) Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)). *Ann For Sci* 68:747–757
- Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant Cell Environ* 33:2101–2111
- Eveno E (2008) L'adaptation à la sécheresse chez le pin maritime (*Pinus pinaster*): patrons de diversité et différenciation nucléotidiques de gènes candidats et variabilité de caractères phénotypiques. Thesis, University of Bordeaux 1, pp 1–390
- Eveno E, Collada C, Guevara MA, Léger V, Soto A, Díaz L, Léger P, González-Martínez SC, Cervera MT, Plomion C et al (2008) Contrasting patterns of selection at *Pinus pinaster* drought stress candidate genes as revealed by genetic differentiation analyses. *Mol Biol Evol* 25:417–437
- Figueroa JA, Lusk CH (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytol* 152:483–489
- Gapare WJ, Ivković M, Baltunis BS, Matheson CA, Wu HX (2009) Genetic stability of wood density and diameter in *Pinus radiata* D. Don plantation estate across Australia. *Tree Genet Genomes* 6:113–125
- Gilchrist AS, Partridge L (2001) The contrasting genetic architecture of wing size and shape in *Drosophila melanogaster*. *Heredity* 86:144–152
- Goudet J, Buchi L (2006) The effects of dominance, regular inbreeding and sampling design on  $Q_{ST}$ , an estimator of population differentiation for quantitative traits. *Genet* 172:1337–1347
- Gould SJ, Lewontin RC (1979) Spandrels of San-Marco and the panglossian paradigm—a critique of the adaptationist program. *Proc R Soc Lond B* 205:581–598
- Guay R, Gagnon R, Morin H (1992) A new automatic and interactive tree ring measurement system based on a line scan camera. *For. Chron.* 68:138–141
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol Evol Syst* 4:97–115
- Hansen TF, Houle D (2004) Evolvability, stabilizing selection and the problem of stasis. In: Pigliucci M, Preston K (eds) *The evolutionary biology of complex phenotypes*. Oxford University Press, Oxford, pp 1–27
- Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genet* 130:195–204
- Jansen S, Lamy J-B, Burrell R, Cochard H, Gasson P, Delzon S (2012) Plasmodesmatal pores in the torus of bordered pit membranes affect cavitation resistance of conifer xylem. *Plant and Cell Environ*. doi: 10.1111/j.1365-3040.2011.02476.x
- Jaramillo-Correa JP, Beaulieu J, Bousquet J (2001) Contrasting evolutionary forces driving population structure at expressed sequence tag polymorphisms, allozymes and quantitative traits in white spruce. *Mol Ecol* 10:2729–2740
- Knap PW (2005) Breeding robust pigs. *Aust J Exp Agric* 45:763–773
- Kosorok MR (1999) Two-sample quantile tests under general conditions. *Biometrika* 86:909–921
- Lamy J-B, Bouffier L, Burrell R, Plomion C, Cochard H, Delzon S (2011) Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS ONE* 6:e23476
- Lewontin RC, Krakauer J (1973) Distribution of gene frequency as a test of theory of selective neutrality of polymorphisms. *Genetics* 74:175–195
- Littell RC, Pendergast J, Natarajan R (2000) Modelling covariance structure in the analysis of repeated measures data. *Stat Med* 19:1793–1819
- Lopez-Fanjul C, Fernandez A, Toro MA (2007) The effect of dominance on the use of the QST-FST contrast to detect natural selection on quantitative traits. *Genetics* 176:725–727
- Lynch M, Walsh B (1998) *Genetics and analysis of quantitative traits*. Sinauer Associates, Sunderland, pp 1–980
- Markestijn L, Poorter L, Bongers F, Paz H, Sack L (2011) Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *N Phytol* 191:480–495
- Martinez-Meier A, Sanchez L, Pastorino M, Gallo L, Rozenberg P (2008) What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. *For Ecol Manag* 256:837–843
- Martinez-Meier A, Gallo L, Pastorino M, Mondino V, Rozenberg P (2011) Phenotypic variation of basic wood density in *Pinus ponderosa* plus trees. *Bosque (Valdivia)* 32:221–226
- Martinez-Vilalta J, Cochard H, Mencuccini M, Sterck F, Herero A, Korhonen JFJ, Llorens P, Nikinmaa E, Nole A, Poyatos R et al (2009) Hydraulic adjustment of Scots pine across Europe. *N Phytol* 184:353–364
- McCulloh KA, Meinzer FC, Sperry JS, Lachenbruch B, Voelker SL, Woodruff DR, Domec J-C (2011) Comparative hydraulic architecture of tropical tree species representing a range of successional stages and wood density. *Oecologia* 167:27–37

- Milton CC, Huynh B, Batterham P, Rutherford SL, Hoffmann AA (2003) Quantitative trait symmetry independent of Hsp90 buffering: distinct modes of genetic canalization and developmental stability. *Proc Natl Acad Sci USA* 100:13396–13401
- Mormede P, Foury A, Terenina E, Knap PW (2011) Breeding for robustness: the role of cortisol. *Animal* 5:651–657
- O'Hara RB, Merilä J (2005) Bias and precision in  $Q_{ST}$  estimates: problems and some solutions. *Genetics* 171:1331–1339
- Petit RJ, Hampe A (2006) Some evolutionary consequences of being a tree. *Annu Rev Ecol Evol Syst* 37:187–214
- Plomion C, Leprovost G, Stokes A (2001) Wood formation in trees. *Plant Physiol* 127:1513–1523
- Polge H (1966) Etablissement des courbes de variation de la densité du bois par exploration densitométrique de radiographie d'échantillons prélevés à la tarière sur des arbres vivants. *Ann Sci For* 23:1–206
- Poorter L, McDonald I, Alarcon A, Fichtler E, Licona JC, Penaclos M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rain-forest tree species. *N Phytol* 185:481–492
- Ribeiro MM, Mariette S, Vendramin GG, Szmídt AE, Plomion C, Kremer A (2002) Comparison of genetic diversity estimates within and among populations of maritime pine using chloroplast simple-sequence repeat and amplified fragment length polymorphism data. *Mol Ecol* 11:869–877
- Richardson DM (1998) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 1–527
- Rosner S, Klein A, Müller U, Karlsson B (2008) Tradeoffs between hydraulic and mechanical stress responses of mature Norway spruce trunk wood. *Tree Physiol* 28:1179–1188
- Sangster TA, Salathia N, Undurraga S, Milo R, Schelienberg K, Lindquist S, Queitsch C (2008) HSP90 affects the expression of genetic variation and developmental stability in quantitative traits. *Proc Natl Acad Sci USA* 105:2963–2968
- SAS II (2008) SAS/STAT<sup>®</sup> 9.2 User's Guide. SAS Institute Inc, Cary
- Satterthwaite FE (1946) An approximate distribution of estimates of variance components. *Biom Bull* 2:110–114
- Spitze K (1993) Population structure in *Daphnia obtusa*: quantitative genetic and allozymic variation. *Genetics* 135:367–374
- Steane DA, Conod N, Jones RC, Vaillancourt RE, Potts BM (2006) A comparative analysis of population structure of a forest tree, *Eucalyptus globulus* (Myrtaceae), using microsatellite markers and quantitative traits. *Tree Genet Genomes* 2:30–38
- Tremblay M, Simon JP (1989) Genetic-structure of marginal populations of white spruce (*Picea glauca*) at its northern limit of distribution in nouveau-Québec. *Can J For Res* 19:1371–1379
- Vendramin GG, Anzidei M, Madaghiele A, Bucci G (1998) Distribution of genetic diversity in *Pinus pinaster* Ait. as revealed by chloroplast microsatellites. *Theor Appl Genet* 97:456–463
- Visscher PM, Hill WG, Wray NR (2008) Heritability in the genomics era—concepts and misconceptions. *Nat Rev Genet* 9:255–266
- Vitasse Y, Bresson CC, Kremer A, Michalet R, Delzon S (2010) Quantifying phenological plasticity to temperature in two temperate tree species. *Funct Ecol* 24:1211–1218
- Waldmann P, García-Gil MR, Sillanpää MJ (2005) Comparing Bayesian estimates of genetic differentiation of molecular markers and quantitative traits: an application to *Pinus sylvestris*. *Heredity* 94:623–629
- Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends Ecol Evol* 21:261–268
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Ann Rev Ecol Syst* 33:125–159
- Whitlock MC (2008) Evolutionary inference from  $Q_{ST}$ . *Mol Ecol* 17:1885–1896
- Whitlock MC, Guillaume F (2009) Testing for spatially divergent selection: comparing  $Q_{ST}$  to  $F_{ST}$ . *Genetics* 183:1055–1063
- Wilson AJ (2008) Why  $h^2$  does not always equal  $V_A/V_P$ ? *J Evol Biol* 21:647–650
- Wortemann R (2011) Etude de la variabilité génétique et la plasticité phénotypique de la vulnérabilité à la cavitation chez *Fagus sylvatica*. Thesis, University of Blaise Pascal, pp 1–154
- Yang RC, Yeh FC, Yanchuk AD (1996) A comparison of isozyme and quantitative genetic variation in *Pinus contorta* ssp. *latifolia* by  $F_{ST}$ . *Genetics* 142:1045–1052
- Zamudio F, Baettyg R, Vergara A, Guerra F (2002) Genetic trends in wood density and radial growth with cambial age in a radiata pine progeny test. *Ann For Sci* 59:541–549
- Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215