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Original article

Genetic control of the tree-ring response of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to the 2003 drought and heat-wave in France

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Abstract – The genetic control of tree ring growth in Douglas-fir in response to the drought and heat-wave that occurred in 2003 in Europe was studied with microdensity profiles in three clonal experiments located in three different French regions. The drought and heat-wave significantly affected Douglas-fir wood formation. The Chassenoix site (Northeast of Massif-Central) was more severely affected that the other two: the 2003 year-ring was narrower and less dense than in the other sites and than the previous (2002) and following (2004) year-rings in the same site: ring growth stopped earlier and latewood did not develop completely. The year-rings 2004 and 2002 were very similar in this site. There was a significant genetic control for all ring parameters in the three sites and during the three years. The heritability was highly variable between years and among sites, without any clear pattern in this variability, except in Chassenoix where it was slightly lower in the 2003 year-ring. Variables measuring the response of trees to the 2003 event, i.e., the difference in ring width between 2002 and 2003, or between 2003 and 2004, showed a very variable degree of genetic control, from very low to relatively high. Douglas-fir seemed plastic enough to acclimate to the drought and heat-wave and then to recover during 2004. Furthermore the level of heritability estimated demonstrates that Douglas-fir has an adaptive potential that could be useful for multi-generation long-term response.

heat-wave / Douglas-fir / microdensity / adaptation

Résumé – Contrôle génétique de la réponse microdensitométrique du Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) à la sécheresse et canicule de 2003 en France. La réponse du douglas à la canicule de 2003 en France a été étudiée à l'aide de profils microdensitométriques obtenus sur des arbres de 3 tests clonaux situés dans 3 régions différentes. La canicule a significativement affecté la formation du bois du douglas. Les arbres du site de Chassenoix, situé dans le Morvan, ont réagi plus fortement que ceux des 2 autres : le cerne de l'année de la canicule est plus étroit et moins dense que le même cerne dans les 2 autres sites et plus étroit et moins dense que les cernes immédiatement antérieur (2002) et postérieur (2004) dans le même site ; la formation du bois s'est arrêtée plus tôt et le bois final ne s'est pas complètement développé. À Chassenoix, le cerne de l'année 2004 ressemble plus au cerne 2002 qu'au cerne 2003, ce qui traduit une récupération. Nous mettons en évidence un contrôle génétique significatif pour toutes les variables intra-cernes dans les 3 sites, pour les 3 années 2002, 2003 et 2004. Les héritabilités sont très variables entre caractères, sites et années, sans structure particulière, sauf à Chassenoix où ces héritabilités sont légèrement plus faibles durant l'année de la canicule. Des variables décrivant la réponse des arbres entre 2002 et 2003 puis 2003 et 2004 sont très irrégulièrement contrôlées génétiquement, avec des héritabilités allant de 0 à près de 0,5. Le douglas semble avoir été suffisamment plastique pour s'acclimater à la sécheresse et canicule puis pour récupérer en 2004 une croissance proche de celle de 2002. De plus, son potentiel génétique démontré par le niveau d'héritabilité estimé lui donne également une capacité adaptative multi-génération à plus long terme.

canicule / Douglas / microdensité / adaptation

1. INTRODUCTION

Summer 2003 was characterized by extremely high temperatures over several European countries, including France, breaking in some cases all-time maximum records [18, 19]. This heat wave had also an extraordinary duration [20]. According to Chuine et al. [5], it was the most severe heat wave in France since at least 1370. This phenomenon was accompanied by low precipitation, which failed to compensate for the elevated evapotranspiration, resulting in a large water balance deficit. Many trees were affected by this phenomenon, with reactions ranging from partial foliage necrosis to tree death [1, 34].

With the forecasted global climate change, such extreme climate events are likely to become more frequent [19, 32]. They may become major limiting factors for tree growth in the future.

The consequences of the global climate change on our forest are being widely studied. For example, the temperature increase associated with the global climate change has a

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Table I. Main features of the three Douglas-fir trial sites used in this study.

Sites	Latitude	Longitude	Elevation (m)	[1] Max–Min temperature (°C)	[2] Precipitation (mm)	Number of clones
Lartimache	45.65	0.84	415	16.8–6.3	1206	30
Chassenoix	47.34	4.19	470	15.3–5.0	1212	23
Sorèze	43.26	2.08	710	18.6–8.8	929	22

[1] Mean daily maximum and minimum temperature for the period 1994–2004.

[2] Mean annual precipitation for the period 1994–2004.

demonstrated effect on tree phenology, especially at the beginning of the growing season [4, 5, 25, 37]. Little is known however about the effect of the climate change on other traits related with wood formation. Cambial activity is affected by variations of water balance during the growing season, which results in variation of the morphology of the produced xylem cells [11, 16, 38]. Rozenberg et al. [27] illustrated this with Norway spruce samples, where early drought during the 1993 growing season left a distinctive imprint in the wood record; moreover, the among-tree difference in reaction intensity was under strong genetic control. In general, the impact of climate fluctuations may be minimized due to the ability of a given genotype to adjust its phenotype: i.e., phenotypic plasticity [24]. Changes in wood formation during cambial activity can be interpreted as a plastic response to climate variation.

Pseudotsuga menziesii var. *menziesii* (Douglas-fir) is one of the tree species that showed partial or complete foliage necrosis during and after the heat-wave. It is a highly productive forest species currently abundantly planted in France, typically in sites with at least 400 mm between May-September. Douglas-fir is particularly sensitive to a reduction of water availability [8, 29].

Preliminary results obtained from samples collected on a small number of Douglas-fir trees immediately after the 2003 drought and heat-wave showed a conspicuous effect on the 2003 year-ring [28]. Indirect X-ray microdensitometry revealed large differences in the 2003 ring as compared to the rings 1999 to 2002: the 2003 ring was narrower with a thinner and less dense latewood.

The objective of this study was to improve our understanding of Douglas-fir responses to extreme drought and heat, using indirect X-ray microdensity profiles in the wood as a record of cambial activity subjected to environmental variations [16, 38].

For this, we analysed wood microdensity records on samples from a Douglas-fir clonal experiment with replicates in three distinct sites. We compared the rings formed under extreme weather conditions in the year 2003 with the rings immediately preceding and following, arbitrarily chosen as references. The primary benefit of selecting 2002 and 2004 as reference years is minimizing the cambial age effect when comparing rings.

The replication of several genotypes over the three sites allowed us to separate the genetic effect from the site effect in the estimation of the response to the drought and heat wave and to quantify the degree of genetic control.

The reaction was measured not only by observing the characteristics of the single rings, but also using the difference between ring variables of successive rings 2002 and 2003, and of successive rings 2003 and 2004. *Difference 2002–2003* is a quantification of immediate tree reaction to drought and heat wave, while *difference 2003–2004* is assumed to be a blend of recovery and delayed reaction. The *difference 2002–2004* was also analysed but finally discarded since no consistent trend was detected in the results.

2. MATERIAL AND METHODS

2.1. Site and climate description

Wood microdensity data were obtained from three clonal tests of Douglas-fir planted in France by AFOCEL (Association Forêt Cellulose, www.afocel.fr). Table I summarizes some climate parameters for the three sites located at Lartimache (West of Massif-Central, Limousin), Chassenoix (Northeast of Massif-Central, Morvan) and Sorèze (South of Massif-Central, Midi-Pyrénées). Chassenoix is the site with the youngest trees and with the lowest plantation density. This plantation was installed during March 1988 at 4 × 3 m spacing, while Sorèze and Lartimache were planted during March 1986 and December 1984 respectively, at 3 × 3 m.

Climate data was provided by Météo-France, from the closest meteorological stations to the experimental sites. Of the three sites, Sorèze showed the lowest mean annual precipitation for the period 1994–2004 and the highest maximum and minimum mean annual temperatures. Chassenoix and Lartimache received similar precipitations. But Lartimache displayed higher annual mean temperature than Chassenoix. We computed an aridity index (Eq. (1)) based on the index of De Martonne [7]:

$$AI_{ij} = \frac{T\max}{P} \tag{1}$$

where: AI_{ij} = climate index of $site_i$ during $year_j$, $T\max$ = sum of maximum daily temperatures, and P = annual precipitation. Taking into account the range of Aridity Indices (AI) of the period 1994–2004, the probability associated with each year's AI was computed from Normal statistics as a measure of the likelihood of each year's aridity.

2.2. Wood sampling

Three to five trees were sampled from each clone in each site. Samples consisted of 5 mm increment cores taken at breast height. The number of clones per site was between 22 and 30 (Tab. I), with nine clones common to the three sites. Increment cores were dried to moisture equilibrium and subsequently analysed by indirect X-ray densitometry [21]. The resulting X-ray films were scanned at a

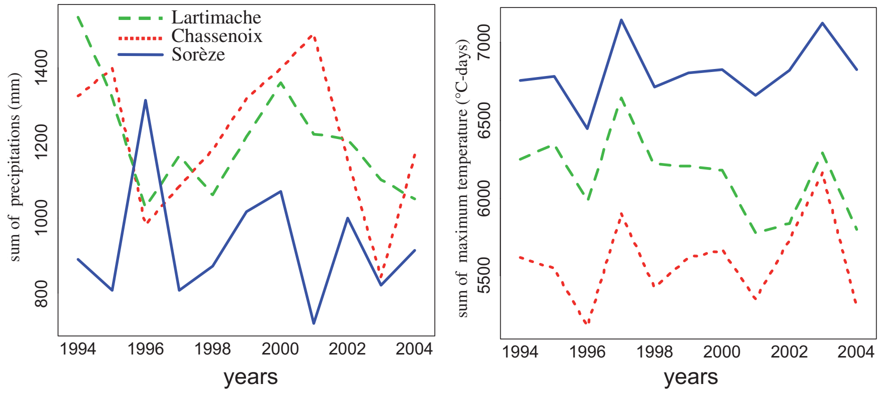

Figure 1. Time course of annual rainfall (mm) and sum of daily maximal temperatures (°C-days) during the 1994–2004 period in Lartimache, Chassenoix and Sorèze.

1000 dpi resolution with 8 bits per pixel. The digital images were processed with the WinDENDRO software [13], obtaining a spatial resolution of 25 µm. The last step of the data processing used a computer routine written in *R* language [22] to compute following variables for each year-ring:

- ring width (RW),
- mean ring density (MRD),
- minimum ring density (MID),
- maximum ring density (MAD).

2.3. Data analysis

The ring formed during 2003 was compared to the neighbouring rings formed during 2002 and 2004, in the three clonal sites. We assumed that the between-ring variation for the three year-rings is related to environment rather than to changes in cambial age, as defined by Zobel and van Buijtenen [39].

Rather than using a unique and complete year-site-clone ANOVA model, with only 9 clones common to the 3 sites and many complex-to-interpret interactions, we decided to split the analysis into two steps:

In a first step, inter-annual variations were analysed independently in the 3 sites using all available clones in each site (thus increasing the statistical power of the analysis), by means of the following ANOVA model:

$$y_{ijk} = \mu + \tau_i + \beta_j + (\tau\beta)_{ij} + \varepsilon_{ijk} \qquad (2)$$

where $y_{ijk} = {}_k$th observation during $_i$th year and the $_j$th level of factor clone, μ = overall mean effect, τ_i = fixed effect of $_i$th year, β_j = fixed effect of the all $_j$th level of factor clone in each site, $(\tau\beta)_{ij}$ = interaction between the $_i$th level of factor year and the $_j$th level of factor clone, and ε_{ijk} = random error.

In a second step, inter-site analysis was conducted independently for each year, using the 9 clones common to the three sites:

$$y_{ijk} = \mu + \tau_i + \beta_j + (\tau\beta)_{ij} + \varepsilon_{ijk} \qquad (3)$$

where $y_{ijk} = {}_k$th observation of the microdensity parameters taken under the $_i$th level of factor site and the $_j$th level of factor clone, μ = overall mean effect, τ_i = fixed effect of the $_i$th level of factor site, β_j = fixed effect of the $_j$th level of factor clone (nine clones in common to the three sites), $(\tau\beta)_{ij}$ = effect of interaction between the $_i$th level of factor site and the $_j$th level of factor clone, and ε_{ijk} = random error.

The between-site cambial age effect related with the differences in plantation dates is taken into account in this inter-site ANOVA model, as well as all the environmental effects associated with the sites.

The response of each ring property to the extreme climate of year 2003 was calculated as the difference between the 2003 and the 2002 values (*difference 2002–2003*). The recovery of ring properties during 2004 was computed similarly as the *difference 2003–2004*. Thus eight *differences* variables were associated to the four ring variables: RW, MRD, MID and MAD. The following model was used to assess the degree of genetic control of the *differences traits*:

$$\Delta y_{ij} = \mu + \tau_i + \varepsilon_{ij} \qquad (4)$$

where $\Delta y_{ij} = {}_{ij}$th difference between the value in year$_{n+1}$ and the value in year$_n$, μ = overall mean, τ_i = random effect of the $_i$th clone and ε_{ij} = random error.

We used the same model to assess the degree of genetic control for ring variables in each site and year. The models were treated with the AOV function of *R* statistical software [22].

We calculated genetic determination coefficient of broad sense heritability as [10]:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_\varepsilon^2}; \qquad (5)$$

where: σ_g^2 = genetic component of variance, and σ_ε^2 = error component of variance. The corresponding standard error of the heritability was estimated as [10]:

$$s.e.(H^2) = \sqrt{\frac{(2 \times 1 + har - 1) \times H^2)^2 \times (1 - H^2)^2}{(har \times (har - 1) \times (n) - 1)}}; \qquad (6)$$

where: *har* = harmonic mean of individuals in each clones, and n = number of clones.

3. RESULTS

3.1. Climate data

The annual cumulated daily maximum temperature during year 2003 was 567 °C-days, 151 °C-days and 314 °C-days above the mean value over the 1994–2004 period in Chassenoix, Lartimache and Sorèze, respectively, while cumulated

Table II. Annual Aridity indexes. Means and standard error for the period 1994–2004, and probability (in percentage) of occurrence of a larger Aridity index.

	Aridity index					Probability × 100		
	AI_{2002}	AI_{2003}	CI_{2004}	$AI_{1994-2004}$	s.e.	$AI_i > AI_{2002}$	$AI_i > AI_{2003}$	$AI_i > AI_{2004}$
Lartimache	4.82	5.72	5.52	5.15	0.61	**70.7**	**17.6**	**27.1**
Chassenoix	4.97	7.32	4.55	4.75	1.02	**41.78**	**0.6**	**57.9**
Sorèze	6.83	8.69	7.48	7.53	1.28	**70.8**	**18.1**	**51.6**

rainfall was 371, 106 and 110 mm below the 1994–2004 average (Fig. 1). Year 2003 was clearly exceptional in Chassenoix with respect to the low probability of reaching higher values displayed in Table II.

3.2. Comparisons between years

The results of ANOVA for the comparison by pairs of years are presented in Table III: year 2003 differed significantly from year 2002 for all ring parameters in the three sites, and from year 2004 for all variables in Chassenoix, for 3 variables in Sorèze and for 3 variables in Lartimache. The year effect was significant when we compare 2002 and 2004 for all ring variables except for RW in Lartimache.

The most severe impact of year 2003 was recorded in Chassenoix, particularly for RW and MID (Tab. III). For 2002 and 2004, the year effect was much stronger in Sorèze for all ring variables except for RW.

Figure 2 shows the change of ring characteristics from 2002 to 2004, in the 3 sites. The site Chassenoix had the most distinctive behaviour of the three sites for the 4 variables. In Chassenoix, RW diminished between 2002 and 2003, but increased steeply in 2004. A similar but attenuated trend was visible in Lartimache. In Sorèze, RW decreased continuously between 2002 and 2004. For the variables MRD and MAD, Chassenoix showed the same trend in 2003 as for RW. In Lartimache and Sorèze, however, the between-year variation for these variables was smaller, and 2003 was generally not the year with the lowest value. MID was the only variable with a maximum value in 2003 in Chassenoix.

3.3. Site, clone and site-clone interaction effects on ring variables

The site effect was strongly significant for all ring variables except for MID during 2004 (Tab. IV). The clone effect was always strongly significant for all years and ring variables. There was no noticeable trend in the variation of the clone effect between years. The interaction effect was significant except for MID (in 2002 and 2003) and MAD (in 2004). When site×clone effects were significant, the associated probabilities were always larger than for the main effects (data not shown).

3.4. Genetic control of ring variables

Table V presents the broad-sense heritability estimates in the 3 sites and during the 3 years for the 4 ring variables.

Table III. Results of the fixe-effects analysis of variance (F value and code for associated probability) for comparison by pairs of years, using all clones in each site.

	RW	MRD	MID	MAD
Between 2002 and 2003				
Lartimache				
Year	23.88***	54.09***	44.19***	68.57***
Clone	7.53***	9.25***	6.36***	10.89***
Year×clone	0.18 ns	1.18 ns	0.61 ns	1.65*
Chassenoix				
Year	119.76***	106.62***	77.99***	243.47***
Clone	5.88***	9.77***	5.22***	4.86***
Year×clone	0.58 ns	1.65*	0.92 ns	0.88 ns
Sorèze				
Year	12.77***	122.32***	30.23***	136.02***
Clone	5.59***	11.26***	5.20***	4.92***
Year×clone	0.71 ns	2.57***	0.38 ns	2.76***
Between 2003 and 2004				
Lartimache				
Year	8.90***	25.18***	0.07 ns	23.30***
Clone	6.43***	9.36***	5.89***	5.23***
Year×clone	0.24 ns	3.01***	0.90 ns	1.59*
Chassenoix				
Year	392.70***	599.99***	36.01***	72.21***
Clone	6.14***	11.05***	3.96***	4.01***
Year×clone	1.79*	3.22***	0.96 ns	1.80*
Sorèze				
Year	16.15***	420.03***	3.35 ns	93.45***
Clone	5.86***	16.04***	6.43***	3.24***
Year×clone	1.19 ns	3.43***	0.58 ns	0.91 ns
Between 2002 and 2004				
Lartimache				
Year	2.14 ns	154.90***	35.17***	127.25***
Clone	6.33***	8.35***	5.14***	6.24***
Year×clone	0.19 ns	1.54*	0.88 ns	0.85 ns
Chassenoix				
Year	111.58***	149.75***	7.53**	55.14***
Clone	5.69***	11.01***	4.09***	6.27***
Year×clone	2.14**	5.29***	1.73*	1.85*
Sorèze				
Year	61.14***	1180.98***	51.58***	439.84***
Clone	3.95***	13.60***	6.87***	5.59***
Year×clone	1.02 ns	4.28***	0.98 ns	1.28 ns

Codes for associated probability: between 0 and 0.001 = ***, between 0.001 and 0.01 = **, between 0.01 and 0.05 = *, and > 0.5 = ns.

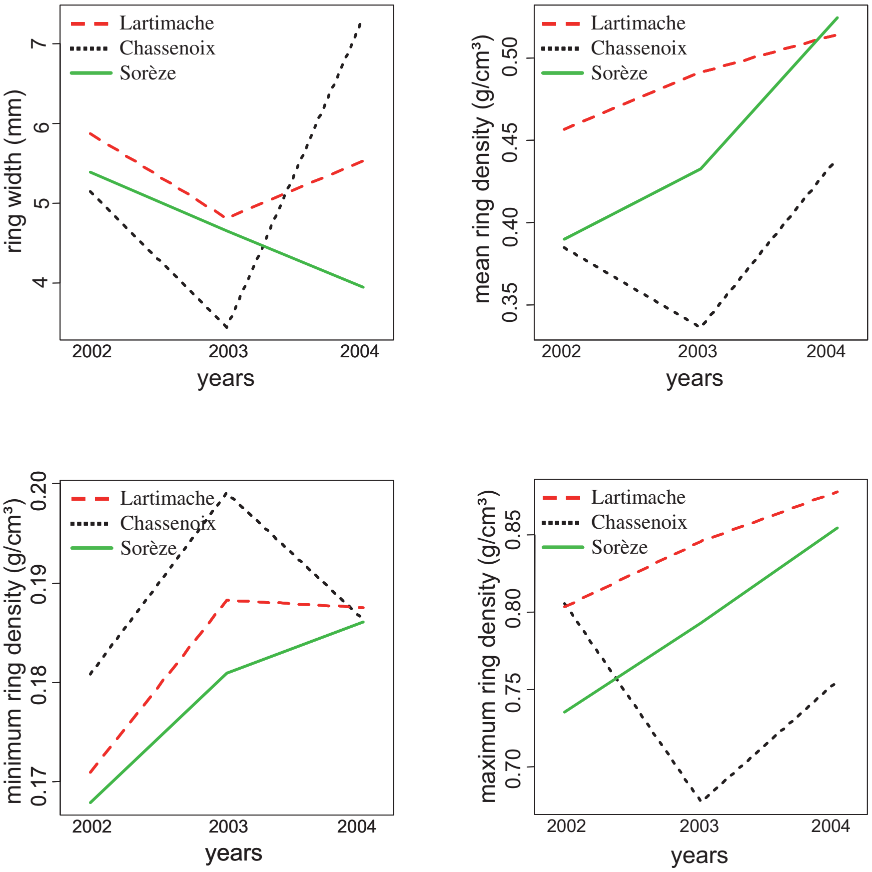

Figure 2. Time course during 2002-2004 of tree ring properties: RW (ring width), MRD (mean ring density), MID (minimum ring density) and MAD (maximum ring density), in young Douglas-firs planted at three sites.

Table IV. Results of fixed effect analysis of variance (F value and code for associated probability) for site (degree of freedom = 2), clone (degree of freedom = 8) and site×clone interaction (degree of freedom = 16), using the 9 clones common to the 3 sites, for the 4 ring variables.

	RW	MRD	MID	MAD
2002				
Site	5.25***	44.29***	6.54***	44.36***
Clone	8.94***	6.98***	5.82***	7.68***
Site×clone	2.27***	2.87***	1.56 ns	3.11***
2003				
Site	9.94***	183.61***	7.22***	90.06***
Clone	7.84***	10.12***	4.45***	4.09***
Site×clone	1.91*	1.90*	1.66 ns	3.46***
2004				
Site	37.17***	136.69***	2.94 ns	49.03***
Clone	6.56***	8.03***	3.54***	3.67***
Site×clone	2.43***	2.46***	2.21**	1.51 ns

Codes for associated probability: between 0 and 0.001 = ***, between 0.001 and 0.01 = **, between 0.01 and 0.05 = *, and >0.5 = ns.

The variable with the strongest genetic control was MRD, followed by MID, MAD and RW. However, there was more variation between years and between sites than between variables. No particular trend can be identified for the between-year or between-site variation.

3.5. Response to 2003 drought and heat-wave

Figure 3 shows the mean values and standard errors of the *difference* for all clones in each site. This suggested that the response to the 2003 drought and heat-wave in Chassenoix was different of that in Lartimache and Sorèze. In Chassenoix, all *differences 2002–2003* were negative, except *difference 2002–2003* for MID, and were opposite to the *differences 2003–2004*.

Table VI presents the results about the genetic control of the *difference traits*. There was a significant genetic control for most *difference traits* in Chassenoix and Sorèze, but not for *difference 2002–2003* for RW and MID in Lartimache and MAD in Chassenoix, nor for *difference 2003–2004* for RW in Lartimache, MID in Chassenoix and MAD in Sorèze. Corresponding values for heritability ranged from non-significantly different from zero (for the same variables) to moderate to quite high values (reaching a maximum of 0.48 in Sorèze for difference 2002–2003 for RW and MAD).

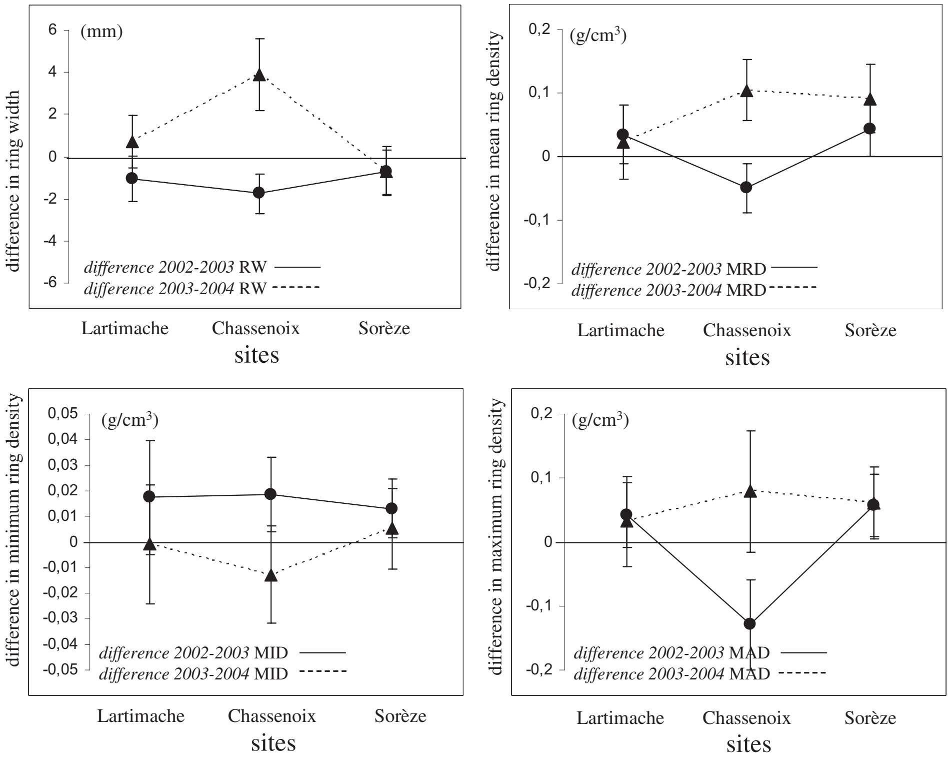

Figure 3. Inter-annual differences in ring properties of young Douglas-firs in the different sites *difference* RW (ring width), *difference* MRD (mean ring density), *difference* MID (minimum ring density) and *difference* MAD (maximum ring density).

Table V. Coefficient of genetic determination (H^2 broad sense heritability) and associated errors (s.e.H^2) for the 4 ring variables in the 3 sites during the 3 years.

	RW		MRD		MID		MAD	
	H^2	s.e.H^2	H^2	s.e.H^2	H^2	s.e.H^2	H^2	s.e.H^2
Lartimache								
2002	**0.37**	0.13	**0.40**	0.13	**0.34**	0.13	**0.55**	0.12
2003	**0.35**	0.13	**0.54**	0.12	**0.54**	0.12	**0.55**	0.12
2004	**0.29**	0.13	**0.52**	0.13	**0.28**	0.13	**0.22**	0.13
Chassenoix								
2002	**0.33**	0.15	**0.55**	0.14	**0.36**	0.15	**0.44**	0.15
2003	**0.32**	0.15	**0.43**	0.15	**0.26**	0.15	**0.23**	0.15
2004	**0.41**	0.15	**0.67**	0.12	**0.30**	0.15	**0.38**	0.15
Sorèze								
2002	**0.26**	0.15	**0.43**	0.16	**0.34**	0.16	**0.59**	0.14
2003	**0.39**	0.16	**0.61**	0.13	**0.25**	0.15	**0.18**	0.14
2004	**0.26**	0.15	**0.69**	0.12	**0.55**	0.14	**0.19**	0.15

4. DISCUSSION AND CONCLUSION

During summer 2003 temperature was exceptionally high and precipitations were low, but the magnitude of the drought and heat-wave was not uniform over the whole French territory [23]. Of the three sites, Chassenoix was the most severely affected, with the highest maximum temperature and lowest precipitations. In Chassenoix, the 2003 Aridity Index had the lowest probability of occurrence, considering a period of 11 years. This confirms that 2003 climatic conditions were most atypical for this site.

Douglas-fir response to drought and heat

In Chassenoix, the ring 2003 was narrower and less dense than the others. Earlywood showed a higher minimum density during 2003, while latewood had lower maximum density than the other neighbouring rings, which determined together a decrease in within-ring density variation for 2003.

These results support the idea that during 2003, in Chassenoix, ring formation stopped earlier than during 2002 and 2004, resulting in a ring with incomplete latewood. Similar features were observed by Rozenberg and Pâques [28] in a Douglas-fir stand located south of Orléans, in France. In Lartimache, the 2003–ring was different from the previous and following ones for nearly all properties, but ring width and ring density variables were only slightly modified (respectively decreased and increased, Fig. 2), with no specific tendency. In Sorèze, the trends (shown in Fig. 2) were different from Chassenoix and Lartimache and moderate, despite the fact that the climatic conditions during 2004 were much closer to mean values than during 2003. This suggests that in Sorèze the abnormal climatic conditions during 2003 may have impacted wood formation during the year 2004.

One of the consequences of the 2003 drought and heat-wave was a dramatic reduction of water availability in the

Table VI. Coefficient of genetic determination (H^2 broad sense heritability) and associated error (s.e.H^2) for the *differences* (2002–2003 and 2003–2004) describing the impact of the 2003 drought and heat wave. All clones were used in Lartimache, Chassenoix and Sorèze.

	Difference 2002–2003		*Difference* 2003–2004	
	H^2	s.e.H^2	H^2	s.e.H^2
Lartimache				
difference RW	**0.01**	0.09	**0.06**	0.10
difference MRD	**0.19**	0.13	**0.41**	0.13
difference MID	**0.05**	0.10	**0.29**	0.13
difference MAD	**0.35**	0.13	**0.27**	0.13
Chassenoix				
difference RW	**0.34**	0.15	**0.38**	0.15
difference MRD	**0.34**	0.15	**0.42**	0.15
difference MID	**0.28**	0.15	**0.08**	0.12
difference MAD	**0.06**	0.12	**0.22**	0.14
Sorèze				
difference RW	**0.48**	0.15	**0.47**	0.15
difference MRD	**0.32**	0.16	**0.40**	0.16
difference MID	**0.17**	0.14	**0.24**	0.16
difference MAD	**0.48**	0.15	**0.05**	0.12

soil. According to Bréda et al. [2, 3], a first reaction to decreased soil water availability, is the reduction of transpiration by stomatal closure. This is generally accompanied by a reduction of tree growth. When the length and the intensity of the drought increase, cavitation may occur in xylem vessels, followed by early mortality of roots and twigs and, finally, by tree death [3]. Thicker cell walls and smaller diameter lumens (higher density wood) increase resistance to drought-induced cavitation and thus help trees to maintain the integrity of their hydraulic system [9, 14, 33]. In Chassenoix, ring density was lower during 2003 because, as hypothesized above, ring formation stopped earlier in 2003 than in 2002 and 2004, without giving the trees the opportunity to form a high-density cavitation-resistant latewood. This is consistent with the fact that the heat-wave started at the beginning of August 2003, which is close to the end of the growing season (the date of cessation of cambial activity is variable among species and among years and is believed to occur generally in August–September under northern-hemisphere temperate climates [16]). We plan to develop an in-depth analysis of the within-year variation of climate conditions and ring structure to improve our understanding of the time course of the effects of the 2003 climate.

The among-site variation for the four ring variables was also significant in rings 2002 and 2004. This regional variation was larger for the years 2003 and 2004 than for the year 2002.

Our results demonstrate that there was a significant genetic control over all ring variables in the 3 sites and during the 3 years. Heritability estimates are consistent with results previously published by several authors for ring width and ring density in Douglas-fir [12, 15, 26, 35, 36]: the highest heritability estimates are found for ring density, while the lowest are found for ring width.

Broad sense heritability varied among years and sites. It was not affected by the 2003 drought and heat-wave, except in Chassenoix. In this later site heritability was always slightly lower during 2003 than 2002 and 2004. Some authors [30, 31] suggested that the expression of genetic control in quantitative characters could be related with resources availability.

An important finding of our study is that almost all *difference traits* were under genetic control. The *difference traits* in this study are indexes of phenotypic plasticity which appeared as having heritability values close to those of ring variables. Assuming that a considerable part of this genotypic variation (note we estimated broad sense heritabilities) is additive, it would be eventually possible to select genotypes with a more favourable plastic reaction to similar climate disturbances, resulting in an improved fitness.

Anatomical changes in wood may confer altered hydraulic properties to the tree [6, 9, 33]. Our study demonstrates that some Douglas-fir genotypes had the potential to acclimate to new, unfavourable climate conditions. In a future work we will try to identify the new hydraulic properties that the plastic density response could confer to Douglas-fir submitted to climate change, and the possible consequences on this species fitness.

Our results show that Douglas-fir was plastic enough to acclimate to the 2003 drought and heat-wave and then to recuperate in 2004 a behaviour comparable to the one observed in ring 2002. But no information is available on possible delayed response, nor on the effect of recurrent, cumulated climate hazards as suggested for other conifer species [17].

Our results also show that Douglas-fir has an adaptive potential that could be useful for multi-generation long-term response. The results of this study are preliminary and have to be followed by new studies, because it is necessary to monitor the possible delayed response of Douglas-fir to the 2003 drought and heat-wave. Also, no information is available yet about the cumulated effect of new heat waves, like the one which was newly observed in July 2006 in France.

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