Growth and microdensity responses of multiple Douglas fir provenances to drought events in Southern France

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To cite this version:

Valentin Bouttier. Growth and microdensity responses of multiple Douglas fir provenances to drought events in Southern France. Silviculture, forestry. 2020. hal-03328830

HAL Id: hal-03328830
https://hal.inrae.fr/hal-03328830v1

Submitted on 30 Aug 2021

Growth and microdensity responses of multiple Douglas fir provenances to drought events in Southern France

Dominante d'approfondissement

Gestion Forestière

Présenté par : Valentin BOUTTIER

Stage effectué du 17/02/2020 au 30/02/2020

Dans l'UMR BioForA INRAE-ONF (Unité Mixte de Recherche Biologie intégrée pour la valorisation de la diversité des arbres et de la forêt, UMR 0588), 2163 avenue de la Pomme de pin, 45075 Orléans CEDEX 2, France

Maître de stage : Brigitte MUSCH

Enseignant référent : Yves EHRHART

Soutenu le 30/09/2020

Année 2019/2020

Picture: Jean Ladier (ONF) – Douglas provenancy test in the “Forêt domaniale de l’Homol” (Gard)

AgroParisTech

UMR BioForA
INRAE-ONF

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FICHE SIGNALÉTIQUE D'UN TRAVAIL D'ÉLÈVE

AgroParisTech	**TRAVAIL D'ÉLÈVE**
TITRE : Growth and microdensity responses of multiple Douglas fir provenances to drought events in Southern France	Mots clés : Douglas, Pseudotuga menziesii, dendroecologie, sécheresse, changements climatiques, tests de provenances
AUTEUR : Valentin BOUTTIER	Année : 2020
Caractéristiques : 27 pages ; 2 tableaux ; 11 figures ; 10 annexes ; bibliographie	

CADRE DU TRAVAIL		
ORGANISME DE STAGE : Office National des Forêts, département Recherche, Développement et Innovation : Unité Mixte de Recherche Biologie intégrée pour la valorisation de la diversité des arbres et de la forêt (UMR BioForA INRAE-ONF, UMR 0588) Nom du responsable : Brigitte MUSCH Fonction : Responsable du Conservatoire Génétique des Arbres Forestiers, directrice adjointe de l'UMR BioForA		
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Résumé :

La forêt joue un rôle essentiel à la fois économique et écologique mais ces rôles sont menacés par les changements climatiques. Une meilleure connaissance et compréhension des processus permettant aux arbres de survivre dans un climat plus chaud et plus sec mais surtout à des événements extrêmes est donc primordial. Le douglas (*Pseudotsuga menziesii* (Mirb.) Franco) qui possède une vaste aire naturelle a largement été planté en Europe. Dans sa vaste aire naturelle, le douglas est confronté à différents climats. La compréhension de la variabilité des réponses du douglas à ces contextes environnementaux dans son aire d'introduction est un enjeu clé afin de sélectionner les provenances les plus adaptées pour de futures plantations. Cette étude se concentre sur la réponse du douglas de quatre régions de provenance : Oregon, Washington, Californie intérieure et Californie côtière plantées sur deux sites en 1992. Le premier site, considéré comme le site "sec" se situe en Corse et le second, considéré comme le site "humide" se situe dans le Gard. La réaction aux évènements de sécheresse des arbres a été étudiée par dendroécologie en utilisant les indices de résistance, récupération et résilience de Lloret sur les 5 années les plus sèches de chaque site. Les résultats montrent l'importance de l'effet du site sur la réponse à la sécheresse. Sur le site humide, il y a peu de différence de résilience entre provenances sur les caractères étudiés alors que sur le site sec, les provenances Californienne ont eu une plus grande résilience de leur croissance radiale pour l'évènement le plus sec. Deux compromis entre la résistance et la récupération ont été trouvés entre la largeur de cerne et la densité maximale du cerne avec des stratégies différenciées entre les provenances Californiennes et les autres. La densité maximum du cerne apparait comme un très bon indicateur de la sécheresse pour les deux sites et quelle que soit la région de provenance. Les provenances Californiennes semblent les plus adaptées à des plantations sur site sec ou sur lesquels de la sécheresse est attendue car elles ont une meilleure résilience et croissance lors d'événements de sècheresse. En revanche pour les sites lesquels le risque de sécheresse est faible, la plantation de provenances Californiennes induit un sacrifice de production non justifiée par rapport aux provenances de l'Oregon ou du Washington.

Abstract:

Forest plays an essential role with strong economic and ecologic values. However, these roles are threatened by the oncoming climate changes. Thus, a better comprehension and assessment of trees' ability to survive in warmer and dryer climate but mostly to stronger drought event is important. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is one of the most important planted trees in Europe and has a vast natural range. In its vast natural range Douglas fir faces various climates. Thus, understanding the variability of Douglas fir's responses within its natural range is a key to select well-adapted provenances for future plantations. Here, the response of Douglas fir coming from four regions is studied: Oregon, Washington, interior California and coastal California planted on two dry differing sites in 1992. The first site considered as the "dry" site is located in Corsica and the second considered as the "wet" site is located in the Gard. The response to drought events is studied using dendroecology and more specifically the resistance, recovery and resilience indices defined by Lloret on the 5 driest years of the dataset. The results show the importance of the testing site when studying drought responses. Similar drought response was obtained between all provenance regions on the moist site but not for the driest site where provenance coming from California showed highest radial growth resilience to the driest years. A trade-off between resistance and recovery is found for the ring width and the maximum density with differing strategies between Californian provenances and the others. Maximum density of the tree ring appears to be a strong marker of the drought events for all sites and provenance regions. As Californian provenances showed the highest overall growth for the dry site combined with the highest drought resilience, these provenances seem to be the most adapted for future plantation on dry sites. On moist site however with low drought risk, planting Californian provenances may result in unnecessary production loss compared to more productive Oregon or Washington provenances.

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Acknowledgements:

I gratefully thank all those without whom the redaction of this report wouldn't have been possible:

Brigitte MUSCH, my apprenticeship master who was always understanding, ready to listen and present to correct my mistakes when writing this report.

Thibaud CHAUVIN, former PhD student of my unit, for providing me all the data used in this report, for the time he granted to help me and answer all my questions.

Philippe ROZENBERG, research director, for the immense help provided when analyzing the data and the time he granted me.

Yves EHRHART, my school referent for his understanding and availability.

Contents

List of Tables

List of Figures

1 Introduction

European forests, cover 10.155 million km^2 of land for 44.3% of its surface (Keenan et al. 2015). In the European Union, 56% of the population lives in rural areas with natural resources and especially forest management being one of their main income sources (Wolf-Crowther et al. 2011). Its economic value is not negligible with forestry and wood sector accounting for approximately 1% of EU GDP and provide 2.6 million jobs (Nègre 2020). Moreover, as it has been shown that declining forest may lose their role as carbon sink (Yang et al. 2018), keeping our forest as healthy as possible will play an important role in mitigating climate change.

This ongoing climate change poses many threats to forest productivity and survival. Although changes in precipitation regimes remain uncertain, it is now clear that the shift in temperature will have an impact on climate all around the world (Beck et al. 2018). As a result, models predict an increase in drought frequency, severity and duration (Burke and Brown 2008, Trenberth et al. (2014), Spinoni et al. (2018)). The impact of these events on forest die-off is now established (Allen et al. 2015, Neumann et al. (2017)) and ecological shift in forests has already been observed (Brown et al. 2016). The shift in tree species composition is expected to be both spatially generalized and impactful for the most dominant species (Buras and Menzel 2019).

Models focusing on climatic averages tend to underestimate the effect of climate change on forests as extreme events are more important (Bréda and Badeau 2008). It is thus important to be able to assess trees' ability to survive and recover from extreme events in order to ensure good adaptation of trees to changing climate. Multiple mechanisms account in trees' response and adaptation to water deficit such as preventing water deprivation by reducing photosynthetic activity (Martin-StPaul et al. 2017) or redirecting biomass allocation, preventing hydraulic failure by higher resistance to cavitation, preventing starvation by accumulating carbon reserves (Adams et al. 2017). Consequently, drought events causes losses in biomass production with reduction in trees' productivity and trees' mortality (Choat et al. 2018).

One of the major production species in Europe, although it does not originate from it, is Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Having been introduced from Western North America to Europe in the XVIII$^{\text{th}}$ century Douglas fir is now widely planted in Western and Central Europe (Loo and Dobrowolska 2019). Its fast growth and high timber production ability coupled with good timber quality makes it a reliable species for production focused forest (Kohlne 2019). Nowadays, it is a widely spread forest species in Europe and especially in France where it is now the second most planted species after maritime pine (*Pinus pinaster* Aiton) with 9.5 millions planted trees per year (Joyeau 2019). Although Douglas fir only accounts for 7% of French wood production in volume, it represents more than 13.5% of the sold lumber (Agreste 2018), making it one of the most valuable forest species in France. Douglas fir is thought to be less vulnerable to climate-change-induced dieback than other coniferous species such as Scots pine and Norway spruce (Vitasse et al. 2019). However, Douglas fir's ability to cope with extreme drought events may reach its limit, as shown during the drought wave affecting Europe in 2003, when Douglas fir diebacks have been recorded on a large scale (Sergent 2011).

Moreover, it is feared that natural migration and adaptation may be insufficient to cope with climate change. A fast and severe climate change as the one tree populations are likely to face during their relatively long lifespan will probably outpace natural means of adaptations (Isabel et al. 2020). Studies are thus conducted to assess trees' populations' abilities in various climates to prepare artificial migration where needed (Aitken and Bemmels 2016). Such studies usually use experiments on multiple genetic levels, those can take many forms and are usually called with the generic term "common garden". Their goal is to compare multiple species and/or intraspecies populations (hereafter called "provenances") in the same site, sometimes repeated over multiple sites to cover more environmental conditions. Those experiments usually measured at a multi-year/decadal scale does complete well *ex-situ* experiments carried out on younger trees because it allows trees to grow up to their mature age. However, drought mechanisms studied in greenhouses only provide information at young age whereas other means as dendroecology can help us understand these mechanisms through the whole trees' lifespan.

In the case of Douglas fir, although it is not as studied as other coniferous species (Moran et al. 2017), studies already gave some results on its adaptation to drought such as drought adaptation of population occurring at warm and dry sites and at sites with cool winter but also a phenotypic response to dry environment triggering transpiration reduction (Bansal et al. 2015). Those results confirm previous results on Oregon provenances where provenances originating from higher elevation and drier sites were more drought tolerant and with an earlier bud-set (White 1987). Furthermore, while a trade-off between radial growth and frost resistance has been discovered, it does not appear to be the case between growth and drought resistance (Darychuk et al. 2012).

To complete this set of knowledge, as mentioned before, dendroecology can help us look into trees' past. It consists of studying trees' past responses to their environment using tree-rings (usually from wood cores) as a proxy of these responses. This method is commonly used when studying trees' climate sensitivity and event responses. In most studies, it consists in studying links between secondary growth, namely ring width or its derivate and climate conditions, in general, or for a given year. Furthermore, indices have been vastly used to study trees' response to drought such as Lloret's indices (Lloret et al. 2011). Those indices compare trees' growth at different stages of an event (before, during and after) to assess its response to the event.

Such dendroecological studies have already shown great variations of drought responses among species and provenances (Fkiri et al. 2018,Vitasse et al. (2019)). In the case of Douglas fir, it has been shown that drought resistance traits are under genetic control especially ring density (Martinez Meier et al. 2008) which has been confirmed by Sergent (2011) with important differences between provenances' density and radial growth. Californian provenances having the highest radial growth and lowest vulnerability to drought. Martinez-Meier also showed that in France Douglas fir which survived the 2003 drought had higher density than dead ones and that this drought event led to an early stop of radial growth (Martinez-Meier 2009). Sergent (2011) showed the existence of threshold in water deficit inducing growth loss, that growth resilience to drought was also linked to soil fertility and that stands located in wetter region have lower resilience to drought. In 2013, Eilmann *et al.* (2013) found different results with northern provenances being more productive but still less drought vulnerability for Southern provenances. Concerning ring characterstics, microdensity measurements and hydraulic properties of the rings are linked and latewood is more susceptible than earlywood to cavitation (**???**). A trade-off between productivity and drought resilience has been found but no differences in resistance to drought were found (Montwé et al. 2015). Ruiz Diaz Britez found that drought responses were dependent on the studied region and the provenances and that some microdensity variables were heritable (Britez 2017).

Although dendroecology improves our understanding of past event responses, when comparing multiple species or provenances, it is often difficult to disentangle genetic and environmental factors. Thus, dendroecological studies carried out on common gardens and provenance tests are important when focusing on the genetic effect (George et al. 2016). Although common gardens enable suppressing most environmental effects, their interactions with genetic effects might be of interest and cannot be studied when focusing on a single site. Multi-site experimental tests are thus important in the matter of understanding links between environmental and genetic responses (Zas et al. 2020). Some dendroecological studies also choose to focus on a small range of years, sometimes even a single year. A low number of studied years makes it hard to distinguish the importance of each environmental component affecting the studied variables. As these studies usually select only the driest year of their dataset, it is impossible to distinguish within years variations such as spring or summer drought responses. Our understanding of wood responses to drought events might also be improved by studying not only ring width but also intra-ring widths such as earlywood and latewood widths to understand the consequence on trees' growth and to assess its vulnerability. Furthermore, another scarcely considered variable is density even though it is important to understand wood structure and water conduction (Dalla-Salda et al. 2011).

The latest studies on Douglas fir's microdensity were carried out by Chauvin (Chauvin 2019). Where he linked microdensity and cavitation measurements to the provenance's origin climate, but he also linked microdensity measurements to cavitation measurements and branch punctuation. The data used in this article came from these measurements. He found that, provenances from hotter/drier climate have higher density and higher survival. Trees with lesser latewood and with lower wood density variability tend to have higher resistance to cavitation.

Considering all these factors, this study is conducted on two Douglas fir provenance trials in Southern France using 28 provenances coming from its natural range. Also, for each site, multiple drought events will be studied and thus will cover a greater range of climate conditions than a single year study. As the fulfilled microdensity measurements allow recording of intra-ring density both radial growth and density's responses to drought will be studied using Lloret's indices.

This study's goal is to answer to:

I : Is there a provenance effect on Douglas fir's radial growth and density's response to drought events?

II : Do the study site conditions impact Douglas fir's radial growth and density response to drought events?

III : Do the drought characteristics impact Douglas fir's radial growth and density response to drought events?

Such results are important to be able to prepare the future of Douglas' plantations. In France, past experiments, trials and amelioration process have led to the construction of eight Douglas fir's seed orchard providing Frenchs forests in Douglas' seeds. However, when constructing these seed orchard in the 80's, little consideration of drought resistance was taken into account. New projects such as the

"Douglas-Avenir" project aims to create new varieties more suited to climate change (Sanchez et al. 2018). Based on the latest results (Chauvin 2019), some grafts were harvested on the study sites from trees comming from Californian provenances to be included in the next ameliorated population. Furthermore, trees from more northern provenances were also included in other ameliorated populations.

2 Material & Methods

2.1 Study sites

The studied sites are two Douglas-fir provenance trials planted in 1992 in cooperation by the French National Institute of Agronomic Research and the French National Forestry Office replicated both in southern France, in Corsica (41°57'N, 9°00'E) and the Gard (44°18'N, 3°59'E). The Corsican site faces North, North-West exposition at 700m high whereas the Gard site is located in a slope facing West, North-West at height ranging from 600 to 680m. Seeds originating from the natural range were germinated and grown in a nursery. Trees were planted in a randomized block containing a single tree of each provenance, with 60 and 68 blocks respectively for Corsica and the Gard.

2.2 Plant material

The studied Douglas-fir provenances originate from three USA states, namely **Washington (WA)**, **Oregon (OR)** and California. California provenances are divided into two regions: **coastal California (COCA)** and **interior California (INCA)**. Details available on each provenance are shown in Table 1.

Table 1: Characteristics of the studied provenances (from Chauvin 2019)

Code	Full name	State/Region	Latitude	Longitude	Altitude (m)
CAL	Calistoga	COCA	38.38	-122.36	170
CO1	Covelo 1	COCA	39.54	-123.00	170
CO2	Covelo 2	COCA	39.54	-123.00	170
HAC	Happy Camp	COCA	41.46	-123.24	800
HAY	Hayfork	COCA	40.35	-123.16	1000
HOO	Hoopa	COCA	40.53	-123.38	330
PIL	Pillbury lake	COCA	39.23	-123.04	1200
RE1	Redwood Creek 1	COCA	41.14	-123.53	600
RE2	Redwood Creek 2	COCA	41.14	-123.50	800
SCR	Scott River	COCA	41.40	-123.09	1000
STH	Sant Helena	COCA	38.33	-122.20	570
VDR	Van Dusen River	COCA	40.30	-123.44	830
BUR	Burney 2	INCA	40.49	-121.50	1000
CH1	Chico 1	INCA	39.42	-121.39	900
CH2	Chico 2	INCA	39.59	-121.39	1200
IOH	Iowa Hill	INCA	39.08	-120.55	1100
LAS	Lassen Lodge	INCA	40.18	-121.42	1000
ORL	Oroville Lake	INCA	39.36	-121.09	1100
SHA	Shasta Mc Cloud	INCA	41.08	-122.08	1000
WEA	Weaversville	INCA	41.08	-122.16	1200
CV1	Coos Bay VG Elite 1	OR	43.23	-123.50	1000
CV2	Coos Bay VG Elite 2	OR	43.23	-123.50	1200
SV1	Springfield VG Elite 1	OR	44.00	-123.00	170
SV2	Springfield VG Elite 2	OR	44.00	-123.00	170
30	Lot commercial zone 030	WA	46.50	-123.61	170
403	Lot commercial zone 403	WA	48.06	-121.54	170
CA1	Cascade VG Elite 1	WA	47.30	-121.50	170
CA2	Cascade VG Elite 2	WA	47.30	-121.50	170

2.3 Measurements

As described by Chauvin (2019), during late autumn 2016 and winter 2017, respectively for the Corsica trial and the Gard trial, every tree of both trials was cored to the pith. A total of 1464 trees were cored and used for analysis. A single core was taken by tree at breast height using a mechanic Pressler borer of 5mm in diameter (Geremia 2006).

All cores were then stored in polycarbonate honeycomb boxes, oven-dried and sawed to 2mm thick samples following Perrin and Ferrand (1984). Density measures were carried out using X-ray radiography following Polge (1966), those radiographs were then scanned at 1000 dpi. Density chronologies were constructed using grey scaling on the WinDendro software (Inc. 2020) and manual control.

Using R software (R Core Team 2019) microdensity chronologies were verified and ring limits adjusted using designed R functions. Each ring was then separated into three stages (earlywood, transition wood, latewood) using extreme means method firstly on the ring and secondly on each part of the ring obtained (Dalla-Salda et al. 2014). Using these three within ring boundaries, 15 variables were recorded per ring. These 15 variables are shown in Table 2.

Table 2: Description of the microdensity variables

Variable name	Variable description	Unit
Rr	Ring width	mm
Ri	Earlywood width	mm
Rt	Transition wood width	mm
Rf	Latewood width	mm
Dr	Mean ring density	g/cm3
Di	Earlywood mean density	g/cm3
Dt	Transition wood mean density	g/cm3
Df	Latewood mean density	g/cm3
Mi	Minimum ring-density	g/cm3
Ma	Maximum ring-density	g/cm3
Sr	Standard deviation of ring density	g/cm3
Si	Standard deviation of earlywood density	g/cm3
St	Standard deviation of transition wood density	g/cm3
Sf	Standard deviation of latewood density	g/cm3
Cr	Density contrast	g/cm3

Basal area increment was also calculated as: $BAI_i = \pi \times (r_i^2 - r_{i-1}^2)$ where BAI_i is the basal area increment of the ith ring starting from the pith and r_i^2 and r_{i-1}^2 are respectively the cumulative ring width for the ith ring and the $i-1$th ring starting from the pith. The BAI is a measure of radial growth that takes into account the geometry of the rings based on the principle that radial growth is distributed evenly all around the stem (Biondi and Qeadan 2008).

2.4 Detrending

All variables presented above were linearly adjusted from the cambial age effect using the regional curve standardization (RCS) procedure at both sites (as shown in Figure 1) (Rozenberg et al. 2020). This process was done using the *rcs* function in *dplR* package (Bunn et al. 2020) in R. The two adjusted variables resulting of the rcs adjustment, residual RCS and ratio RCS (Esper et al. 2003) and the raw variables were kept in this analysis to compare the final results between the adjustment methods.

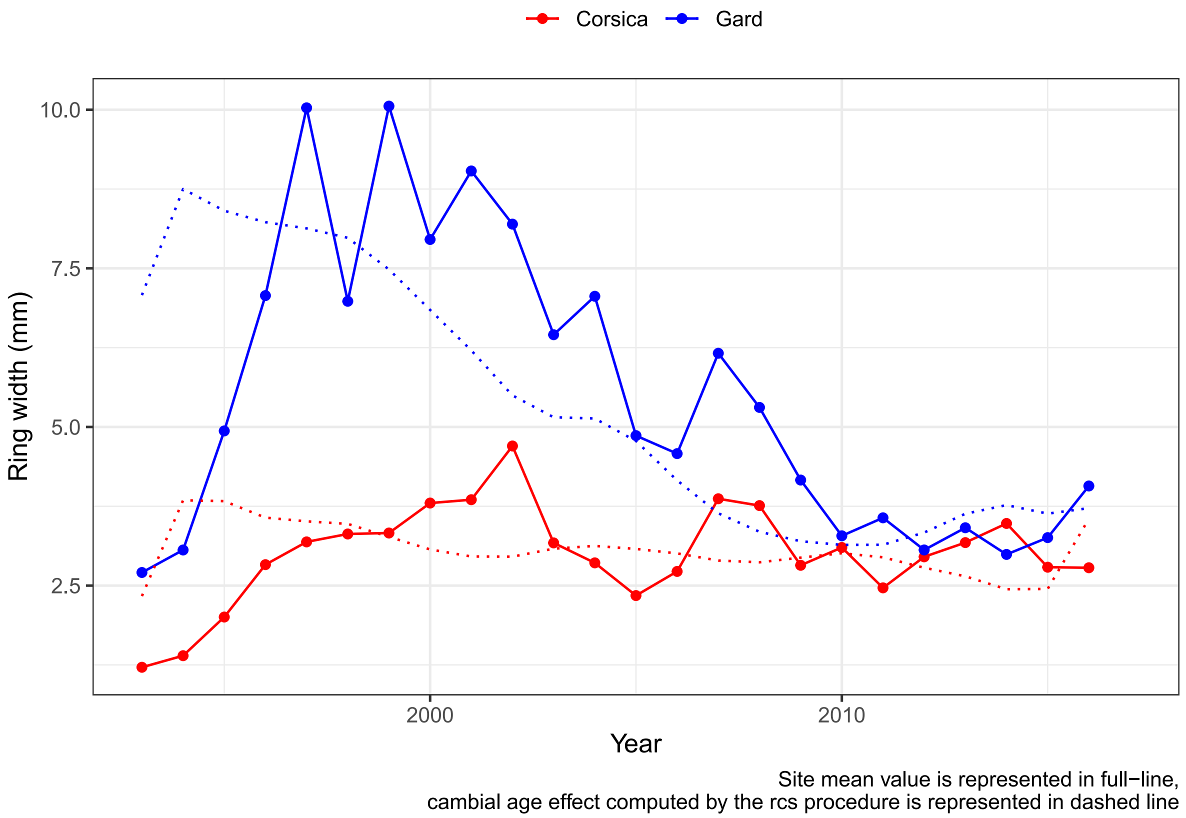


Figure 1: Cambial age effect on ring width (mm)

2.5 Identification of the study periods

Monthly mean temperature and precipitation sum for the period 1992-2015 were obtained from two nearby meteorological stations. Monthly Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) was then calculated using Thornthwaite equation (Thornthwaite 1948) to compute monthly potential evapotranspiration (PET). This process has been done using the *SPEI* package in R (Čadro and Uzunović 2013). SPEI calculations were processed using a 1-month timescale to retain the most variability.

For each site and year, yearly SPEI was then computed as the mean of monthly SPEI values during the vegetation period (April-September) (Escobedo et al. 2018).

In order to select the driest years for each site, these climatic data were then filtered to keep only the five years with the lowest yearly SPEI values. Two to three drought events were kept for each site within those five years. Those two to three events were selected firstly by removing the last years of the dataset because further indices calculation is based on post-drought years. Secondly, the selection was based on their non-proximity to each other in order to minimize the influence of multiple drought events in a single index calculation. However, following years could be grouped into the same drought-event. The selection was then confirmed using a PCA for each site using each monthly SPEI value as variable, thus allowing to describe each year's climate.

For each of the two to three selected periods, a study period was defined as the pre-drought period, the drought period and the post-drought period, in order to calculate further indices based on those periods. Following Schwarz recommendation (2020), multiple timescales (± 2 years to ± 5 years) relatively to the drought years were tested and compared for the pre and post-drought period.

2.6 Trees' response indices

Multiple indices that are usually used to quantify growth response to drought events were calculated for each microdensity variable. These are, as suggested by Lloret *et al.* (2011), the resistance, the recovery and the resilience. The resistance index is used to quantify the ratio of reduction of the variable between the pre-drought period and the drought period. It is calculated by:

$$Resistance_{nij} = Dr_{ij}/PreDr_{nij}$$

with $Dr_{ij}$$ indicating the value of the variable during the drought period i for the variable j and $PreDr_{nij}$ indicating the mean value of the variable during the *n's year* preceding the drought period i for the variable j.

The recovery index quantifies the response following the drought period, it is a ratio of the increment of the variable between the post-drought period and the drought period. It is calculated by:

$$Recovery_{nij} = PostDr_{nij}/Dr_{ij}$$

with $PostDr_{nij}$ indicating the mean value of the variable during the *n's year* periods following the drought period i for the variable j and Dr_{ij} indicating the value of the variable during the drought period i for the variable j. The resilience quantifies the ability of the tree to return to a pre-stress status, it is a ratio of reduction between the post-drought and pre-drought variable. It is calculated by:

$$Resilience_{nij} = PostDr_{nij}/PreDr_{nij}$$

with $PostDr_{nij}$ indicating the mean value of the variable during the *n's year* periods following the drought period i for the variable j and $PreDr_{nij}$ indicating the mean value of the variable during the *n's year* preceding the drought period i for the variable j.

For calculations using the RCS adjustment with residual, site mean was added for each term to ensure the absence of negative values.

2.7 Statistical analysis

Shapiro-Wilk's test and qqplots were used to test normality of the calculated indices. Event effects on the indices were analyzed using a Wilcoxon test to test difference with a reference value (1 for all indices) to ensure every studied variable has significantly reacted to the event. A Kruskal-Wallis test was performed to check significant differences in the indices values among different provenances and provenance regions. Differences between provenance regions' indices were then calculated using paired Wilcoxon test adjusted using Holm method.

3 Results

3.1 Detrending

As the dataset year's range is relatively short (1993 - 2016) compared to other dendroecological studies we can see that differences between detrended and non-detrended (or "raw") values are small (as shown in Figure 2). However, detrending seems to be useful for the first years of the dataset notably on strongly age dependent variables such as BAI accounting for the strong geometrical effect in the first years. As the final results are very similar between the non-detrended and the 2 detrended values, only the values detrended using the residual method will be shown.

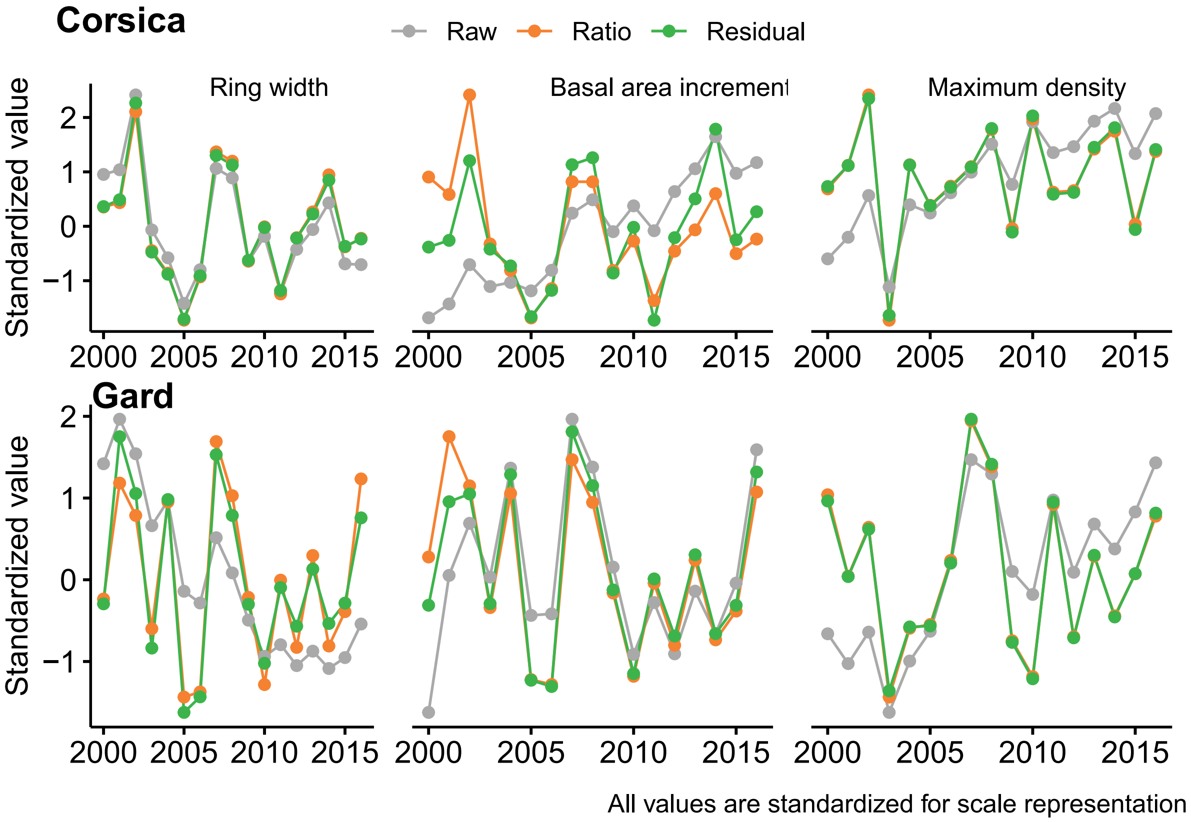


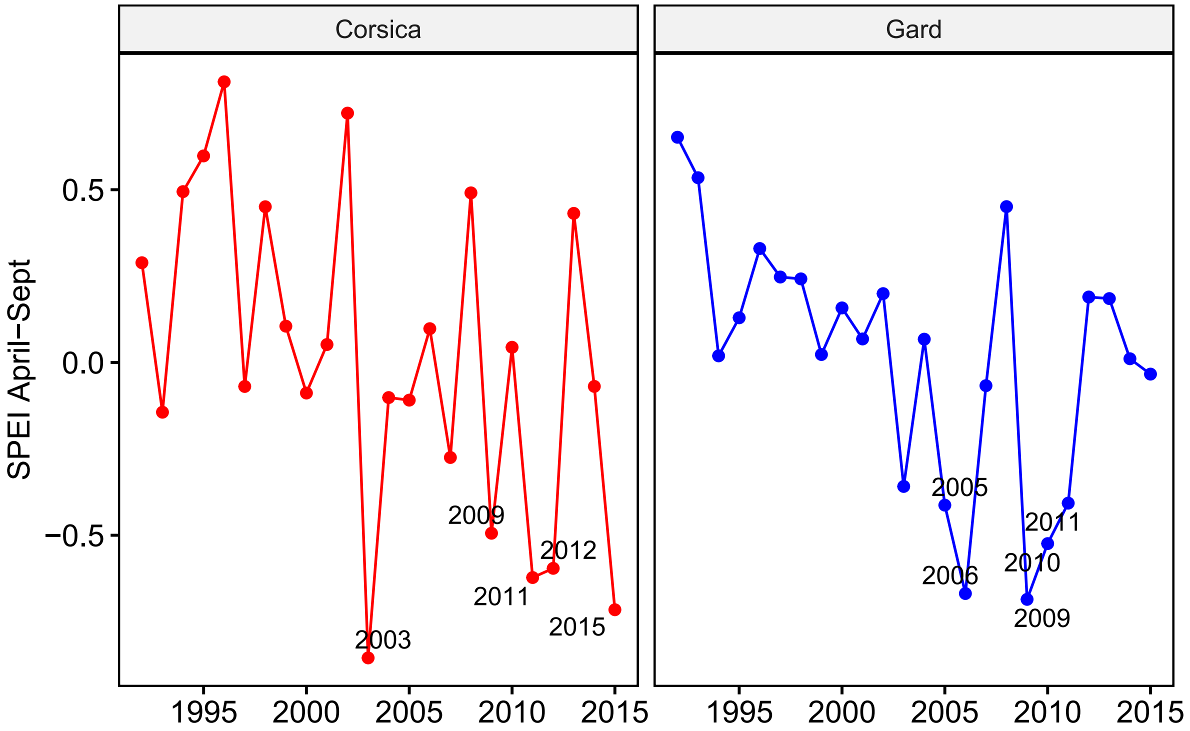
Figure 2: Comparison of the detrending methods for different variables

3.2 Yearly SPEI variations

Annual variation of the SPEI are represented in Figure 3. The mean SPEI during the growing period (April-September) varied from -0.85 to 0.81 with roughly the same extremum values between the two sites although Corsica site experienced more interannual variations.

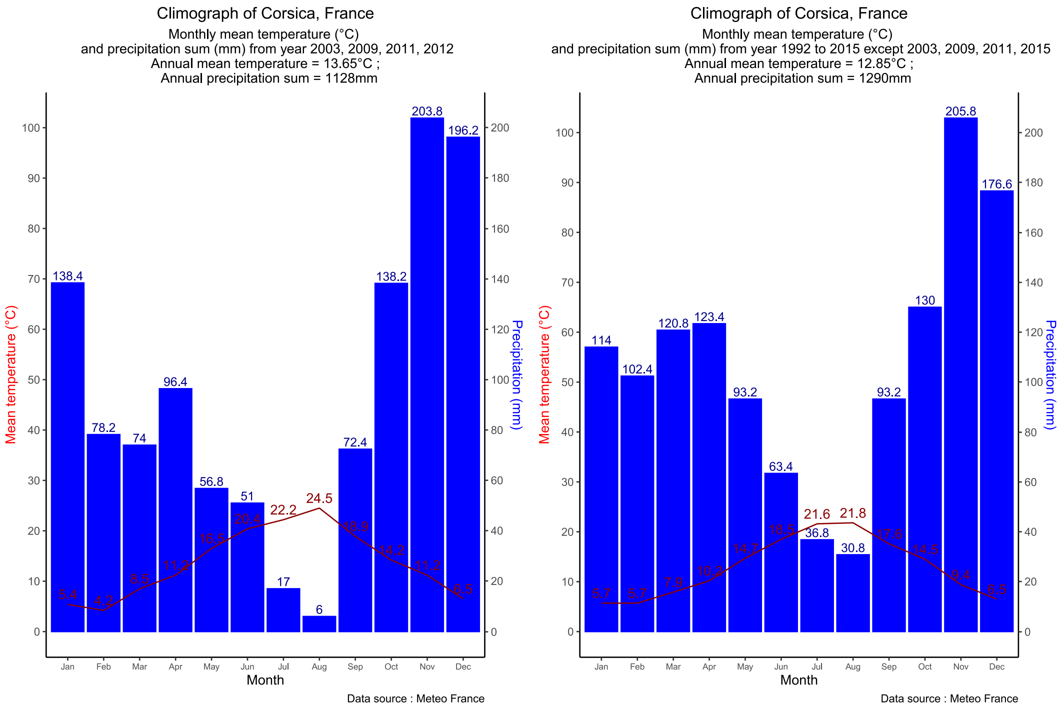
In the Corsica site, the years presenting the lowest mean SPEI are 2003, 2009, 2011, 2012 and 2015 with 2009 having the highest (-0.49) and 2003 the lowest. Out of these fives, the year 2015 has been discarded from the study because of the lack of microdensity measures after 2016. Furthermore, the years 2011 and 2012 have been grouped into a single drought event, leaving us with 3 drought events for this site: 2003, 2009, 2011-2012.

In the Gard site, the years presenting the lowest mean SPEI are 2005, 2006, 2009, 2010 and 2011 with 2005 having the highest (-0.41) and 2009 the lowest. As for the Corsica site following selected years were grouped into single drought events making 2005-2006 and 2009-2010-2011 the two drought events for the Gard site.



The labeled years are the five years with the lowest SPEI values

Figure 3: Annual variation in the Standardized Precipitation-Evapotranspiration Index (SPEI) of the growing period (April-September) in the two sites

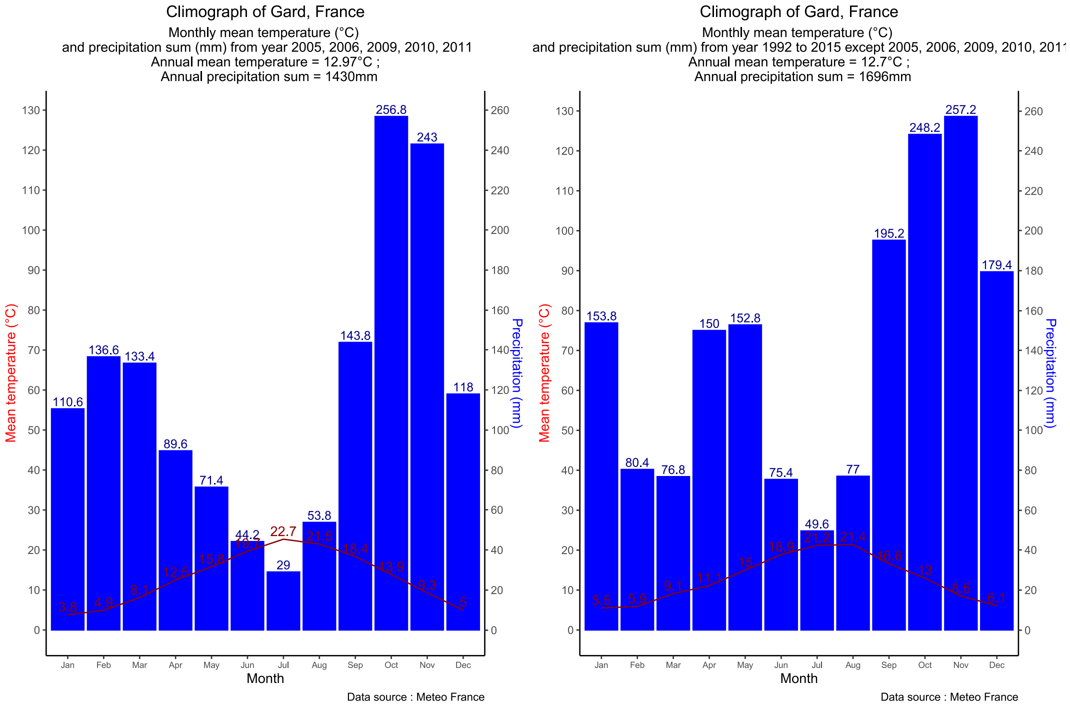

Climograph of Corsica, France
Monthly mean temperature (°C)
and precipitation sum (mm) from year 2003, 2009, 2011, 2012
Annual mean temperature = 13.65°C ;
Annual precipitation sum = 1128mm

Climograph of Corsica, France
Monthly mean temperature (°C)
and precipitation sum (mm) from year 1992 to 2015 except 2003, 2009, 2011, 2015
Annual mean temperature = 12.85°C ;
Annual precipitation sum = 1290mm

Data source : Meteo France

Data source : Meteo France

Figure 4: Climographs of the Corsica site for the selected and non selected years


Climograph of Gard, France
Monthly mean temperature (°C)
and precipitation sum (mm) from year 2005, 2006, 2009, 2010, 2011
Annual mean temperature = 12.97°C ;
Annual precipitation sum = 1430mm

Climograph of Gard, France
Monthly mean temperature (°C)
and precipitation sum (mm) from year 1992 to 2015 except 2005, 2006, 2009, 2010, 201
Annual mean temperature = 12.7°C ;
Annual precipitation sum = 1696mm

Data source : Meteo France

Data source : Meteo France

Figure 5: Climographs of the Gard site for the selected and non-selected years

According to the PCA (not shown) and the mean climographs of these years (shown in Figure 4 and 5), those years are characterized by higher annual mean temperature (respectively +0.8°C/+6% and +0.27°C/+2.1% for the Corsica and the Gard site) and mostly by less annual precipitation (respectively -162mm/-14.4% and -266mm/-15.7%). Looking only at the growing period (April-September), this trend is even more pronounced with +1.6°C/8.9% and 1.1°C/6.1% additional mean temperature for the selected years and -141.2mm/-32% and -268.2mm/-38.3% for the sum of precipitation respectively for the Corsica and the Gard site. We can also see that the Corsica site is climatically drier with comparable mean temperatures but less precipitation. On the climograph of the full dataset it is shown that Corsica site suffers from drought (as defined by Bagnouls and Gaussen (1957)) in June and July which is not the case for the Gard site.

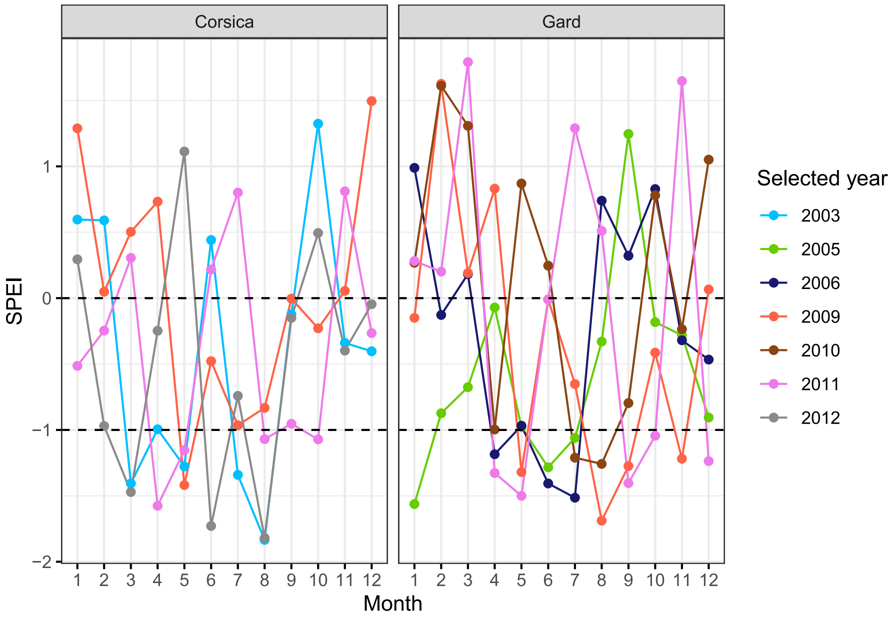


Figure 6: Variation of the Standardized Precipitation-Evapotranspiration Index (SPEI) for the selected years in the two sites

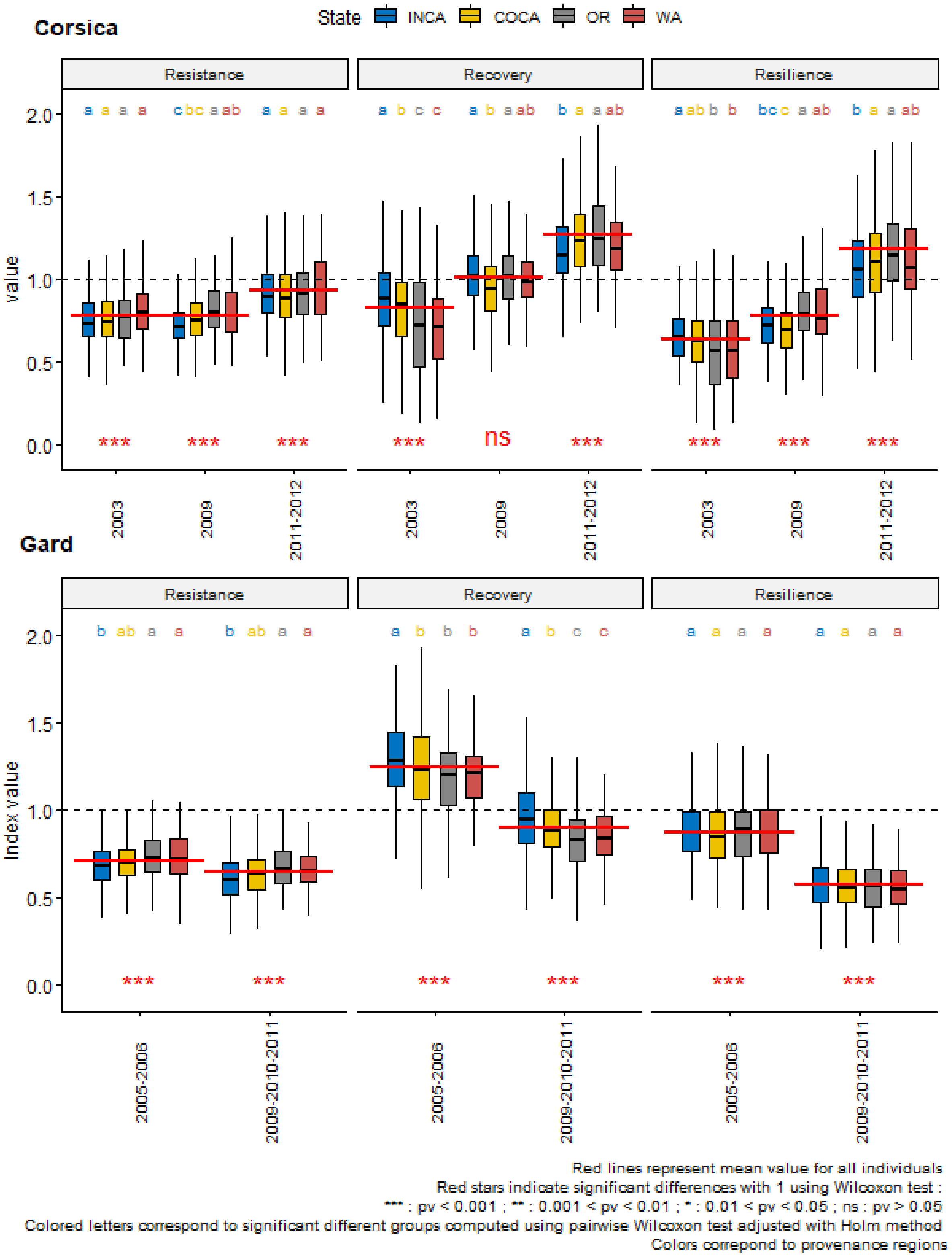
Although differences between selected and non-selected years are important, differences within drought patterns of the selected years can also be important (as shown in Figure 6).
All value comparisons mentioned below are made to the mean value from all years on the specific site. The year 2003 of the Corsica site is the one with the lowest SPEI (-0.85) and is characterized by SPEI values inferior to -1 for the period Mars-August (at the exception of the month June with positive SPEI values due to high precipitation). These months low SPEI values are mostly due to high temperatures with at most +4.5°C for the June month but also a strong lack of precipitation from Mars to May, which is less present in July and August. The month with the lowest SPEI value is August with a SPEI of -1.83 having a mean temperature superior of 3.6°C than average.
The year 2009 of the Corsica site is the one with the highest SPEI values (-0.49) for the selected years of this site and is characterized by only May having SPEI values inferior to -1. May is indeed characterized by

very high mean temperatures (+3.6°C) concurring with a lack of almost half the precipitation (-60mm). June, July and August also have higher temperatures and lesser precipitation than the rest of the dataset's years but in much smaller proportion.
The year 2011 of the Corsica site has a mean SPEI value for the growing period of -0.62 and is characterized by SPEI values inferior to -0.95 for the months April, May, August, September and October. These months low SPEI values are partly due to higher temperature with at most +2.5°C in April and September but also a lack of precipitation of more than half normal values for all these months. However, June and July are not dry months and have below normal temperatures. The end of the year 2011 does not show strong drought with November having almost 40% more precipitation than normal.
The year 2012 of the Corsica site has a mean SPEI value for the growing period of -0.6 and is characterized by SPEI values inferior to -0.75 for the months February, March, June, July and August. As for the year 2011, these low SPEI values are explained both by high temperatures (+3°C at most) and low precipitation (-90mm at most), however on the contrary to 2011, the wet period of this year is located earlier in the growing season (April-May), the month of January being an average January month for this site it does not show drought values.
On the Gard site, the year 2005 has a mean SPEI value for the growing period of -0.41, the highest for the selected years of this site, it is characterized by SPEI values below -0.95 for the months May, June and July. These months low SPEI values are due to a small shortage in precipitation (-66%, -50%, -66% respectively for the months May, June and July) and high temperatures for June (+2.5°C). This year is also interesting because it showed a drought period before the growing period (from November 2004 to March 2005) due to low precipitation.
The year 2006 of the Gard site has a mean SPEI value for the growing period of -0.67 and is characterized by SPEI values below -0.95 for the months April to July. These month low SPEI values are due both to a lack of precipitation (-50%) and high temperatures (+4°C at most in July).

The year 2009 of the Gard site has the lowest mean SPEI values of this site (-0.69) and is characterized by SPEI values below -1 for the months May, August and September. 2009 has experienced high temperatures during all its growing period (+1.4°C on average) but also low precipitation (–42mm/-39% on average) with September and May having the lowest precipitation compared to average years (more than 100mm below the mean for each month). The year 2010 of the Gard site has a mean SPEI value for the growing period of -0.52 and is characterized by SPEI values inferior to -0.95 for the months April, July and August. These low SPEI values during those months are mainly due to low precipitation (-66% for these 3 months) concurring with high temperatures for July (+2°C). The months of May and June present no drought having SPEI values above 0.

The year 2011 of the Gard site has a mean SPEI value for the growing period of -0.41 and is characterized by SPEI values inferior to -1 for the months April, May and September. These months low SPEI values are due both to a lack of precipitation (-70%) and high temperatures (+3.4°C at most in April). June, July and August do not show signs of drought furthermore March experienced very high precipitations (+234mm/+300%).

3.3 Effect of the drought events on growth

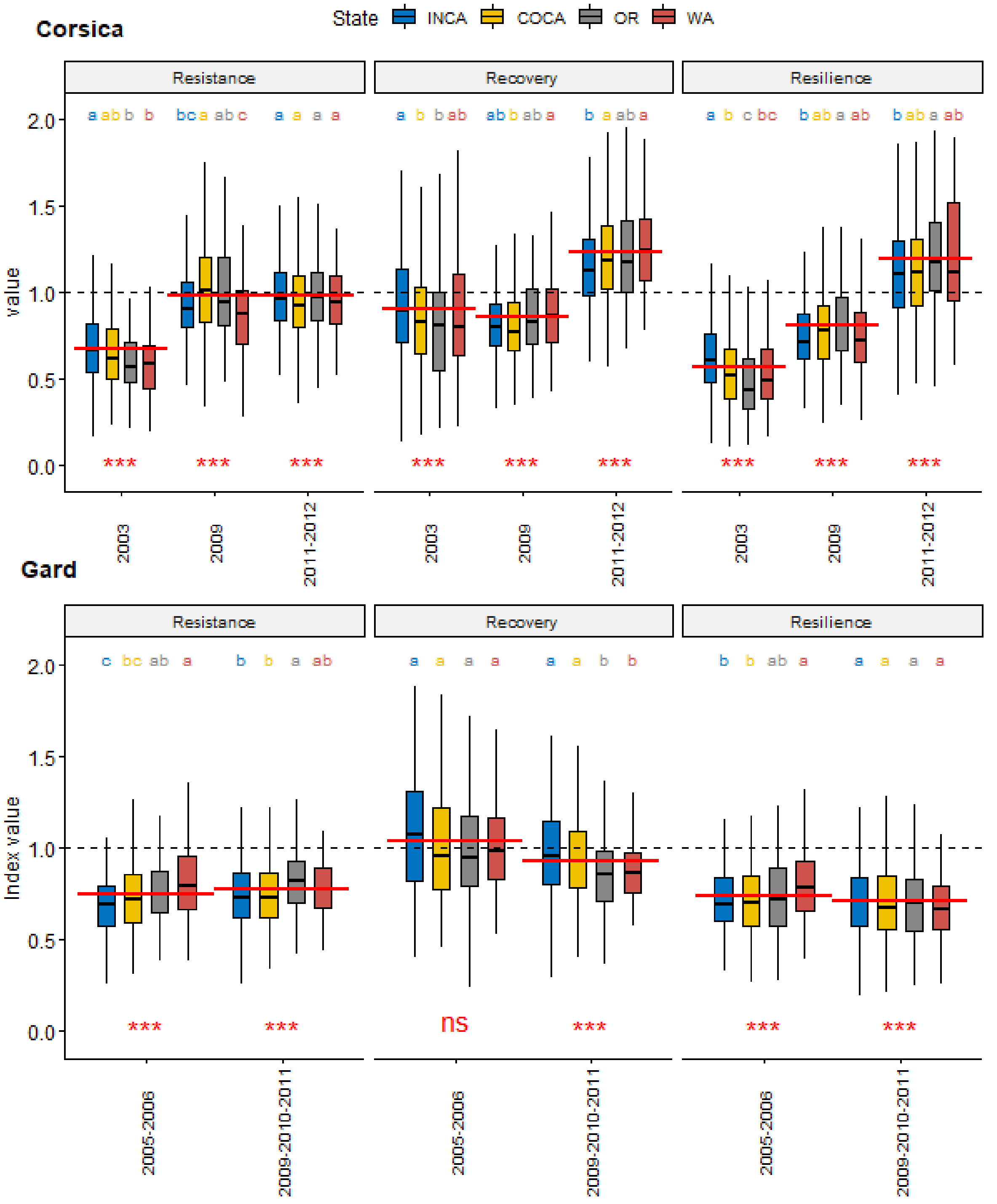


Red lines represent mean value for all individuals
Red stars indicate significant differences with 1 using Wilcoxon test :
*** : pv < 0.001 ; ** : 0.001 < pv < 0.01 ; * : 0.01 < pv < 0.05 ; ns : pv > 0.05
Colored letters correspond to significant different groups computed using pairwise Wilcoxon test adjusted with Holm method
Colors correpond to provenance regions

Figure 7: 2 years response to drought events of the Ring width in both sites and for each provenance region

As all results are similar between 2-year, 3-year, 4-year and 5-year timespan, only 2-year timespan results will be shown in the main document to minimize overlapping between drought events. Also, all results will be shown at the provenance region scale in the main document because there were very few to no significant differences between provenance themselves.

All ring width indices results are shown in Figure 7.
Ring width significantly declined for all the selected years and both sites during the drought events and did not recover in four years (except for the 2011-2012 drought event in Corsica, with ring width significantly higher after the drought event). Ring width reduction during the events was slightly more pronounced in the Gard than in Corsica. Growth responses to the drought events were, however, dependent on the site, drought event and provenance region. Nevertheless, individual variations among those categories are still major with a strong individual component.
In the Corsica site, for all studied years, ring width was reduced by 17.2%. Respectively, mean resistance values are 78% (P-value $= 2 \times 10^{-89}$), 77.5% (P-value $= 4 \times 10^{-93}$) and 92.8% (P-value $= 2 \times 10^{-26}$) for 2003, 2009 and 2011-2012 events. Significant differences in resistance between provenance regions were observed only in 2009 with INCA provenances (74.7%) having lower resistance than both OR provenances (83.9%) and WA provenances (82.5%) and COCA provenances (76.6%) having lower resistance than OR provenances.
Regarding recovery, for the year 2003, values are still significantly below one (P-value $= 6 \times 10^{-50}$) meaning ring width kept decreasing after the event. Differences among provenance regions for this index are great with INCA provenances having significantly greater values than the rest (88.9%), followed by COCA provenances (83.1%) and then OR provenances (73%) and WA provenances (70.9%) with non-significant differences. However, for 2009, recovery is not significantly different from one (P-value $= 0.1$). For 2011-2012, on the contrary to 2003, recovery is significantly higher than one (P-value $= 3 \times 10^{-90}$) with INCA provenances (119.8%) having the lowest value and being significantly inferior to COCA provenances (132.1%) and OR provenances (134.8%) but not from WA provenances (122.5%).
For the resilience, 2003 values are the lowest with 63.4% followed by 2009 with 78.2% and 2011-2012 with 78%. In 2003, INCA provenances significantly showed the highest resilience (66.6%) whereas in 2009 it was OR provenances (86.3%) and WA provenances (82.4%). In 2011-2012, INCA provenances (110.3%) showed the lowest values significantly below COCA provenances (122.3%) and OR provenances (122.6%).
2003 was the only event showing signs of lasting effect of an event on ring width, after the event mean values decreased for 2 years and then started increasing but did not reach pre-event values except for INCA and COCA provenances within the 5 years preceding the 2009 drought (as shown in Appendix A1). However, after 5 years INCA provenances and COCA provenances with the highest ring width did have above one resilience (as shown in Appendix A2).



Red lines represent mean value for all individuals
Red stars indicate significant differences with 1 using Wilcoxon test :
*** : pv < 0.001 ; ** : 0.001 < pv < 0.01 ; * : 0.01 < pv < 0.05 ; ns : pv > 0.05
Colored letters correspond to significant different groups computed using pairwise Wilcoxon test adjusted with Holm method
Colors correpond to provenance regions

Figure 8: 2 years response to drought events of the Latewood width in both sites and for each provenance region

In the Gard site, both events resistance values are below one (70.8%, P-value $= 2 \times 10^{-119}$; 64.5%, P-value $= 10^{-116}$ respectively for 2005-2006 and 2009-2010-2011) with INCA provenances having significantly lower values than OR provenances and WA provenances. For both events, INCA provenances showed significantly higher recovery than the rest although for 2009-2010-2011 COCA provenances also showed higher recovery than OR and WA provenances. 2005-2006 event's resistance values are above one (124.4%, P-value $= 5 \times 10^{-83}$) whereas for 2009-2010-2011 values are below 1 (90%, P-value $= 8 \times 10^{-37}$).
Regarding resilience, values are below one for both events (86.8%, P-value $= 3 \times 10^{-55}$; 57.2%, P-value $= 3 \times 10^{-120}$ respectively for 2005-2006 and 2009-2010-2011) with no significant differences between provenance regions.

When looking at the provenance scale, there were no strong differences between provenances of the same region for each index in the Gard site. However, in the Corsica site, notable differences appear, those differences were higher for the 2011-2012 event inside all provenance regions except INCA with little differences between its provenances. A small trend, although not strongly marked appears, provenances with the lowest resilience values in 2003 tend to have the highest resilience values in 2011-2012 (shown in Appendix A3) seemingly because of a combination of higher resistance and higher recovery.
This trend appears strongly and significantly ($R^2 = 0.48$, p-value = 0.012) for the COCA region where the provenances RE1 and HAC have small resilience in 2003 compared to the mean of the COCA region but high in 2011-2012 compared still compared to the mean, WA provenances show the same trend although not significantly ($R^2 = 0.79$, p-value = 0.11) but no OR and INCA provenances (as shown in Appendix A4).

As the results regarding earlywood width are highly similar to those of the entire ring width (Pearson correlation of 89.6%), they are not shown here, you can refer to the results presented above for this variable.

Focusing on the final-ring width (shown in Figure 8) which sometimes displays dissimilar patterns than ring width. However, as for the ring width, individual variations remain greater than between provenance region variations. In the Corsica site, although mean resistance values are all significantly different from one, they are close to one for 2009 (98.3%, P-value $= 5 \times 10^{-4}$) and 2011-2012 (98.1%, P-value $= 3 \times 10^{-5}$) but not for 2003 where resistance values are much lower (66.9%, P-value $= 2 \times 10^{-96}$). For 2003, INCA provenances have the highest resistance values (69.6%) which are significantly greater than both OR (61.2%) and WA (65.9%). However, for the year 2009 COCA provenances (103%) have significantly greater resistance values than INCA provenances (94.7%) and WA provenances (88.6%) when OR provenances (100.8%) are only significantly greater than WA provenances. No significant differences for the 2011-2012 event are displayed for this index.
For the recovery index, for all events site mean values are statistically different from one, with 2003 (90.3%, P-value $= 3 \times 10^{-18}$) and 2009 (85.2%, P-value $= 4 \times 10^{-57}$) values being below one and above for the 2011-2012 event (123.1%, P-value $= 4 \times 10^{-64}$). INCA provenances have significantly greater values than COCA provenances and OR provenances in 2003 but significantly lower values than COCA provenances and WA provenances for 2011-2012, for 2009, only COCA provenances display significantly lower recovery values than WA provenances.

Regarding the resilience index, as for the recovery, all site mean values are significantly different from one with both 2003 (56.9%, P-value = 8×10^{-108}) and 2009 (81.1%, P-value = 6×10^{-62}) being below and 2011-2012 (118.7%, P-value = 7×10^{-33}) being above. For the year 2003, INCA provenances show resilience values significantly greater than the rest (63.2%) and COCA provenances (55.5%) show higher resilience than OR (47.7%) but not WA (54.3%). As for 2009 and 2011-2012 events, provenance regions responded similarly with OR provenances having the highest values followed by COCA provenances and WA provenances and INCA provenances having the lowest values, significantly different from OR provenances.

As for the Gard, the ring width results are not similar to those of the Corsica site. Both events resistance values are significantly below one (74.3%, P-value = 6×10^{-97} ; 77%, P-value = 3×10^{-92} respectively for the 2005-2006 and the 2009-2010-2011 events). Within those events, INCA provenances and COCA provenances have lower resistance values than OR provenances and WA provenances, although not always significantly.
Recovery in the Gard site does not differ from one for 2005-2006 (103.8%, P-value = 0.2) but does for 2009-2010-2011 (92.8%, P-value = 10^{-18}). For this event, INCA provenances and COCA provenances have significantly higher recovery values (95.8% and 95% respectively) than OR provenances and WA provenances (85.7% and 87.5% respectively).

Both events resilience values are significantly below one (73.7%, P-value = 3×10^{-97} ; 70.5%, P-value = 2×10^{-101} respectively for the 2005-2006 and the 2009-2010-2011 events). The only significant difference between provenance regions is 2005-2006 values for WA provenances (68.7%) which are significantly higher than INCA provenances (71.2%) and COCA provenances (70.5%) but not the OR provenances (70.6%).

When looking at the provenance scale, there are no significant differences between provenances of the same region for each index. However, in the Corsica site, the same trend as ring width appears with a negative correlation between 2003 and 2011-2012 resilience values (shown in Appendix A6) mostly for the COCA region. This negative correlation appears significantly only for the COCA region ($R^2 = 0.41$, p-value = 0.025) but is non significant for other regions (as shown in Appendix A7)

As the results regarding basal area increment are highly similar to those of the entire ring width (Pearson correlation of 95%), they are not shown here, you can refer to the results presented for ring width.

3.4 Effect of the drought events on density

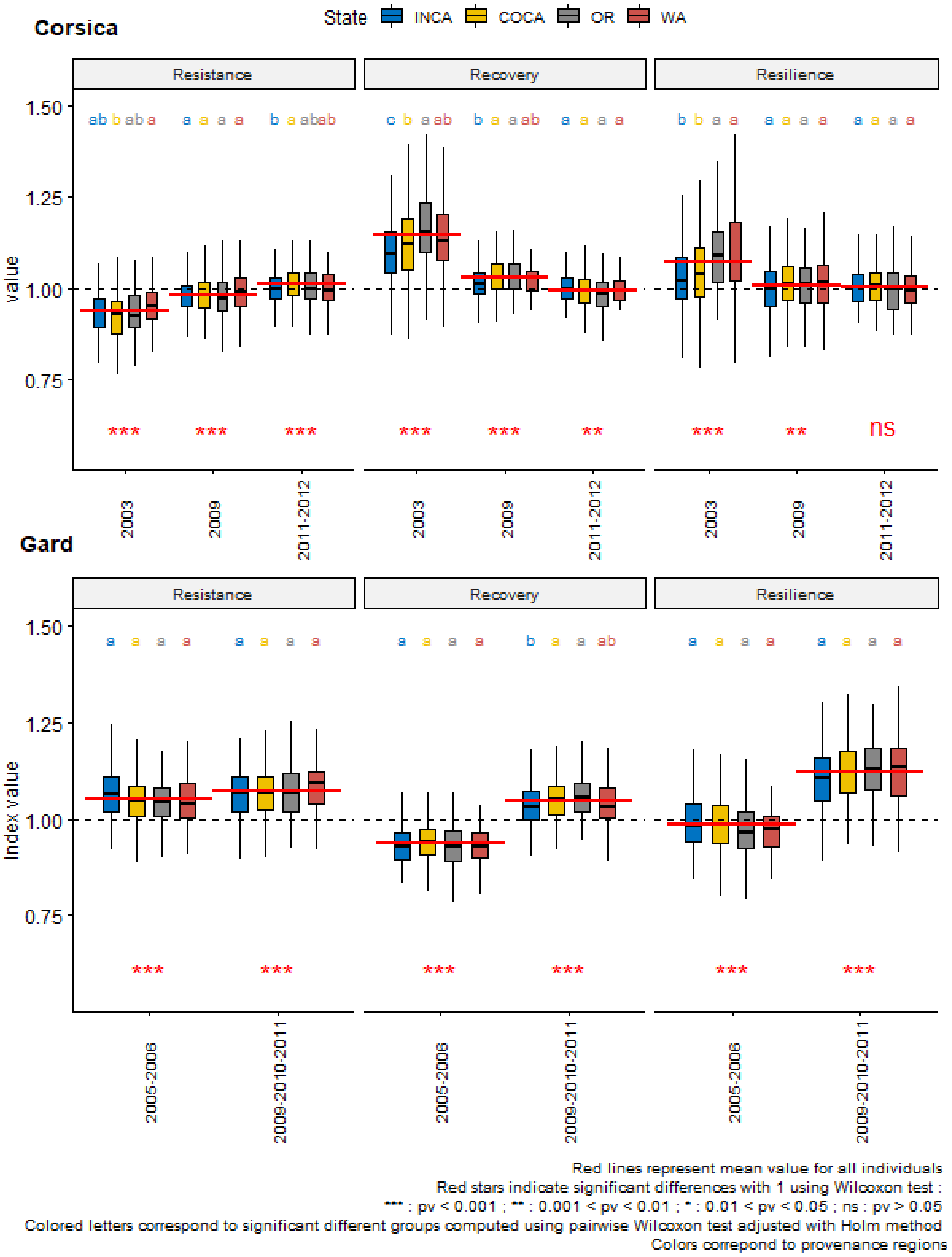


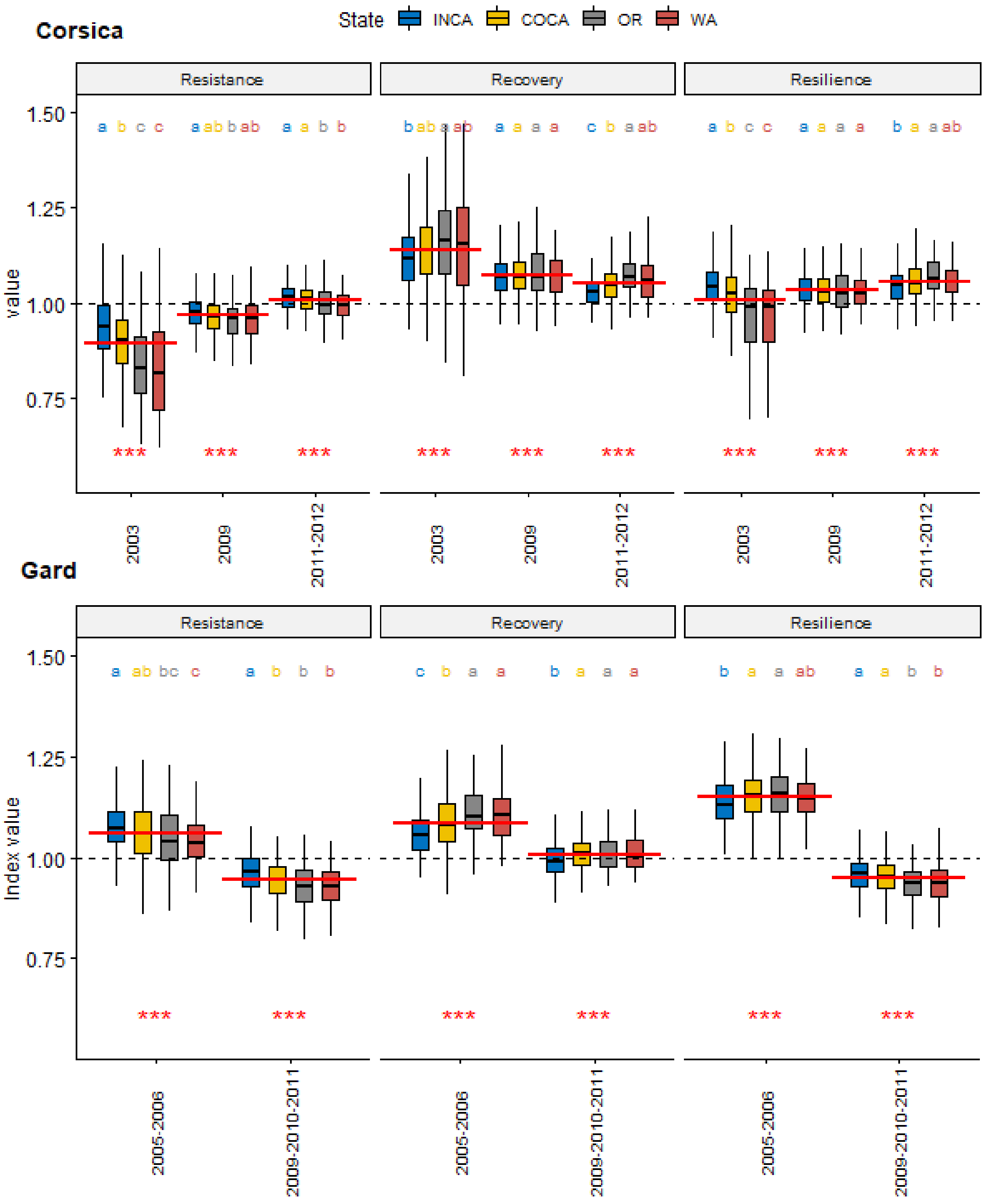
Figure 9: 2 years response to drought events of the minimum ring density in both sites and for each provenance region

Results regarding earlywood mean density and minimum ring-density are strongly correlated (Pearson correlation of 99.2%). As for the maximum ring-density, it is highly correlated with latewood mean density (Pearson correlation of 97.8%), standard deviation of ring density (Pearson correlation of 90%) and ring density contrast (Pearson correlation of 92%). Thus, only minimum and maximum ring-density results will be presented in this study (respectively in Figure 9 and Figure 10), those two variables being easy to measure and easy to interpret.

Regarding minimum density's indices, even more variation among responses is displayed than for radial growth indices. However, the range of these variations is shorter with indices mainly contained in a range of ± 30% around 1. Corsica's mean resistance values are all significantly different from 1 for this variable and range from 93.9% (P-value $= 9 \times 10^{-74}$) for 2003 to 101% (P-value $= 3 \times 10^{-4}$) for 2011-2012 going by 98.1% (P-value $= 10^{-19}$) for 2009. Among those, COCA provenances have significantly lower resistance values than WA for 2003 and greater than INCA for 2011-2012.
Recovery in the Corsica site for the 2003 event shows strong variation both within and between provenance regions, with INCA provenances having significantly lower values than the rest (111.1%) followed by COCA provenances (115%) significantly lower than OR provenances (120.4%) but not than WA provenances (115.9%). As shown in Appendix A9, provenances RE1 and HAC had higher values than other COCA provenances more comparable to those of the OR provenances and WA provenances. Mean values for 2009 and 2011-2012 are closer to 1 although it still differs from it significantly with 103% (P-value $= 9 \times 10^{-39}$) and 99.5% (P-value = 0.005) respectively. INCA provenances (101.7%) have significantly lower values than COCA provenances (103.6%) and OR provenances (103.7%) but not WA provenances (103.9%) for 2009.

As for the resilience, only the 2003 event showed strong significant difference from 1 (107.2%, P-value $= 9 \times 10^{-39}$) with OR provenances (112.2%) and WA provenances (110.7%) having significantly higher values than INCA provenances (104.8%) and COCA provenances (106.5%).

As for the Gard site, no significant differences between provenance regions are displayed (except for the recovery of the 2009-2010-2011 event where COCA provenances and OR provenances have greater values than INCA provenances). However, all site mean values significantly differ from 1. For the resistance both values are above 1 with 105.2% (P-value $= 10^{-64}$) for 2005-2006 and 107.3% (P-value $= 3 \times 10^{-90}$) for 2009-2010-2011.
For the recovery values for the 2005-2006 event they are below 1 (93.9%, P-value $= 10^{-92}$) and above 1 for the 2009-2010-2011 event (104.9%, P-value $= 10^{-71}$). The resilience's values are again below 1 for the 2005-2006 event (98.6%, P-value $= 10^{-8}$) and above for the 2009-2010-2011 event (112.4%, P-value $= 10^{-111}$).
Moreover, minimum density values do not differ significantly between provenance regions in the Corsica site, at the exception of the years 2000, 2011, 2014 and 2015 all with low significant differences. On the other hand, in the Gard site, minimum density values differ significantly for all the time period with INCA provenances and COCA provenances having higher minimum density values than OR provenances and WA provenances (as shown in Appendix A8).



Red lines represent mean value for all individuals
Red stars indicate significant differences with 1 using Wilcoxon test :
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Colored letters correspond to significant different groups computed using pairwise Wilcoxon test adjusted with Holm method
Colors correpond to provenance regions

Figure 10: 2 years response to drought events of the maximum ring density in both sites and for each provenance region

Concerning maximum density's indices, it is the variable that displays the most important variations between provenance values.

For the Corsica site, the resistance values of all events are significantly different from 1 (89.4%, P-value $= 10^{-86}$; 96.7%, P-value $= 5 \times 10^{-57}$; 100.6%, P-value $= 6 \times 10^{-8}$ respectively for the 2003, 2009 and the 2011-2012 events). For all events, INCA provenances and then COCA provenances values are the highest, although their difference to other regions is not always significant (it is strongly significant for 2003).

Conversely, for the recovery values, INCA has the lowest values for both 2003 (111.6%) and 2011-2012 events followed by COCA (114.1%) while there is no difference between provenance regions for 2009. All site mean values are significantly above 1 with 113.7% (P-value $= 7 \times 10^{-92}$), 107.2% (P-value $= 10^{-91}$), 105.1% (P-value $= 3 \times 10^{-85}$) respectively for the 2003, 2009 and the 2011-2012 events. Resilience mean values are all significantly above 1 for each event as well with 100.9% (P-value $= 8 \times 10^{-9}$) , 103.4% (P-value $= 6 \times 10^{-47}$) , 105.6% (P-value $= 6 \times 10^{-88}$) respectively for the 2003, 2009 and the 2011-2012 events. For 2003, INCA provenances values (104%) are significantly higher than the rest, COCA provenances values (101.6%) are also significantly higher than OR provenances (95.5%) and WA provenances (95.3%).

For the Gard site, concerning between provenance regions variations, a similar trend to the Corsica site is displayed with INCA provenances and COCA provenances having the highest resistance values and the lowest recovery values, although it is not always significant for both events.

For the resistance, mean values for both events are significantly different from 1, above for 2005-2006 (106.1%, P-value $= 10^{-77}$) and below for 2009-2010-2011 (94.5%, P-value $= 5 \times 10^{-93}$). For the recovery indice, both mean values for each event are above 1 although the difference with 1 is more pronounced for 2005-2006 (108.6%, P-value $= 4 \times 10^{-111}$) than 2009-2010-2011 (100.7%, P-value $= 5 \times 10^{-4}$). The mean resilience value for 2005-2006 is significantly above 1 (115%, P-value $= 2 \times 10^{-119}$) with INCA provenances having the lowest values (106.1%) although it is not statistically different from WA provenances (110.9%). However, for the 2009-2010-2011, INCA (99.4%) and COCA provenances' (101.2%) values are both significantly higher than those of OR (101.2%) and WA (101.4%). The site mean resilience value for this event is significantly below 1 with a value of 95.1% (P-value $= 3 \times 10^{-81}$).

As shown in Appendix A10, for both sites, INCA provenances and COCA provenances have higher maximum density values than OR provenances and WA provenances, although it is more strongly marked after the 2003 event of the Corsica site. In the Gard site, these differences appear stronger during drought events.

4 Discussion

As expected, ring width significantly decreased for all selected events. It is clear that all these events had a significant impact on tree growth even though variation remains between responses to the different events, between the different provenance regions and between both sites. This impact is due to soil water deficit leading to stomatal closure thus limiting evapotranspiration but also carbon uptake (Aussenac and Bourgois 1984).

On the Corsica site, the event with the lowest decrease in ring width is 2011-2012. However looking at year by year values (shown in Appendix A1), it appears that the year 2011 taken alone would have similar resistance values as the two other events. On the other hand, in 2012 even though it has been selected as a drought year, ring width increased compared to 2011. 2012 is the only selected year with above 1 resistance values for this site. It is also the only year with high SPEI values for the months April and May even though it has low SPEI values for March and June, July and August. It can be hypothesized that ring width on this site is highly dependent on early growing season conditions because of harder conditions during the summer months. For this site, May SPEI values are indeed the most correlated with ring width (14.7%) closely followed by August values (14%). A previous study, in Poland, however, did not give similar result with the main factor influencing radial growth being February and March temperatures (Feliksik and Wilczynski 2004). Those different results can probably be explained by a wetter and colder climate found in Poland than in the two tested site here, thus influencing the growth period.

Concerning differences between provenance regions, variability in ring width between provenance regions is not significant before the first drought event and then tends to decrease during the event but increase in the recovery period of these events. After 2003's drought only INCA and in a lesser extend COCA provenances recovered to their high pre-drought values. As ring width cannot be indefinitely small, in order to maintain its primary purpose of sap conduction, having smaller ring width for OR and WA provenances may imply their resistance to future events to be higher relatively to larger ring width which could explain why their resistance in 2009 was relatively higher than INCA and COCA provenances for this event. As during 2009 events, the differences between the ring width of each provenance regions decreased (and were much less significant), this effect of larger ring width reducing resistance values does not occur for the close event of 2011-2012. Interestingly, these observations do not comply with previous results showing a higher growth reduction during drought years for Interior California provenances and a higher growth for coastal provenances (Anekonda et al. 2004, Sergent et al. (2014a)). However, those previous results are similar to those found on the Gard site where INCA provenances show significantly lower ring width resistance along with lower growth rates, although this observation does not comply with the trade-off between growth and drought resilience observed by Montwe *et al.* (2015). This observed difference both between sites and with previous studies might be explained by the more difficult pedoclimatic conditions of the Corsica site not allowing provenances adapted to wetter climate to express their higher performances. In the Gard site, however, the previously described trend of a resistance advantage to lower ring width does not occur with INCA provenances. They have the lowest ring width but also the lowest resistance values, which is probably explained by an overall larger ring width in the Gard site than in the Corsica site. Indeed, the raw ring width values for the OR and WA provenances in Corsica for the pre-drought period of 2007-2008 are in absolute values almost half those of the INCA provenances in the Gard site for the pre-drought period 2003-2004 (3.3mm and 6.42mm respectively) thus leaving more room for Gard trees' ring width to decrease. Even though INCA provenances' (and COCA provenances which seem to be intermediate between INCA and OR/WA provenances) ring width did not resist as much, its higher recovery makes it at terms equal to the other provenances in terms of resilience. There seems to be a trade-off between resistance and recovery with provenances coming from wetter regions favoring resistance whereas provenances coming

from drier regions favoring recovery.
Another interesting trend similar between both sites is a reduction in ring width variability between provenance regions for the last recorded years. It is not so surprising for the Gard site, where fewer differences were observed for non-dry years. However, in the Corsica site, because of the 2010-2011 event, it would be expected that the recovery period accentuates differences between provenance regions which only occurs in 2012. In can be hypothesized after that point, as before the first event, the trees fully recovered thus not showing any differences in their mean until a new drought event occurs.

When focusing on the latewood width, we can see that, in Corsica, except for certain years with good climate conditions, there are few to no significant differences between provenances region in term of latewood width. It is not the case in the Gard site with strong and significant differences between provenance regions. According to Anderegg and HilleRisLambers (2019), harsh range boundaries tend to be under climatic control, as displayed in the Corsica site, trees cannot express their potential thus showing similar final width growth rate between provenance regions.
Even though latewood width shows significant response for all events, the 2003 year of Corsica show stronger reduction than every other event. During this event, INCA provenances significantly shows both higher resistance and resilience than OR and WA provenances, thus leading to stronger resilience. However, for other events in Corsica, resistance did not react much even though recovery did which could be explained by the climate succeeding the 2009 and 2011-2012 drought event. Indeed, all provenances showed a decline in latewood width in 2010, which was fully recovered only in 2014. This decline could be explained by a strong drought in July 2010. The reduction in latewood width because of 2010 event appears to be higher for INCA and COCA provenances although COCA recovered quicker than INCA. This difference between the response to the 2003 event and the 2010 year might be caused by either the duration of the summer drought, being much longer for 2003 or the location within the year, 2003 drought also affecting August.
In the Gard site, however, the COCA-INCA pair and the OR-WA pair appear to have the same response. There appears to be a trade-off between resistance and resilience with INCA and COCA provenances having higher recovery and OR and WA provenances having higher resistance. Though, both strategies seem to give the same results in terms of resilience. The absence of recovery for the 2005-2006 event at the site level seems to appear because of the between provenances variability with positive recovery for most INCA and COCA provenances and negative for half of the OR and WA provenances.

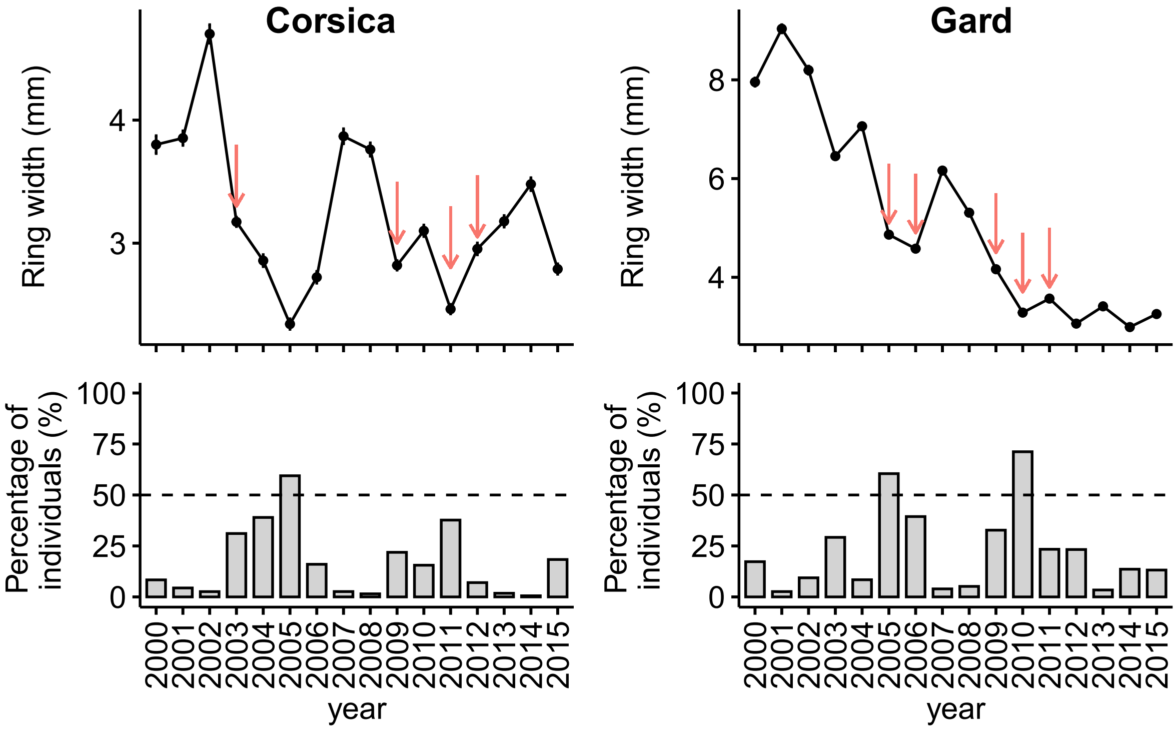
Regarding the minimum density, it is interesting to note that on the site with no significant differences between provenance regions (i.e. Corsica), differences of response to drought events appear stronger than in the site with strong differences between provenance regions values. The strongest differences are displayed for the 2003 event in the Corsica site when INCA and COCA provenances has lower resilience values than OR and WA provenances, mainly because of lower recovery. OR and WA provenances thus reacted more strongly to the event, focusing on increasing their wood density to cope with a drier environment which was probably not required for more drought resistant INCA provenances and COCA provenances. On the Gard site, where the climatic constraint is lower, all provenances regions reacted the same with a decrease in minimum density at the beginning of the drought event followed by an increase. As for earlywood width, this pattern does not strongly appear when looking at the index for the selected years. It is due to some years with a decrease in minimum density not being selected (2003 and 2008) because of smaller drought for these years compared to the selected year.

On the contrary, maximum density variations appear to be a good indicator of drought as steep decrease in maximum density occurs during the selected years with quick recovery after the event for both sites and all provenance regions. Although some events would show different trends, those are easily explainable, the 2011-2012 event of Corsica showed a decrease for the year 2011 but the mean resistance is higher than 1 because it is also calculated using the 2009 low values. It is the same for the 2005-2006 event of the Gard site, where resistance values also include the 2003 year, which although not being selected was also a dry year (the 6th dryer year for the Gard site), especially when focusing only on summer drought. During those events, there appears to be a trade-off between resistance and recovery with INCA provenances and COCA provenances having higher resistance but lower recovery than OR provenances and WA provenances. On the driest events, which are the 2003 event of the Corsica site and the 2011-2012 event of the Gard site, the resistance strategy maintains the highest maximum density with higher resilience values for the INCA provenances and COCA provenances. For the other events, the difference between the strategies is less clear with both strategies having the same resilience after two years.
As latewood is more vulnerable to embolism than early wood (Domec and Gartner 2002, Dalla-Salda et al. (2014)) and some links have been found between rings with little density variations and drought resistance (Chauvin 2019), the reduction of the maximum ring density during a drought event seems to be a clear adaptation from the trees to cope with the event.

It could be hypothesized that all these results may suffer to a certain extent of the survivorship bias. Indeed, dead trees have not been cored thus not giving their values for the selected events. As the lowest survival rate is found for the WA and OR provenances on the Corsica site (48% survival), it is likely that the remaining individuals (i.e. the studied individuals) are more adapted to the site than the dead ones. If drought is the main death factor, then the results may overestimate drought tolerance at the provenance region level by selecting only the most drought tolerant individuals. As tested by Chauvin (2019), although the Corsica site has the lowest survival rate, it is the one with the greastest variation in phenotypical vulnerability to cavitation. However, as the same provenances are in average less vulnerable to cavitation on the Corsica site than in the Gard site, it is likely that a selection over vulnerability to cavitation occured in the Corsica site.

As well described by Schwarz (2020), studies using Lloret indices to study drought responses do not use a homogenized method of year selection. Drought events can be identified by using either climatic data or reduction in trees' growth data or a combination of both. As suggested, to be sure to have a consistent method through both sites and to be able to characterize the drought events, here only climate data were used to select the studied years. However, if tree growth reduction was chosen as a method for selecting the data, it would not have selected the exact same year, as shown in Figure 11. A selection using pointer years, a commonly used approach (Becker et al. 1994, Weigel et al. (2018), Matisons et al. (2019)) based on the percentage of trees having the same ring width tendency for a given year at a given site would have given misleading results concerning the 2003 drought event of Corse. Indeed, this event seemingly caused lagged drought response on ring width, which was still decreasing in 2005. It confirms that a method based on climatic data only is a more generalizable solution although the addition of hydrological data may be of strong interest to account for the variability in soil water capacity.

However, when studying the ring width components such as latewood, obtained results do not appear consistent with the methodology, favoring longer drought period within the year. If a single month drought can influence a given variable, as the July month does in the Corsica site for the latewood width, then results do not coincide with the selected years thus granting misleading results. In this case, the recovery in 2009 and 2011-2012 does not result from those years but from the drought of the non-selected year 2010.



The y−axis corresponds to the percentage of individuals showing a reduction of at least 30% of their ring width compared to the 3 years prior ; Red arrows represent selected years for this study using Standardized Precipitation−Evapotranspiration Index (SPEI)

Figure 11: Pointer years for the Corsica and the Gard site based on raw ring width

Schwarz also suggested to use other indices (2020) in complement of the ones used here. As described by Thurm *et al* (2016), he suggested to use an index called the *recovery period*, being the time necessary to reach pre-drought growth level and the *total growth reduction*, being the sum of the growth loss for all of the recovery period. These were not used here because this study aimed to select multiple events on a short timespan, thus not allowing for recovery periods to be independant between events.

Ring width and density respond similarly to drought events with a strong reduction in growth and in density for each part of the ring. However, maximum density reacts more rapidly with a higher recovery compared to ring width which can also have some multi-years effect as shown for the 2003 event of Corsica. Although this multi-year effect has not been observed for Douglas fir (Sergent et al. 2014b) it has already been observed on other species such as silver fir (Becker 1989) and may be explained by irreversible damage on foliage, fine roots, twigs or xylem cavitation (Bréda et al. 2006).

As the responses differ greatly between the two sites, it appears that the pedoclimatic constraint leads to different responses of the trees. On the drier site of Corsica, INCA provenances showed the highest resilience to drought for the most extreme event in term of radial growth accompanied by the highest overall productivity and the highest maximum density. COCA provenances closely followed those of INCA both in terms of resilience and productivity at the exception of the RE1 and HAC provenances reacting similarly to OR or WA provenances. On the other hand, on this site, the OR and WA provenances usually considered more productive showed a higher mortality rate, a lower growth rate and a lower resilience to drought events.

On the Gard site, the drought constraint is smaller than on the Corsica site because of higher precipitation, on this site, the OR and WA provenances can express their growth potential. The differences between trees density are larger (for minimum density) or similar (for maximum density) to those of the Corsica site, but the differences in radial growth are bigger. On this site, the OR and WA provenances high production does not come along with lower resilience.

In the perspective of selecting more drought resistant provenances for a future breeding program, a single set of provenances cannot be advised. In the case of a current or future drought prone site, it appears that selecting provenances from the INCA region is the most secured choice even though it can lead to slightly less productive stands. In the case of a moist site, selecting provenances from the INCA or COCA region seems to be detrimental in term of production when the gain in drought resilience is low to null, thus using conventionally used provenances such as WA or OR seems to be the right choice. COCA provenances seem to be more suited for intermediate site or to minimize risks compared to OR and WA provenances on intermediary sites.

5 Conclusion

This study has shown that growth, density and its responses to drought depend both of the tested site, on the origin of the seeds and on the event we are looking at. On the drier site, during the driest event, Californian provenances performed best in terms of growth, density and resilience to drought. On the moister site, Oregon and Washington provenances performed best in terms of growth with little differentiation in terms of resilience to drought between provenances. On this site, provenances from the driest environments showed the lowest growth during the driest years. A trade-off between ring width and maximum ring density resistance and recuperation have been observed with reverse patterns between Californians and Oregon plus Washington provenances. More investigation will be necessary to link these results to geographic and climatic adaptation of the provenance regions and to investigate further at the provenance or individual scale. These deeper investigation appear especially useful in the context of creating new seed orchard using clones from the best individuals.

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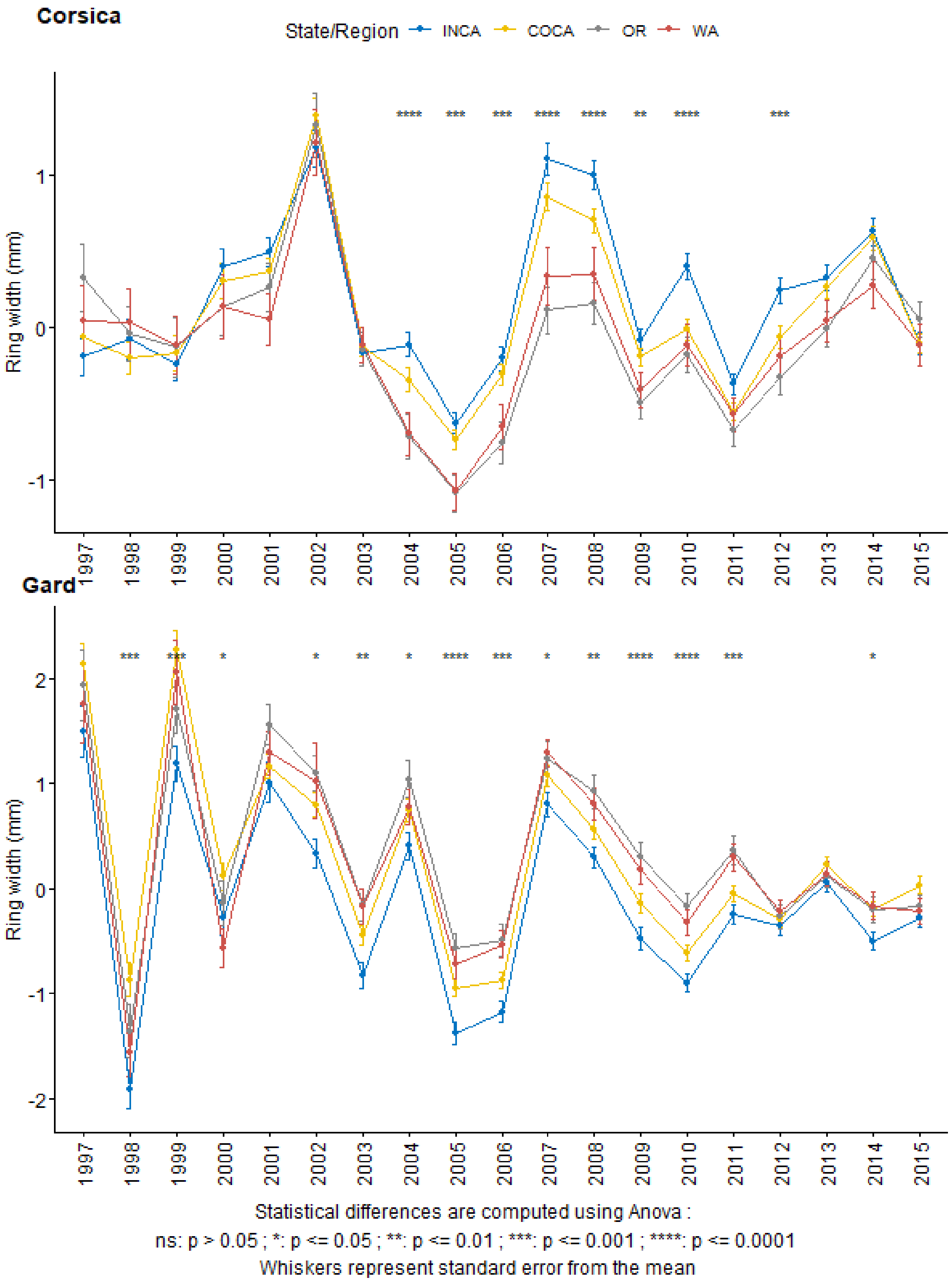
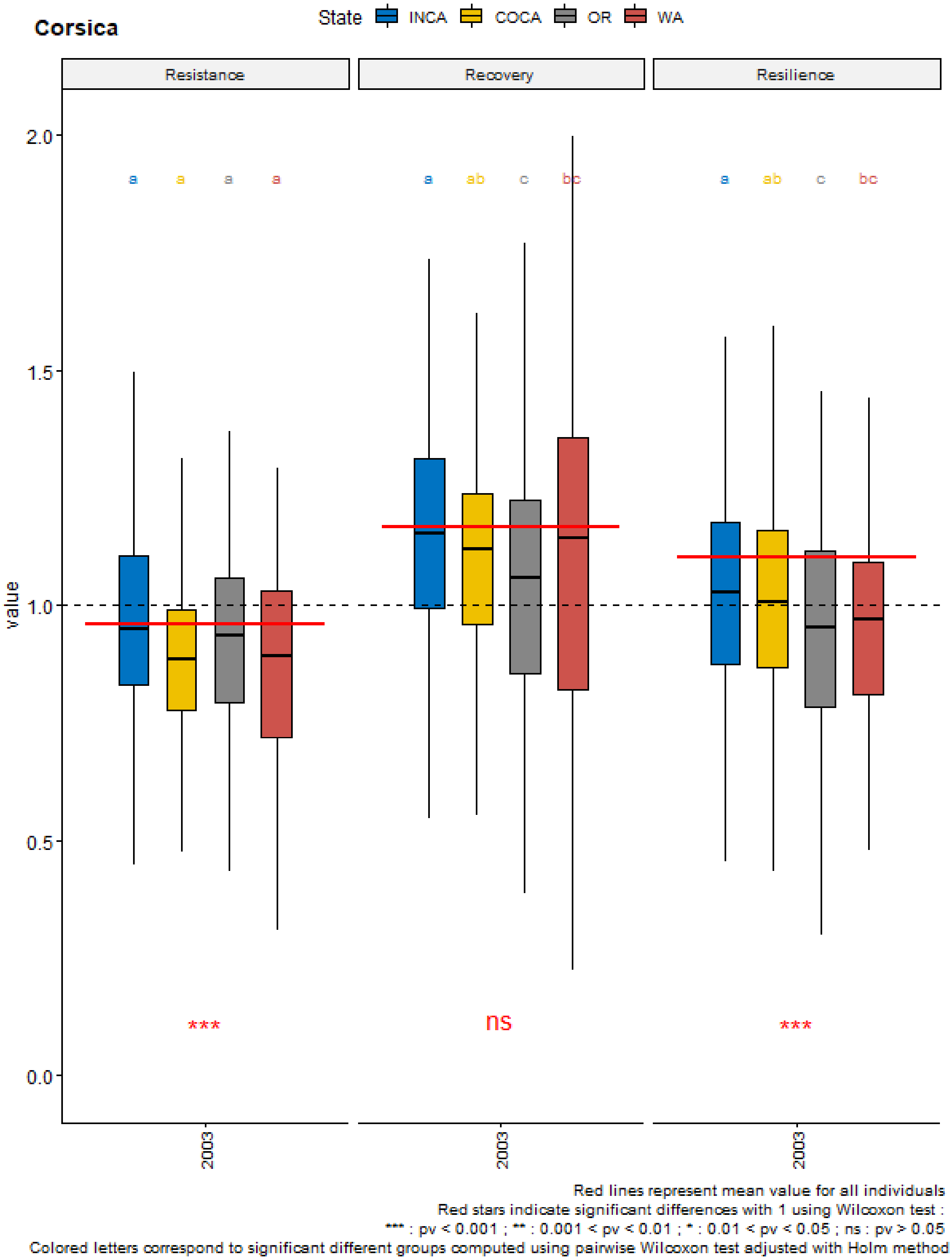
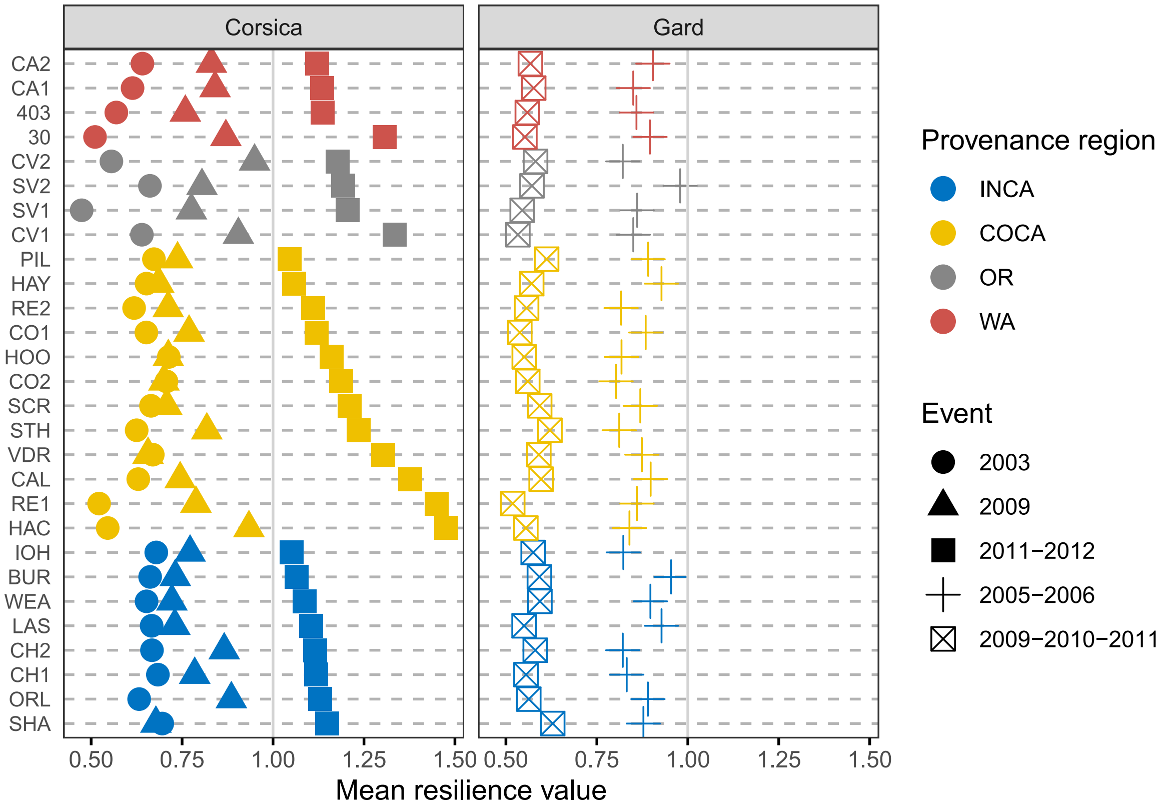


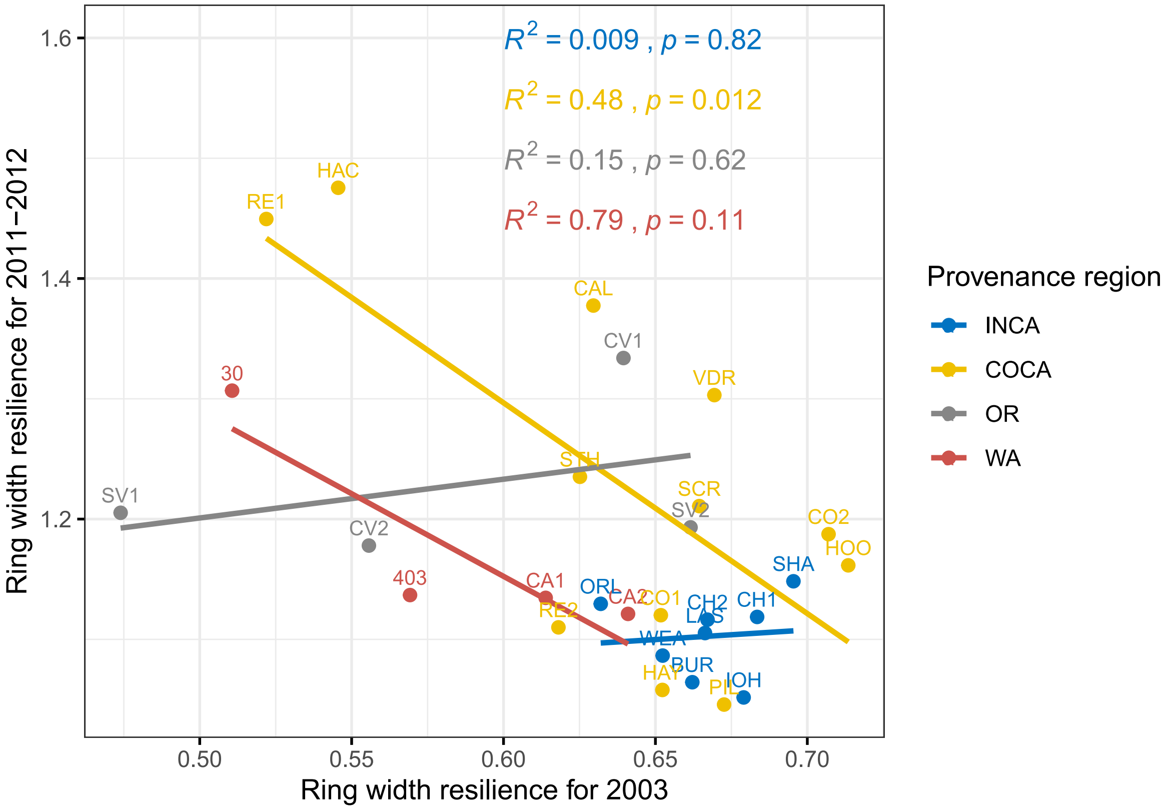
Appendix A1: Plot of the evolution of standardized ring width for both sites and all 4 provenance regions



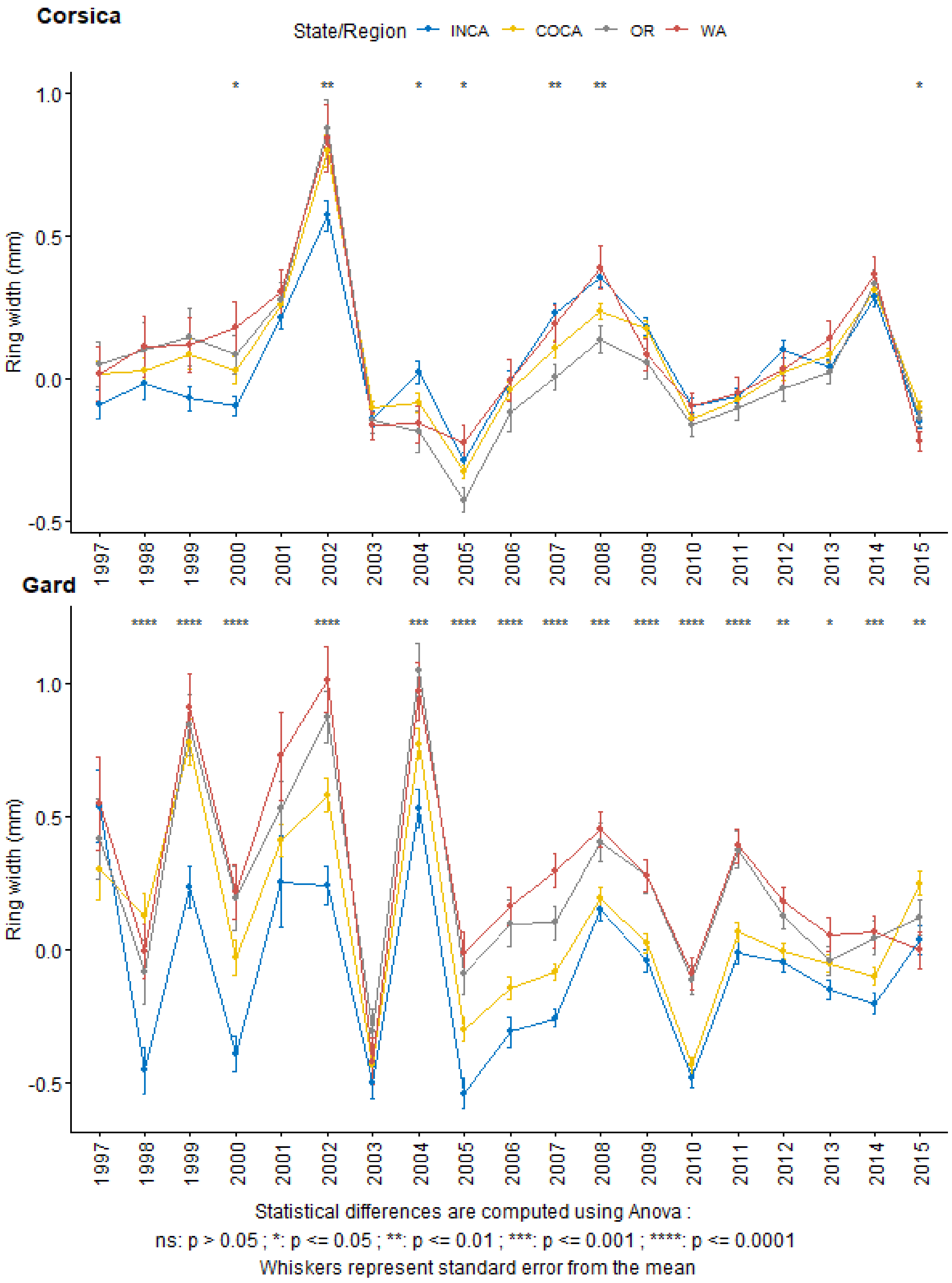
Appendix A2: 5 years response to 2003 drought events of the Ring width for the Corsica site and for each provenance region



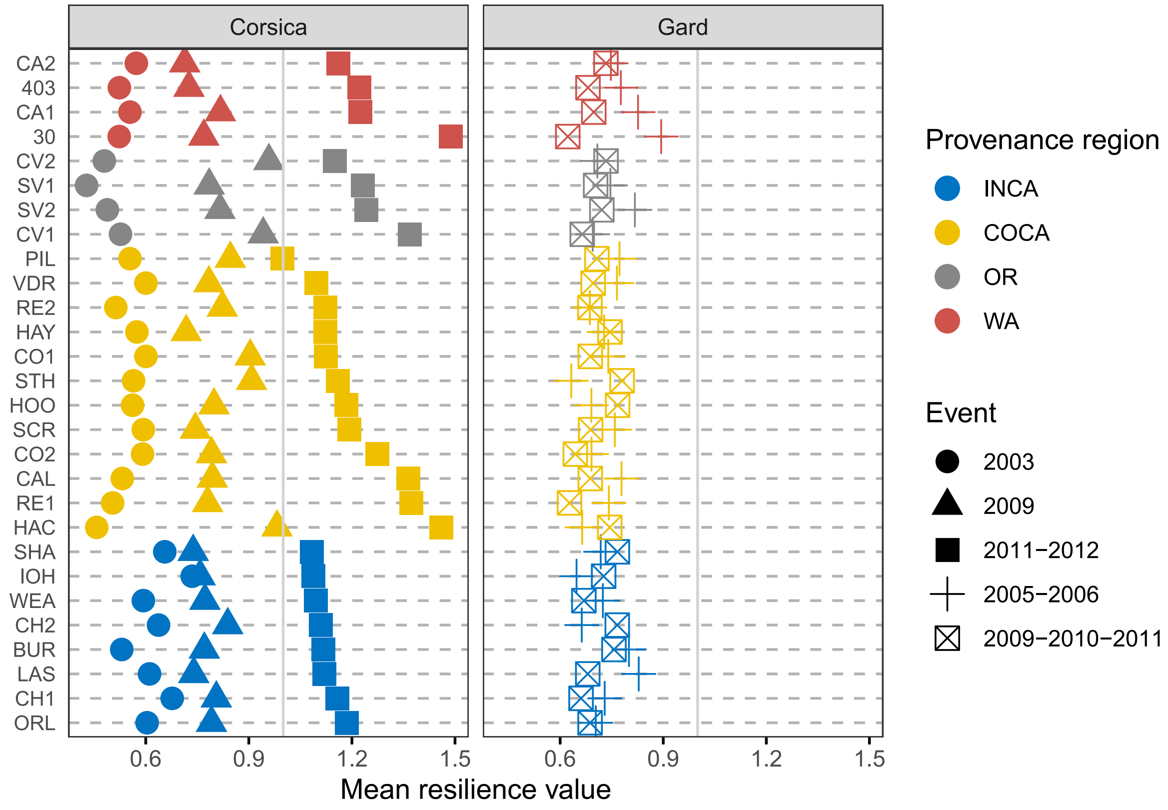
Appendix A3: 2 years resilience to drought events of the Ring width in both sites and for each provenance



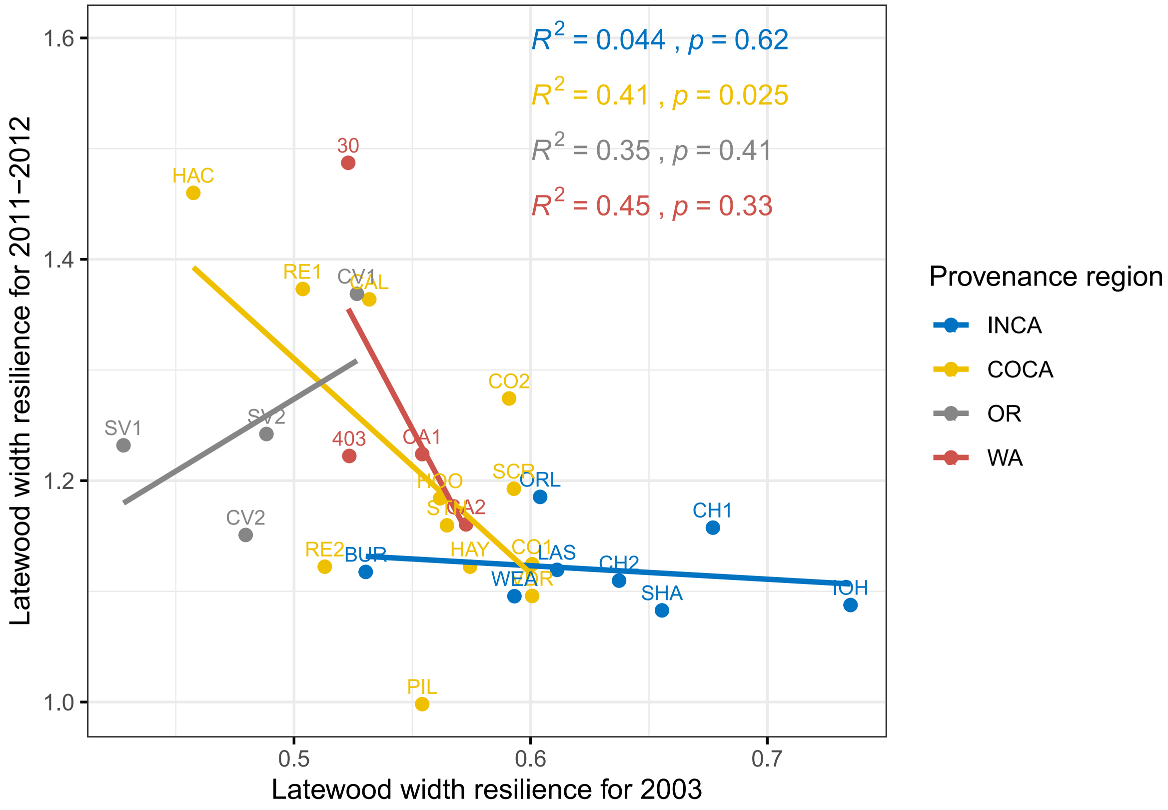
Appendix A4: 2 years ring width resilience of each provenance for 2011-2012 compared to 2003 in the Corsica site



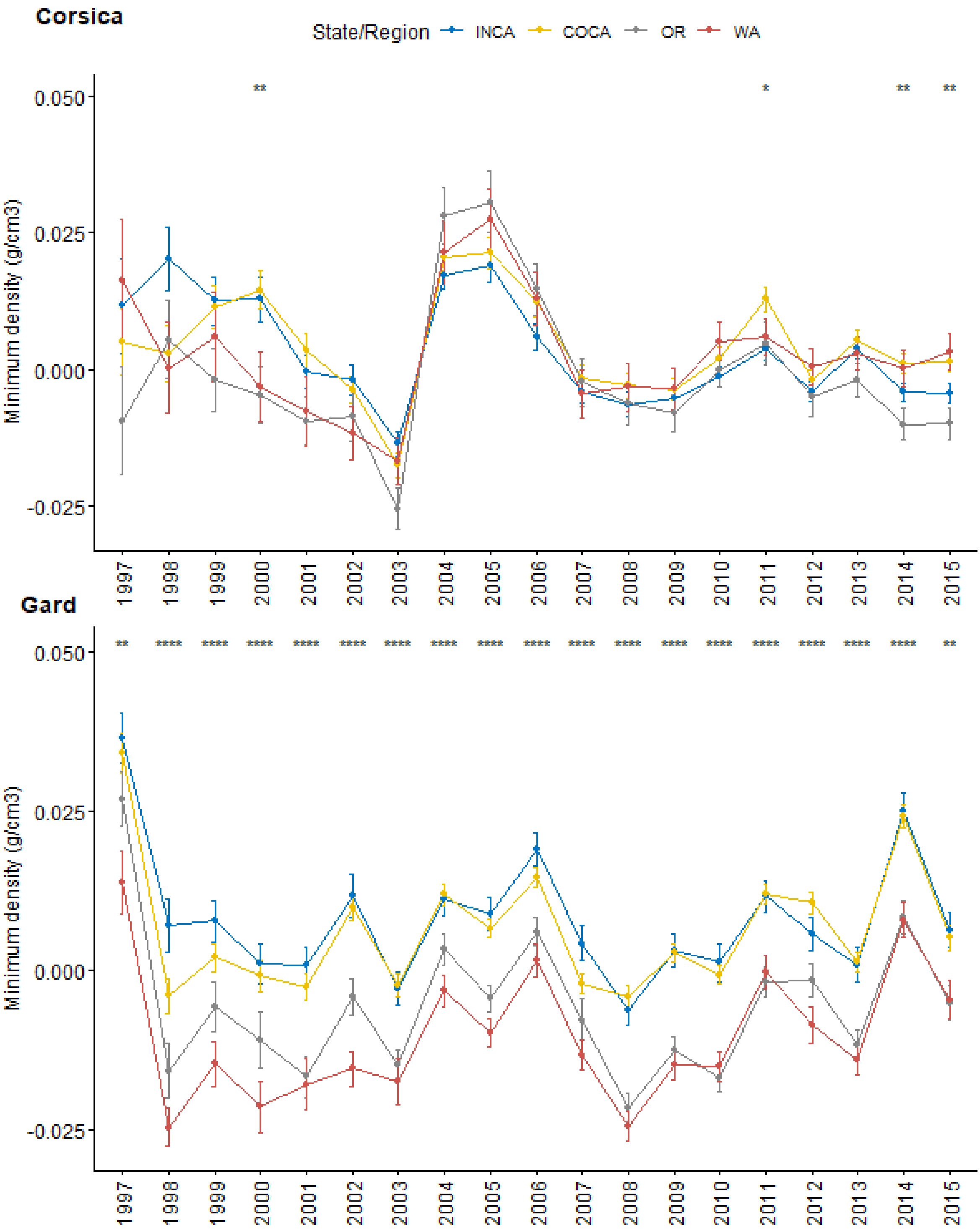
Appendix A5: Plot of the evolution of standardized latewood width for both sites and all 4 provenance regions



Appendix A6: 2 years resilience to drought events of the latewood width in both sites and for each provenance

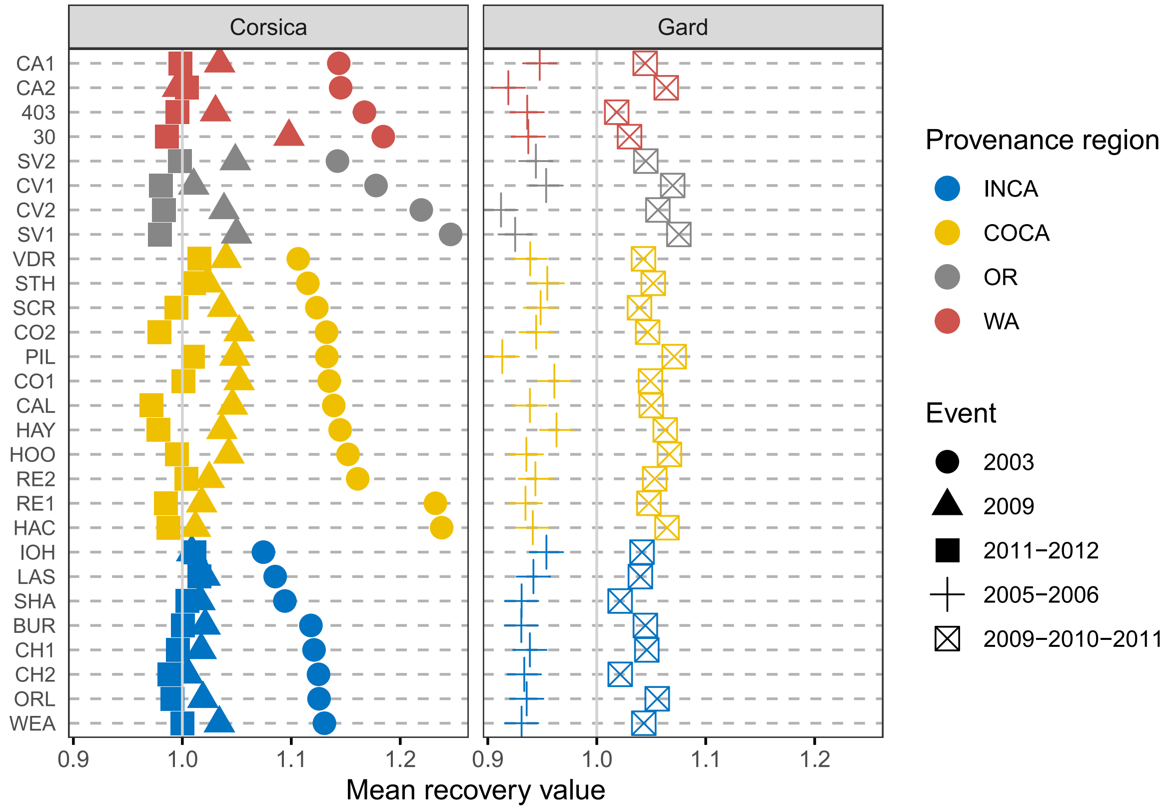


Appendix A7: 2 years latewood width resilience of each provenance for 2011-2012 compared to 2003 in the Corsica site

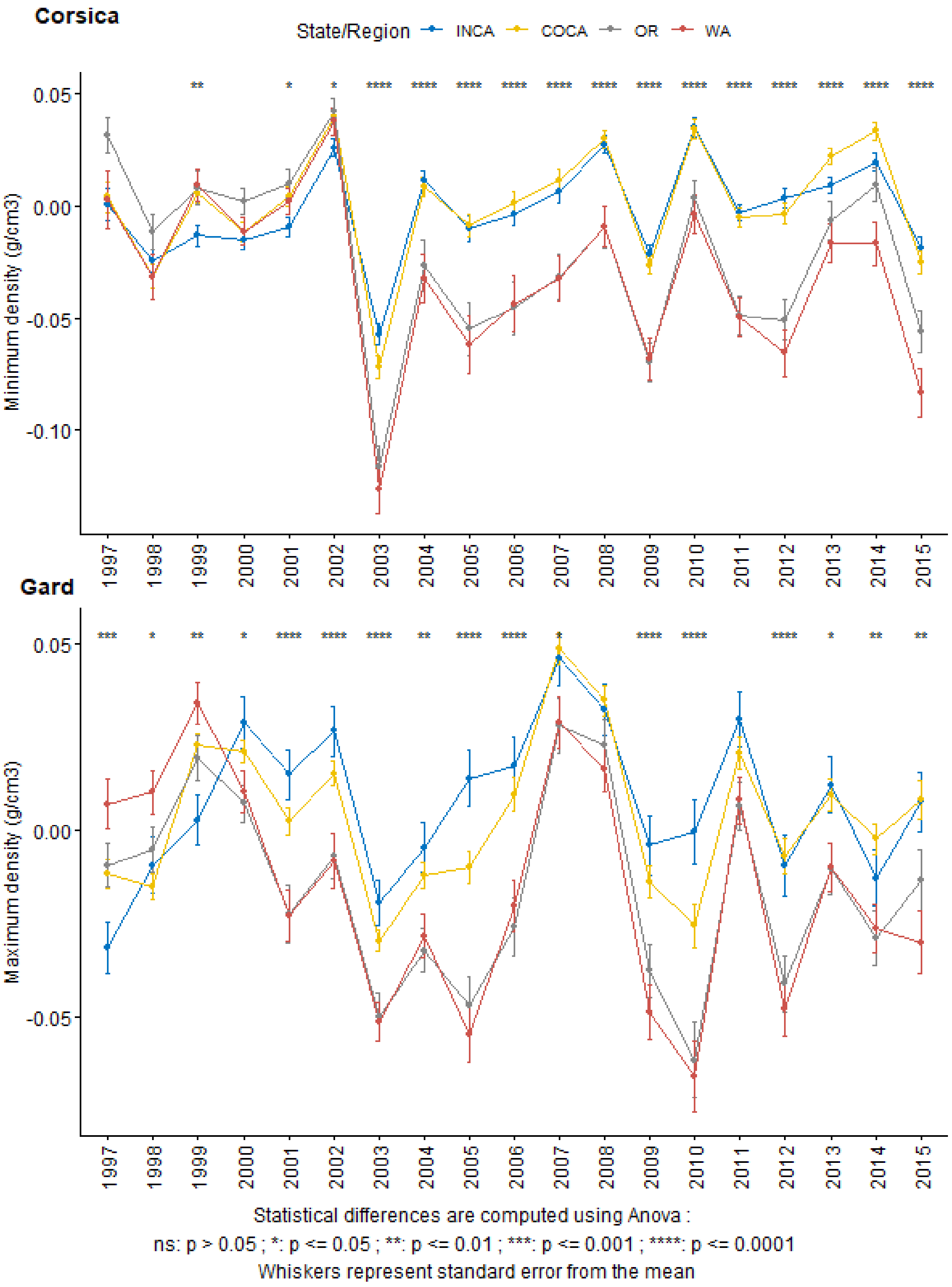


Statistical differences are computed using Anova :
ns: p > 0.05 ; *: p <= 0.05 ; **: p <= 0.01 ; ***: p <= 0.001 ; ****: p <= 0.0001
Whiskers represent standard error from the mean

Appendix A8: Plot of the evolution of the minimum density for both sites and all 4 provenance regions



Appendix A9: 2 years recovery to drought events of the minimum density in both sites and for each provenance



Statistical differences are computed using Anova :
ns: p > 0.05 ; *: p <= 0.05 ; **: p <= 0.01 ; ***: p <= 0.001 ; ****: p <= 0.0001
Whiskers represent standard error from the mean

Appendix A10: Plot of the evolution of the maxmimum density for both sites and all 4 provenance regions