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Original article

Genetic variation of the pilodyn–girth relationship in Norway spruce (*Picea abies* L [Karst])*

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Summary – Genetic variability in the relationship between pilodyn pin penetration (an indirect measure of wood density) and stem girth of individual trees was assessed at three levels (provenance, family [half-sib] and clone) in 15-year-old Norway spruce. The relationship between pilodyn and girth was found to be linear at all three levels, but estimated parameters of the linear regression differed among genetic entities at the three genetic levels: provenance, family and clone. Hence, accuracy of models relating wood density to stem growth is increased when using parameters specific to the genetic entity of interest. Nevertheless, model parameters for specific genetic entities were moderately correlated with mean values for pilodyn and girth. Therefore, and at least at clone level, selecting for high girth is a way to select for low intra-clone variability for wood density.

spruce / pilodyn–girth relationship / genetic variation / wood / growth

Résumé – Variabilité génétique de la relation pilodyn–circonférence chez l'épicéa commun (*Picea abies* L [Karst]). *La variabilité génétique de la relation entre la profondeur de pénétration de l'aiguille du pilodyn (une méthode indirecte de mesure de la densité du bois) et la circonférence de la tige a été étudiée aux niveaux provenance, famille (demi-frères) et clone chez des épicéas communs âgés de 15 ans. Cette relation peut être décrite de façon satisfaisante pour tous les génotypes à tous les niveaux par un modèle linéaire simple. Mais il existe des différences significatives entre génotypes pour les paramètres de cette relation linéaire aux trois niveaux génétiques provenance, famille et clone. Donc la précision d'un modèle décrivant la relation entre densité du bois et croissance en grosseur de la tige est accrue quand on utilise les paramètres calculés au niveau du génotype plutôt que ceux calculés au niveau général. La forte relation entre paramètres des modèles et moyennes des génotypes pour les variables étudiées suggère l'idée que les modèles génotypiques peuvent se déduire d'un modèle général. Cette relation signifie également qu'en sélectionnant pour une circonférence élevée on sélectionne des génotypes ayant une plus faible variabilité intraclone pour la densité du bois.*

épicea / relation pilodyn–circonférence / variabilité génétique / bois / croissance

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INTRODUCTION

Modeling wood quality using a low number of easy-to-measure forest tree traits has been applied to several forest tree species. Objectives may vary from simulation (Leban and Duchanois, 1990) to prediction (Colin and Houillier, 1991, 1992; Owoundi, 1992). Variation between stands in model shape or in model parameters is known and sometimes taken into consideration (Nepveu, 1991; Zhang et al, 1993).

Genetic variation at different levels within species for wood quality, growth, form and adaptation traits is well known. This variation is used in forest tree breeding programs to select and create new genotypes (Kremer, 1986; Cornelius, 1994). For Norway spruce (*Picea abies* L [Karst]) in France, improved genotypes must combine adaptability, fast growth and straight stems with good or at least acceptable wood quality (Ferrand, 1986).

The presence of genetic variation in wood quality raises a number of questions with regards to its modeling: Is there genetic variation in the shape of models (eg, in the analytical expression) or their parameters (eg, regression coefficients) when relating wood quality to other traits? What is the range of this variation at different genetic levels? What happens if this variation is not taken into account in models?

Few attempts have been made to answer these questions. Colin et al (1993) and Dedeckel (1994) tried, and they found no clear evidence of differences, respectively, between provenances and families for model parameters; however, few provenances and families were investigated. On 21 Norway spruce clones, Chantre and Gouma (1994) found a significant clonal effect on the residuals of a general basic density–ring width relationship. In our study, three genetic levels within Norway spruce were investigated, with a large number of entities within each genetic level. Wood quality was assessed through depth of pilodyn pin penetration, an indirect way to measure wood density. The pilodyn is widely used in forestry (Cown, 1981) and in forest tree breeding programs (Villeneuve et al, 1987; Chantre et al, 1992; Adams et al, 1993). Tree growth was assessed through girth measurements. The strong negative relationship between wood density and radial growth in Norway spruce is often reported, and is believed to be a major question for Norway spruce breeding (Zobel and Jett, 1995). A detailed study of this unfavorable relationship could help the breeder to better understand it and, consequently, better deal with it.

MATERIALS AND METHODS

The material was composed of 991 clones (from central Poland) representing 321 families and 25 provenances. Trees were planted in spring 1981 in Reix, Creuse (central France, alt 530 m), at a spacing of 2 x 3 m and using a single-tree plot incomplete block design (33 blocks x 200 trees = 6 600 trees, completely random assignment of ramets). The objectives of these plantings were to select about 50 fast-growing clones, taking wood quality and shape of stems into account. Results of the first analysis (Van de Sype, 1994) demonstrated that provenances, families and clones (within families) are significantly different for growth and wood density, and that these differences can be used to select families or clones with high performance in both traits.

Stem height and girth and pilodyn pin penetration at breast height were measured in 1992, 11 growing seasons after planting (when trees were 15 years old). The Pilodyn penetrometer is an indirect tool for measuring wood density. Originally developed to test soundness of wood poles in Switzerland, it is a hand-held instrument which propels a spring-loaded needle into the wood. Depth of needle penetration is read directly from the instrument, and is assumed to be well correlated with wood density (Hoffmeyer, 1978, 1979; Cown, 1981). Because wood density can be measured at low cost, it is often used in tree breeding studies (Loblolly pine, Sprague et al, 1983; Jack pine, Villeneuve et al, 1987; Norway spruce, Van de Sype, 1991; Chantre et al, 1992; Douglas fir, Adams et al, 1993; Schermann 1994, etc). The instrument used was 6 joules, with a pin size of 2.5 mm diameter and 60 mm length. Pin penetration was recorded through the bark on two opposite sides of the bole, perpendicular to the direction of the prevailing wind (to avoid compression wood). The mean of the two readings on each tree was used in all subsequent analysis.

The following steps were taken in analyzing the data (in the following, *pilodyn,* as a trait, means *depth of pilodyn pin penetration).*

First, data for individual trees were adjusted to environmental (block) effects through analysis of variance (model: $X_{ij} = \mu + C_i + B_j + \varepsilon_{ij}$, with clone effect ($C_i$) having a random effect and the block effect (B_j) a fixed effect, and ε_{ij}, a residual error). Inbalances were taken into account by conducting analysis using the type I sum of squares analysis of variance (ANOVA) procedure of the MODLI software, an INRA procedure developed using S-plus statistical software (Anonymous, 1990). Type I sum of squares was chosen because of a strong genetic effect on the high mortality rate (dead trees were not randomly distributed on the field; Van de Sype, 1994).

Next, the shape and strength of relationships between the three measured traits were studied at each genetic level. We calculated linear correlation coefficients among individuals within each provenance, family and clone (phenotypic correlations), and the associated probability (*P* value) of the correlation coefficient given the actual coefficient is zero, and we drew *x–y* plots of the relationships.

Due to the unbalanced design and the high mortality rate, the number of trees within genetic entities was very different from one genetic entity to another; for example, at the clone level, this number varied from 1 to 12; less than 3, calculation of correlation is not possible, and greater than 3, the sample size influences the precision of the estimated linear correlation coefficient (*r*) and of the estimated means for the study traits. Thus, for some genetic entities, sample size was not sufficient to reliably estimate correlations and means. Selecting genetic entities only on the basis of the probability value (*P*) of the correlation between pilodyn and girth did not seem reasonable, as it was easy to find genetic entities with very few trees, low *P* value and high negative *r* value (obviously nonrealistic), and as there is no evident link between *P* and the precision of estimation of the mean, a *size-of-genetic-entity* criterion (N) seemed necessary. That is why we selected genetic entities not only on the *P* value basis, but also on this N criterion. We tried to estimate N, the minimum number of trees required to correctly estimate the pilodyn–girth correlation and the mean values for pilodyn (pi) and girth (gi), assuming that it was not necessarily the same at each genetic level. At each genetic level, and for the genetic entities with the maximum number of individuals (ie, 22 provenances with at least 30 trees, 32 families with at least 20 trees and 29 clones with at least 12 trees), N was estimated: *r*, *P*, pi and gi were calculated for, at first step, a randomly selected subsample of three trees. Then one randomly selected new observation was added at each sample, and *r*, *P*, pi and gi were re-estimated. The computation was reiterated until the sample size reached, respectively, 12, 20 and 30 at clone, family and provenance level. The procedure was repeated 30 times, enough to observe a general trend. Mean *P* and variance of *r*, pi and gi where calculated for each sample size. Graphs of the evolution of mean *P* and variances of *r*, pi and gi against N where drawn. We assumed that N was the same from one genetic entity to another within each genetic level. N, then the *P* value, were used to select the genetic entities composing the sample (sample 1) used to calculate the models and the pilodyn and girth means.

Then, four linear models were considered with girth or a transformation of this variate:

pilodyn = $a + b$ x girth
pilodyn = $a + b$ x (1/girth)
pilodyn = $a + b$ x log (girth)
pilodyn = $a + b$ x (1/girth^2)

These models were chosen as they seemed able to accurately describe the shape of the pilodyn–girth plots. It did not seem helpful to investigate possible use of a nonlinear model.

Improving the first of these models by adding height as an independent variable was also considered (pilodyn = $a + b$ x girth + c x height). The single linear model type which best fit the observations for all genetic entities, whatever the level, was chosen.

The correctness of the models for describing the pilodyn–girth relationship was evaluated by calculating the model R^2 and the associated *P* value, the *P* value of models parameters, and plots of residuals (residuals vs girth and residuals vs adjusted pilodyn). At each genetic level, regressions were based on measurements of individual trees. In other words, at provenance and family level, we did not use family or clone means in the regressions. Why? First, whatever the genetic level, we wanted to consider each genetic entity as an independent population, as was done by researchers building models relating wood quality and growth (eg, Leban and Duchanois, 1990; Colin and Houillier, 1991, 1992; Nepveu, 1991; Owoundi, 1992; Zhang et al, 1993). Second, due to the high mortality rate, the number of families within provenances and of clones within families was very different from one genetic unit to another, and often very low: it was not possible to study the pilodyn–girth relationship at provenance level using family means, nor at family level using clone means.

We selected a second sample (sample 2) to conduct a covariance analysis to test differences between the genetic entities for the slope coefficient of the previously calculated models at each genetic level. This sample was selected using the following criteria: clones with more than four trees, and families with more than three clones per site (at least 12 trees per family). Hence, inbalances are reduced and the sample better matches the linear model conditions: conclusions from the ANOVA can be drawn with better confidence. Because of this selection, sample 2 is not a random sample, and covariance analysis was conducted using a fixed effect ANOVA.

Analysis of variance on pilodyn trait was conducted with the sample 2, using least square estimation and various combinations of covariates: 1: girth; 2: 1 + girth at provenance level; 3: 2 + girth at family level; and 4: 3 + girth at clone level.

The models are as follows:

$Y_{ijkl} = m + \alpha (X_{ijkl} + \varepsilon_{ijkl})$[1]

$Y_{ijkl} = m + (\alpha + \beta_i) (X_{ijkl} + \varepsilon_{ijkl})$ [2]

$Y_{ijkl} = m + (\alpha + \beta_i + \gamma_{ij}) (X_{ijkl} + \varepsilon_{ijkl})$ [3]

$Y_{ijkl} = m + (\alpha + \beta_i + \gamma_{ij} + \delta_{ijk}) (X_{ijkl} + \varepsilon_{ijkl})$ [4]

where Y_{ijkl} and X_{ijkl} are the pilodyn and girth measurements, respectively, on the *l*th tree of the *k*th clone (C) of the *j*th family (F) *j* of the *i*th provenance (P), *m* is the general pilodyn mean; α, β_i, γ_{ij} and δ_{ijk} are, respectively, pilodyn–girth covariation coefficients at the site, provenance, family and clone levels; and ε_{ijkl} is residual error.

According to Azais et al (1991), slope differences among genetic entities can be tested by successively comparing the models [1] to [3] to the model [4] using the *F* statistic:

$$F = \frac{(RSS_n - RSS_g) / p - q}{RSS_g / q}$$

where RSS_n and RSS_g are, respectively, the residual sum of square of the model (*n*) and of the general model [4], and *p* and *q* are the degrees of freedom of these model residuals.

For example, comparison of the model [4] and [5], the null hypothesis is: $\delta_{ij1} = \delta_{ij2} = \ldots = \delta_{ijk}$.

We computed

$$> F = \frac{(RSS_3 - RSS_4) / p - q}{RSS_4 / q} >$$

then we computed the *P* value associated with *F*, and according to the result, we accepted or rejected the null hypothesis.

$$Y_{ijkl} = m + (\alpha + \beta_i + \gamma_{ij} + \delta_{ijk}) \times (X_{ijkl} + P_i + F_{ij} + C_{ijk} + \varepsilon_{ijkl}) \quad [5]$$

is the model used to test the existence of a remaining genetic effect on pilodyn when data are adjusted for the girth at all genetic levels.

RESULTS

Sampling of genetic entities

The study of the influence of the sample size (number of trees within genetic entity) on the strength of the relationship between girth and pilodyn and on the estimation of mean pilodyn and girth showed evidence that there exists a limit where the *P* value becomes higher than the usual 5% limit (fig 1) and where mean linear correlation coefficient, pilodyn and girth becomes very *unsteady* (that is when variance of estimation of the coefficient of correlation and of the mean is high; fig 2). Results from figures 1 and 2 are summarized in table I. This limit was chosen to decide what should be the minimum number of trees in the genetic entities applied in this study.

N was chosen equal to 20 for provenances, 12 for families. According to table I, N should be equal to eight or ten for clones; however, too few clones had ten, or even eight, and more trees. One hundred ten clones have six and more trees. Thus, N was chosen equal to six for clones, a compromise between the number of trees per clone and the number of clones. N was used to select all genetic entities in sample 1.

Table I shows the number of genetic entities selected within each genetic level

Table I. Sample 1: minimum number of trees allowed per genetic entity according to the level and the chosen criteria (number of trees per genetic entity).

Genetic level	*Mean* P *value*	*Variance of* r	*Variance of pi*	*Variance of gi*	*Minimum number*	*No of genetic entities in sample 1*
Provenance	> 12	> 14	> 20	> 20	20	24
Family	> 12	> 10	> 11	> 11	12	114
Clone	> 8	> 6	> 10	> 10	6	110

(sample 1). There were 248 different genetic entities studied. Sample 2 was used for the covariance analysis. There were more clones, but less families in sample 2 than in sample 1: 337 clones (vs 110 in sample 1), 79 families (vs 114 in sample 1) and 21 provenances (vs 24 in sample 1).

Choice of the model (sample 1)

Observation of R^2 and residuals of calculated models demonstrated that 'pilodyn = $a + b$ x girth' was the most general model, and was usually as good as or better than models with more independant

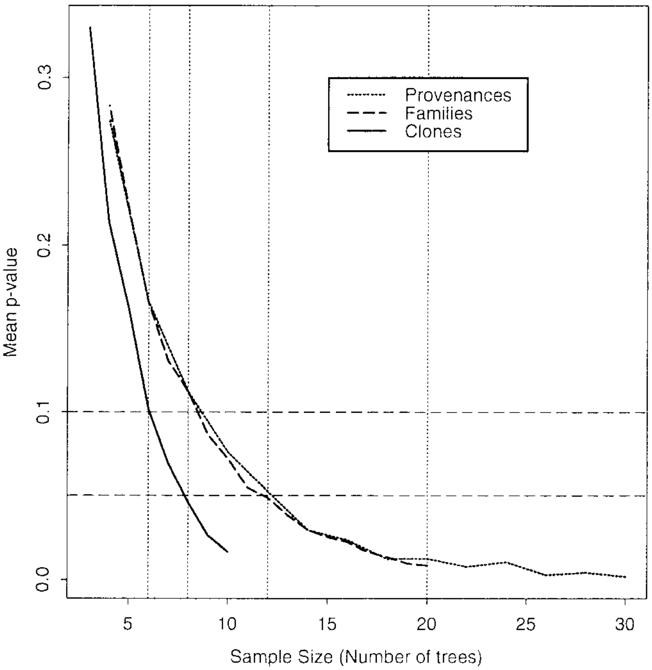


Fig 1. Relationship between mean *P* value (over 30 simulated data sets) associated with the linear correlation coefficient between girth and pilodyn pin penetration, and the number of trees in the sample.

Table II. R^2 of calculated regressions (summary).

Genetic level	*Minimum*	*Median*	*Mean*	*Maximum*
Provenance	0.088	0.355	0.363	0.660
Family	0.187	0.535	0.545	0.891
Clones	0.448	0.761	0.748	0.981

variables. Introduction of height improved R^2 significantly in only five of 248 cases, and transformation did not significantly increase the fit of the model in any case. Table II shows a summary of values of R^2 for chosen model at all levels, and the results are illustrated in figures 3–5.

Covariance analysis (sample 2)

Genetic variation for the slope of the pilodyn–girth relationship and ANOVA of pilodyn with girth as a covariate (tables III and IV):

Model [1]: girth as a covariate. The R^2 of this model is 0.521.

Model [2]: girth and girth at provenance level as a covariate. The R^2 increase from model [1] to [2] is only 0.017.

Model [3]: girth, girth at provenance level and girth at family level as a covariate. The R^2 increase from model [2] to [3] is 0.027.

Model [4]: girth, girth at provenance level, girth at family level and girth at clone level as a covariate: complete model to test differences among genetic entities for the slope of the pilodyn–girth relationship. The

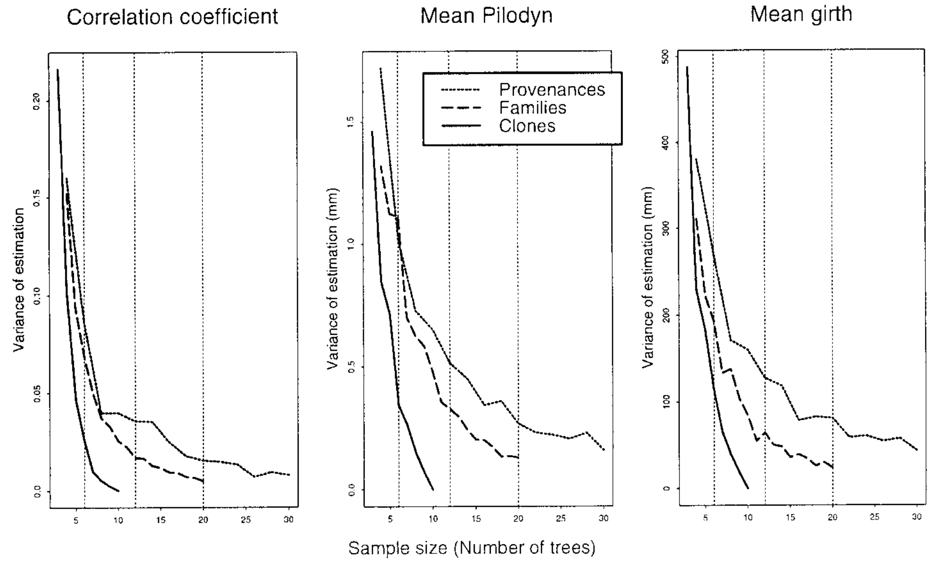


Fig 2. Variance of estimation of linear correlation coefficient between girth and pilodyn, of mean pilodyn and of mean girth is increasing when the number of trees within the study genetic entities decreases. Thus, the quality of the estimation of these correlation coefficients and means is decreasing.

Table III. *F* statistic and associated *P* value for the comparison of the incomplete and general covariance models.

Comparaison	F *statistic*	*DF of the submodel residuals*	P *value*
Models [1] and [4]	1.45	4 080	< 0.001
Models [2] and [4]	1.42	4 052	< 0.001
Models [3] and [4]	1.25	3 772	< 0.001

The degree of freedom (DF) of the residuals of model [4] is 3090. None of the three submodels can be accepted instead of the model [4], hence there are significant differences among genetic entities for the slope of the *within-genetic-entity* pilodyn–girth relationship.

R^2 increase from model [3] to [4] is 0.086. The results in table III demonstrate that the slope of the pilodyn–girth relationship significantly differs among provenances, families and clones (successively adding terms in the models [1], [2] and [3] significantly improved them, even if the R^2 increase from one model to another was sometimes low).

Model [5]: general model. The results from table IV show that there are still differences among provenances for pilodyn, but no longer among families and clones. In this sample (sample 2), therefore, most differences

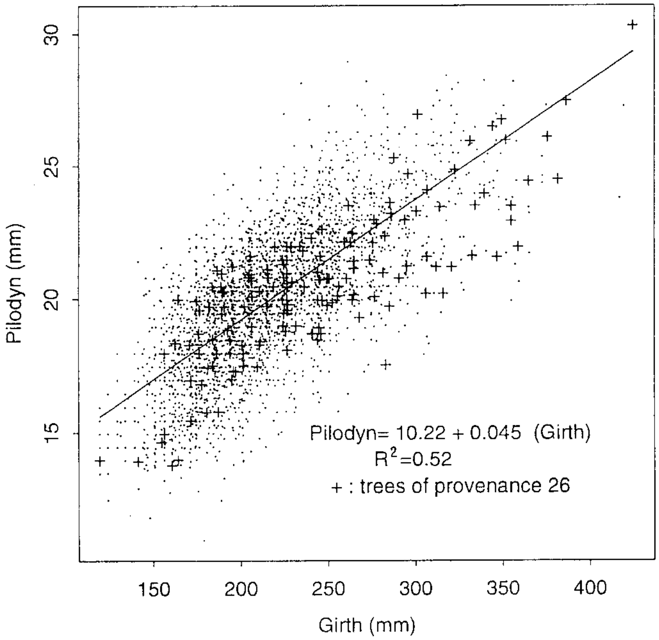


Fig 3. Pilodyn–girth relationship based on all trees (n = 4 092) in the study. Trees of provenance 26 are indicated by +.

Table IV. *F* statistic for different independent variables included in analysis of covariance models.

Independent variables	*Model 1 (0.521)*	*Model 2 (0.538)*	*Model 3 (0.565)*	*Model 4 (0.651)*	*Model 5 (0.739)*
α	2 027***	2 083.1***	2 142.9***	2 281.3***	2 385.9***
β_i		3.6***	3.7***	3.9***	4.1***
γ_{ij}			1.9***	2.0***	2.1***
δ_{ijk}				1.4***	1.5***
Provenance					2.0**
Family/provenance					1.2 NS
Clone/famille					1.2 NS

The R^2 for each model is shown in parentheses. ***Significant *F* value at 0.1% level; **significant *F* value at 1% level; *significant *F* value at 5% level; NS: not significant. α, β_i, γ_{ij} and δ_{ijk} are, respectively, pilodyn–girth covariation coefficients at the site, provenance, family and clone levels.

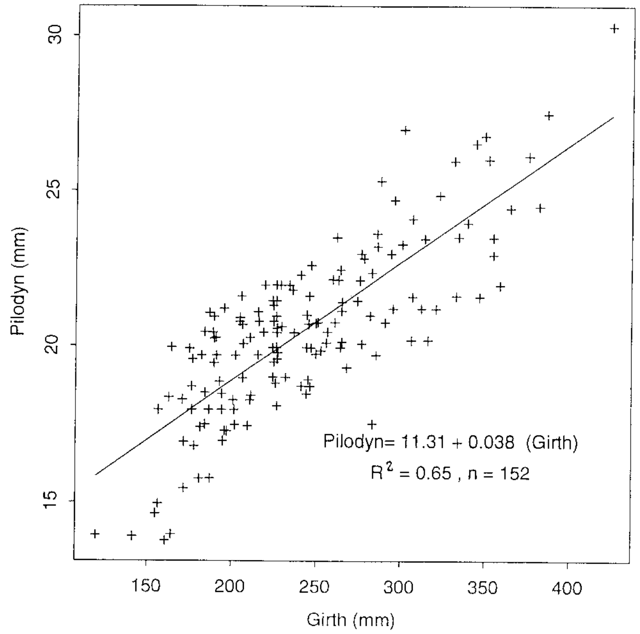


Fig 4. Example of a fitted linear regression of pilodyn versus girth for trees from a single provenance (provenance 26).

among families and clones for pilodyn are in fact differences for diameter growth.

A test was conducted to tell if leaving the terms 'family' and 'clone' in the model improved its fit significantly: *F* statistic = 1.16, *P* value = 0.0252, hence the fit increase is significant.

Relationships between model parameters (sample 1)

Whatever the genetic level and the site, there are strong or very strong linear relationships between model parameters: slope is high when intercept is low (fig 6 and table V at all levels). Intercept does not have a biological meaning. This strong relationship between slope and intercept reflects the fact that regression lines all intersect each other in a restricted zone. This zone is within the range of the two variates, around 200–250 mm girth and 20 mm pilodyn.

In addition, slope alone explains nearly all the variability of the pilodyn–girth relationship.

There is also a significant moderate relationship between pilodyn and girth and model parameters (table V and fig 7) – in particular, slope is moderately and negatively correlated with girth.

DISCUSSION AND CONCLUSION

There is a general relationship between growth and wood density assessed by the pilodyn. Globally, a satisfactory linear model to represent the pilodyn–girth relationship was found within the range of pilodyn–girth observations in this study. However, with data from a wider range, we believe that this model might be less satisfactory than a model allowing a curvilinear trend, slightly perceptible in figures 3 and 6. Chantre and Gouma (1994) found that a good description of the relationship

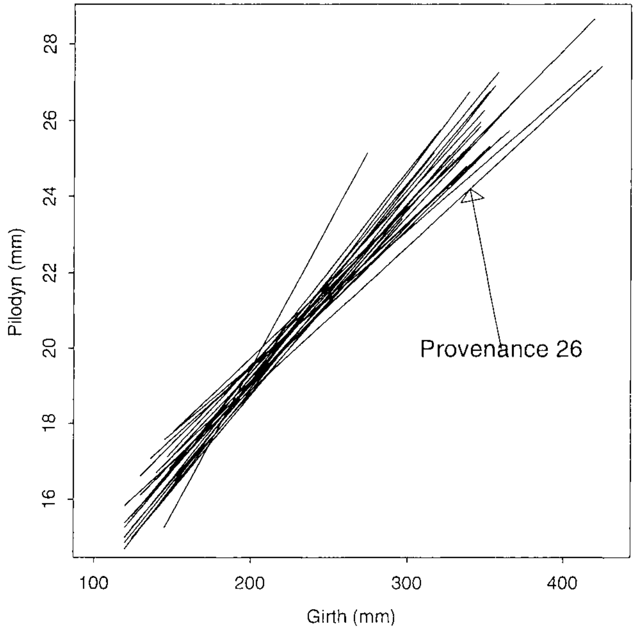


Fig 5. Complete set of linear regressions of pilodyn versus girth measurements for different provenances.

between basic density (d) and ring width (w) in Norway spruce was $d = a.\log(w)+b$ (where a and $b > 0$), while Chantre et al (1992) found that, in the same species, pilodyn (p) and basic density relationship could be described by $d = c.p + d$ (where $c < 0$ and $d > 0$). Combining both expressions, it can be written $p = \alpha.\log(w) + \beta$ (where α and $\beta > 0$); this could be the analytical expression of the curvilinear model mentioned earlier.

Unlike Colin et al (1993) and Dedeckel (1994), and like Chantre and Gouma (1994), genetic entities were significantly different for at least one parameter of the linear model between girth and pilodyn at the provenance, family and clone level (in our case, slope, as demonstrated by the covariance analysis, table III).

Most differences among genetic entities for pilodyn values are explained by the pilodyn–girth relationship (table IV). When the pilodyn data is adjusted for girth, and girth at all genetic levels, there are still provenance differences, but no family nor clone effect. For some different trees with the same girth, pilodyn partly depends on genetic identity. The absence of family and clone effect may be related with the selection of sample 2; further studies on better structured samples could help decide.

A general relationship between intercept and slope and structure of the regression lines suggest that error of estimation of wood density occurs when a model is used to predict wood density of individual trees or genetic entities. The accuracy of the model is increased when using a *genetic entity* model rather than a *general* model. The precision increase is 13% on average (0.651 for model [4] – 0.521 for model [1]; table IV).

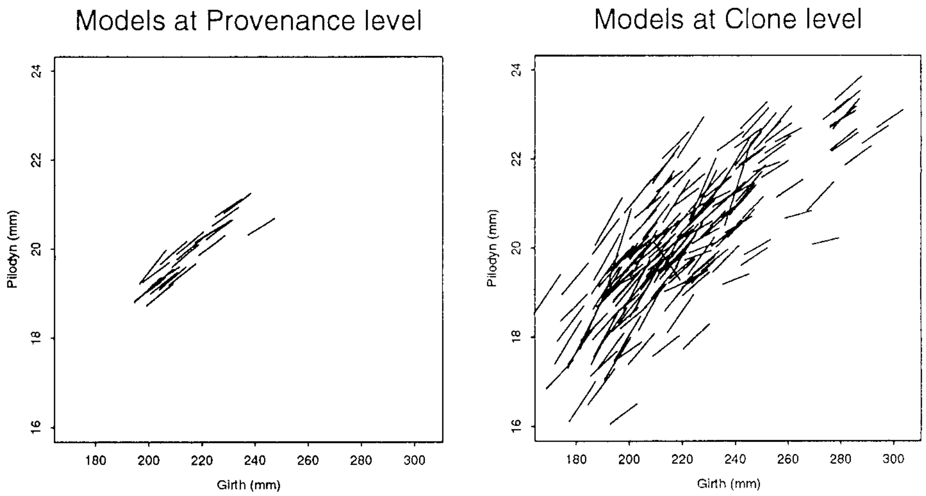
The relationship between the intercept and the slope of the models is very strong (fig 7). This relationship seems to be the same at each genetic level. There is also a significant relationship between parameters of models and mean values of the studied traits at genetic entity level; thus, specific model parameters for individual genetic entities could be deduced from a general model (genetic-entity-slope = f (genetic-entity-mean-girth)). This trend can be seen in figure 6.

At the clone level, all trees representing a clone are genetically alike. Considering that girth is a microsite fertility index and that trees of the same clones are different for girth and pilodyn (even after adjustment

Table V. Relationships between traits and parameters on site 2.

Level		*Mean girth*	*Mean pilodyn*	*Intercept*
Provenance	Mean pilodyn	0.915***		
	Intercept	0.576**	0.502*	
	Slope	– 0.536**	– 0.407*	– 0.988***
Family	Mean pilodyn	0.833***		
	Intercept	0.518***	0.502***	
	Slope	– 0.519***	– 0.396***	– 0.978***
Clones	Mean pilodyn	0.794***		
	Intercept	0.339***	0.238*	
	Slope	– 0.366***	– 0.155NS	– 0.979***

Linear correlation coefficient. ***Significant at 0.1% level; **significant at 1% level; *significant at 5% level; NS: not significant.



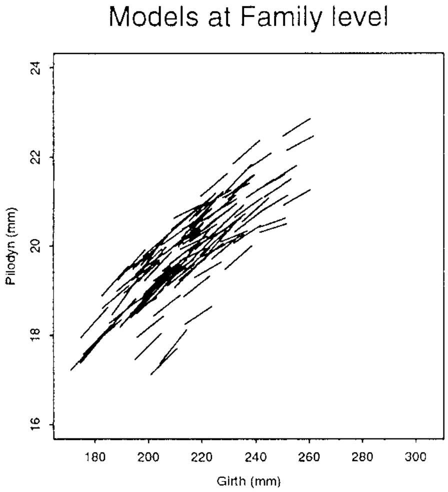
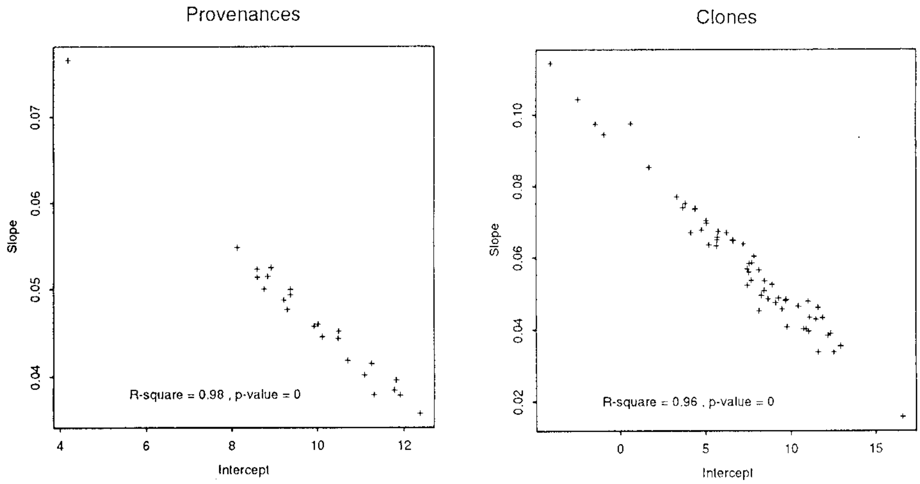


Fig 6. Complete set of calculated models at the three genetic levels: provenance, family and clone.

of block effect), these remaining differences are small-scale environmental differences. Thus, the within-clone relationship between girth and pilodyn is an environmental relationship. The same relationship calculated using mean girth and mean pilodyn at clone level is quite strong (table V): fast-growing clones will always have, in the same site conditions, wood with lower density than slow-growing clones.

At a given level for girth, however, there is some variability for mean pilodyn, and thus possibilities for selection. The range of this variation is between less than 1 (provenances) and more than 4 (clones) mm of pilodyn pin depth of penetration in our study (fig 6). Chantre et al (1992) found that the relationship between the pilodyn pin depth of penetration and the wood basic density was a simple linear one (Norway spruce). According to this relationship, the range of the variation is between 12 to 48 g/dm^3 in terms of basic density: this is not negligible, and the breeder can use the value of the pilodyn as a selection criteria, before or after selecting for girth.

Nevertheless, there is also a low, negative and highly significant genetic relationship between slope of the within-clone relationship and clone mean girth (table V). The range of this relationship is quite high: for example, slope ranges from 0.08 for slow-growing families (mean girth = 180 mm) to 0.02 for fast-growing families (mean girth = 240 mm) (fig 8). Thus, as the fertility of a site increases by 1 cm in terms of girth,



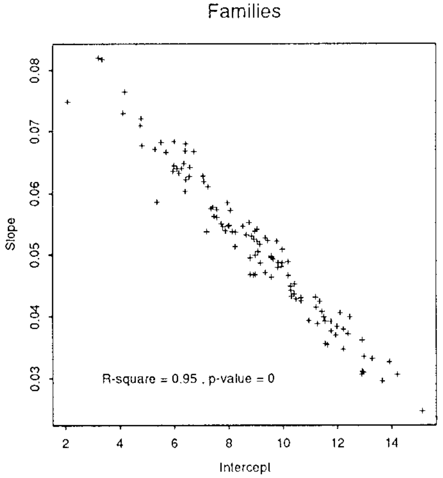


Fig 7. Relationships between slope and intercept at provenance, family and clone levels.

basic density will decrease on an average of 0.6 to 0.8 g/dm^3 for a slow-growing family, according to Chantre et al (1992). On the other hand, a fast-growing family will only loose 0.3 to 0.4 g/dm^3 for the same site fertility increase. This trend is still higher for clones: the basic density decrease may range from 1.0 to only 0.2 g/dm^3.

In others words, clones with high production and low density have a less unfavorable environmental relationship between girth and pilodyn, and thus a lower intraclone variability for wood density, than clones with low production and high density. In the same environment, wood density of the trees of such a clone will be more homogeneous among individuals; this is a constant request from the wood industry (Zobel and Jett, 1995). The slope of the pilodyn–girth relationship can be used as a secondary selection criteria, behind girth and pilodyn.

There is no significant relationship between pilodyn and slope at clone level (table V); thus, selecting for a low slope at a given level of girth will have no effect on wood density. Concurrently, this implies that selecting for a low slope at a given level of density will cause a small girth increase.

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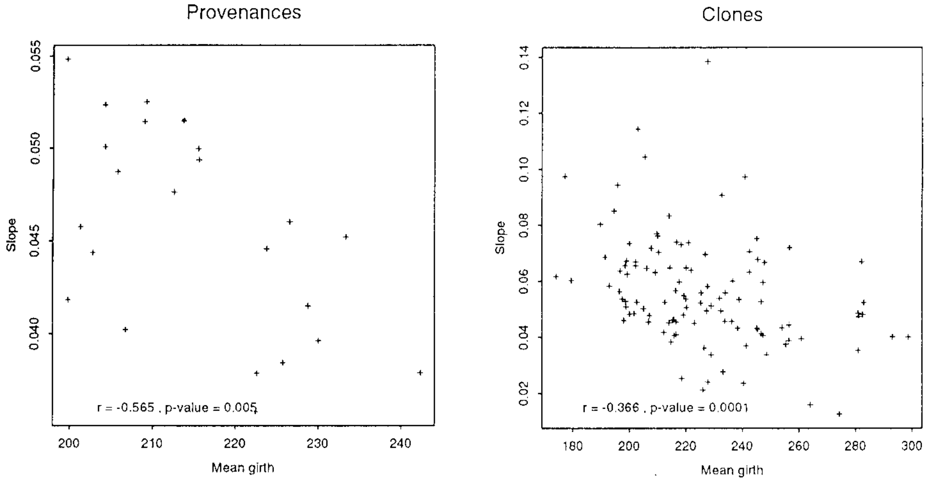

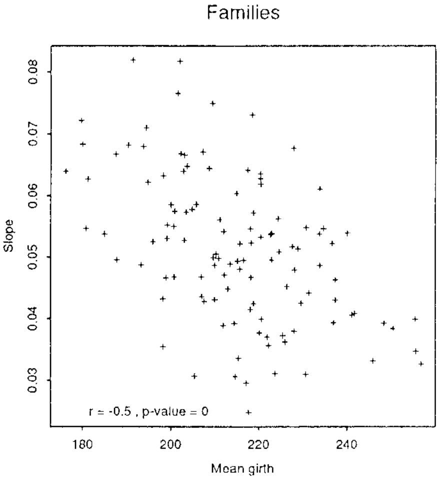

Fig 8. Relationship between estimated slope and girth for individual provenances, families and clones.

REFERENCES

Anonymous (1990) S Modli. BAO/Document N°09/90, NCY/GL, Département d'informatique, Inra, Paris, France, 21

Adams T, Aitken S, Balduman L, Schermann N (1993) Pilodyn repeatability study. In: *Pacific Northwest Tree Improvement Research Cooperative Annual Report 1992–93*. Oregon State University, Corvallis, OR, USA, 29-35

Azais JM, Bastien C, Berthier G, Chabanet C, Durier C, Gasqui P, Goyeau H, Griveau Y, Hébert Y, Hommet G, Hulmel M, Lefort-Buson M, Membre JM, Moisan A, Pellerin S, Pinochet X, Solari A, Volaire F, Turkheim E, Lavergne JC (1991) *Modèle linéaire, Manuel du formateur*, Module 2-3, Inra, Formation permanente, Paris, France

Chantre G, Sutter-Barrot E, Gouma R, Bouvet A (1992) De l'intérêt de l'utilisation du pilodyn dans l'étude de la qualité du bois: application à l'épicéa commun et à l'épicéa de Sitka. *Ann Afocel* 1992, 145-177

Chantre G, Gouma R (1994) Influence du génotype, de l'âge et de la station sur la relation entre l'infradensité du bois et la vigueur chez l'épicéa commun (*Picea abies* Karst). *Ann Rech Sylv* 61-89

Colin F, Houillier F (1991) Branchiness of Norway spruce in north-eastern France: modeling vertical trends in maximum nodal branch size. *Ann Sci For* 48, 679-693

Colin F, Houillier F (1992) Branchiness of Norway spruce in north-eastern France: predicting the main crown characteristics from usual tree measurements. *Ann Sci For* 49, 511-538

Colin F, Houillier F, Joannes H, Haddaoui A (1993) Modélisation du profil vertical des diamètres, angles et nombres de branches pour trois provenances d'épicéa commun. *Silvae Genet* 42, 206-222

Cornelius J (1994) Heritabilities and additive genetic coefficient of variation in forestry. *Can J For Res* 24, 372-379

Cown DJ (1981) Use of the pilodyn wood tester for estimating wood density in standing trees–influence of site and tree age. Forest Research Institute, New Zealand Forest Service, bulletin n° 13

Dedeckel A (1994) La densité du bois de douglas (*Pseudotsuga menziesii* Mirb [Franco]): la variabilité des facteurs microdensitométriques et l'effet génétique. DEA sciences du bois, Inra-Nancy, Engref, France, 24

Eyono Owoundi R (1992) Modélisation de la rétractibilité du bois, en relation avec des paramètres de la structure de l'accroissement annuel et de la position dans l'arbre chez *Quercus robur* L et *Quercus petraea* Liebl. Thesis, École nationale du génie rural des eaux et forêts, Nancy, France

Ferrand JC (1986) Le programme d'amélioration de l'épicéa commun. *Amél Génét Arbres For* 125-129

Hoffmeyer P (1978) The pilodyn instrument as a non-destructive tester of the shock resistance of wood. Non-destructive testing meeting, Vancouver, WA, USA, August 1978

Kremer A (1986) Méthodes et stratégies de sélection. *Amél Génét Arbres For* 89-101

Leban JM, Duchanois G (1990) SIMQUA: un logiciel de simulation de la qualité des bois. *Ann Sci For* 47, 483-493

Nepveu G (1991), La variabilité du bois. In: *Le matériau bois*. Arbolor, Nancy, France, 56

Schermann N (1994) Étude des paramètres génétiques de trois populations de douglas vert (*Pseudotsuga menziesii* [Mirb] Franco), analyse d'un diallèle 16 x 16, conséquences pour la stratégie d'amélioration génétique de l'espèce. Thesis, INA-PG-INRA Orléans, France, 117

Sprague JR, Talbert JT, Jett JB, Bryant RL (1983) Utility of the pilodyn in selection for mature wood specific gravity in Loblolly pine. *For Sci* 29, 696-701

Van de Sype H (1994) *Clones* (Compte rendu des premiers résultats des tests INRA 6.352.1, 6.352.2 et 6.351, Document Interne), INRA-Orléans, France

Villeneuve M, Morgenstern EK, Sebastian LP (1987) Estimation of wood density in family tests of jack pine and black spruce using the pilodyn tester. *Can J For Res* 17, 1147-1149

Zhang SY, Eyono Owoundi R, Nepveu G, Mothe F, Dhôte JF (1993) Modelling wood density in European oak (*Quercus petraea* and *Quercus robur*) and simulating the silvicultural influence. *Can J For Res* 23, 2587-2593

Zobel B, Jett J (1995) *Genetics of Wood Production*. Springer-Verlag (Springer series in wood science), Berlin, 337