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Context: As a widespread species, sessile oak (*Quercus petraea*) populations occupy a wide range of ecological conditions, with large gradients of soil water availability. Drought acclimation involves a plastic increase in water-use efficiency (WUE), a trait that is easily measured using the carbon isotope composition (δ^{13}C). However, the question remains whether WUE is an adaptive trait that impacts the fitness of trees in natural environments.

Objectives and Methods: To investigate whether WUE was a drought-adaptive trait, we studied a sample of 600 trees originating from 16 provenances, grown for 21 years in a common garden. Intrinsic WUE (WUE$_i$), estimated from tree ring δ^{13}C, was compared among and within populations for three climatically contrasted years. The adaptive character of WUE$_i$ was evaluated by relating population mean WUE$_i$, as well as its plasticity to drought, to the pedoclimatic conditions of their provenance sites. The contribution of WUE$_i$ to tree and population fitness was finally assessed from the relationship between WUE$_i$ and tree radial growth (GI).

Results: Significant differences in WUE$_i$ were found among populations but a much larger variability was observed within than among populations. The population WUE$_i$ of the juvenile oak trees growing in the relatively mesic conditions of the common garden showed no relationship with a modeled water deficit index for the provenance sites. However, a higher population WUE$_i$ plasticity to severe drought was related to a higher proportion of silt and carbon and a lower proportion of sand in the soil of the provenance sites. In response to severe drought, populations with a higher increase in WUE$_i$ showed a lower decrease in GI. Populations with lower GI reduction were from sites with higher vapor pressure deficit in May–July (VPD). For the wet year only, populations with a higher WUE$_i$ also had a higher GI.

Conclusion: The correlations observed at the common garden site between (i) population means of WUE$_i$ plasticity to drought and soil texture of the provenance sites, and (ii) GI plasticity to drought and VPD, suggested a local adaptation of sessile oak.

Keywords: local adaptation, soil texture, vapor pressure deficit, phenotypic plasticity, wood carbon isotope composition, social status, relative extractable water, drought response strategy

INTRODUCTION

Drought-induced diebacks of forest trees are commonly observed and affect nearly every forest biome in all parts of the world (Hartmann et al., 2018b). Extreme drought events are expected to be more frequent and intensive in the forthcoming decades due to climate change (Spinoni et al., 2018), and those observed between 2015 and 2018 in Europe have no equivalent in the past two millennia (Büntgen et al., 2021). In Europe, the loss of forest area due to drought-induced mortality has been estimated at 500,000 ha between 1987 and 2016 (Senf et al., 2020). Many forest tree species are affected, especially when they grow under limiting environmental conditions (Allen et al., 2010; Urli et al., 2015). Although considered as rather drought-resistant (Friedrichs et al., 2009; Härdtle et al., 2013; Kunz et al., 2018; Perkins et al., 2018), sessile oak [*Quercus petraea* (Mattuschka) Lieblein, 1784] already experienced recent diebacks in the most continental part of its distribution area (Petritan et al., 2021) and is expected to suffer future declines on sites with warmer and drier conditions (Bert et al., 2020).

Over the past millennia, migration allowed white oak species, as many others, to respond to climate changes caused by the glacial-interglacial cycles (Kremer et al., 2002; Petit et al., 2002; Cheddadi et al., 2005), with a mean migration rate estimated at 1.5 km per year for the last glacial migration (Brewer et al., 2005). However, climate change models predict an unprecedentedly rapid temperature change over the next 100 years, which would require a much faster migration pace. Assisted migration (Aitken and Bemmels, 2016; Sáenz-Romero et al., 2016) could accelerate range shifts through human intervention; however, this requires detailed information about genetic adaptive variation within the species. As a widespread species, sessile oak populations occupy a wide range of ecological conditions with different local selection pressures favoring local adaptation and resulting in genetic differentiation, as observed by Kremer and Petit (1993). Such genetic differentiation can include genetic diversity for phenotypic plasticity, which contributes to responses to short-term changes in environmental conditions. Higher phenotypic plasticity is expected in tree populations from sites subjected to more variable conditions over time, and especially to larger amplitudes of pedoclimatic conditions (Aitken et al., 2008).

Species with a large diversity in functional traits show a high capacity to adapt and/or acclimate to increasing aridity (Anderegg et al., 2021). The adaptive character of traits is commonly established by linking the among-population differences in traits observed in a common garden with the difference in climate or geographical characteristics of each population (Wang et al., 2010; Aitken and Bemmels, 2016; Sáenz-Romero et al., 2019; Bert et al., 2021). For sessile oak, significant among-population differentiation was observed for radial growth (Bert et al., 2020), height and survival (Grotehusmann and Schönfelder, 2011; Sáenz-Romero et al., 2017; Mátyás, 2021), and leaf functional traits (Vitasse et al., 2009a; Bruschi, 2010; Bresson et al., 2011; Torres-Ruiz et al., 2019). Leaf flushing and senescence dates were earlier for sessile oak populations originating from warmer sites (Vitasse et al., 2009b). Bruschi (2010) showed that the temperature and precipitation of the

provenance sites contributed to the among-population variation in sessile oak height, root–shoot ratio, leaf size, and thickness. However, other studies reported no significant differentiation among sessile oak populations, established along an aridity gradient, for leaf unfolding and senescence (Vitasse et al., 2010), leaf area, carbon and nitrogen isotope discrimination, leaf C and N content, stomatal density, xylem pressure inducing 50% loss of hydraulic conductivity due to embolism, vein density and wood density (Torres-Ruiz et al., 2019). These discrepancies illustrate the complex relationship between traits observed in a common garden and provenance site conditions, partly due to the much lower diversity observed among than within sessile oak populations (Bresson et al., 2011), which has also been observed for many other tree species (Hamrick et al., 1992; Ramirez-Valiente et al., 2010; Aranda et al., 2017).

Water-use efficiency (WUE) is a functional trait expressing at the tree level the trade-off between biomass production and water loss by transpiration. Because WUE reflects the link between tree carbon assimilation and water loss, studying among-population variation in WUE allows characterizing tree's strategies to face drought events (Brendel and Epron, 2022). The corresponding trait at the leaf level is called intrinsic water-use efficiency (WUE_i), i.e., the ratio between net CO_2 assimilation (A) and stomatal conductance for water vapor (g_{sw}). WUE_i is linked to the carbon isotope composition ($\delta^{13}C$, ‰) of the photosynthesis products (Farquhar and Richards, 1984). $WUEi$ and $\delta^{13}C$ are positively related, i.e., when WUE_i increases, $\delta^{13}C$ values become less negative. Although post-photosynthetic fractionation processes have been identified between leaf carbon assimilates and wood (Gessler et al., 2014), tree-ring $\delta^{13}C$ is considered as a valid estimator of foliar WUE_i integrated over the growing season and at the tree level (Ponton et al., 2002; Roussel et al., 2009). To our knowledge, the only study assessing variation among populations of sessile oak did not detect any significant differences in $\delta^{13}C$ measured in leaves sampled in mid-June (Torres-Ruiz et al., 2019), whereas significant differences were observed for many other forest tree species (Zhang and Marshall, 1995; Ferrio et al., 2003; Aranda et al., 2010). Several studies on broadleaved and conifer species observed a negative correlation between populations WUE_i (directly calculated from gas exchange measurements or estimated with $\delta^{13}C$, or both) and precipitation at their provenance sites (Li et al., 2000; Cregg and Zhang, 2001; Bekessy et al., 2002; Zhang et al., 2005; Duan et al., 2009), suggesting higher WUE_i for populations from drier sites. Conversely, a lower WUE_i for populations from the drier sites was observed in conifer species (Aitken et al., 1995; Guehl et al., 1996; Nguyen-Queyrens et al., 1998; Fan et al., 2008) but also in *Castanea sativa* (Lauteri et al., 2004; Eriksson et al., 2005) and *Quercus ilex* (Ferrio et al., 2003). These discrepancies among observations might suggest that there is no simple relationship between adaptation to dry environments and WUE. However, as suggested by Brendel and Epron (2022), the relationship between population mean WUE and pedoclimatic characteristics of provenance sites could be an indicator of different drought adaptation strategies. Further, most relationships between population mean WUE and site conditions are based on meteorological data only, whereas the soil water

availability depends strongly on the soil characteristics, which should be the main selection force for adaptation to soil drought.

Plant fitness is associated with several traits linked to reproduction and survival, including leaf phenology and vertical and radial growth (Gárate-Escamilla et al., 2019). Therefore, tree fitness could be linked to WUE_i by associating it with radial growth. The direction of this relationship allows some inferences about its underlying cause. A variation in photosynthetic capacity among populations would affect both their WUE_i and productivity in the same direction, i.e., an increase in photosynthetic capacity could increase WUE_i, resulting in less negative values of $\delta^{13}C$, and could also result in an increase in radial growth, at least under optimal conditions of water availability, light intensity, CO_2 concentration, and temperature. Thus, a variation in photosynthetic capacity would result in a positive correlation between WUE_i and growth. In contrast, a variation in stomatal conductance would result in an inverse relationship between WUE_i and radial growth: a lower stomatal conductance increases WUE_i (and results in more negative values of $\delta^{13}C$) but would either decrease growth (because of stomatal limitations of A) or result in no relationship. Summarizing studies about intra-specific association between WUE_i and tree productivity, Fardusi et al. (2016) showed that, for shrubs and conifers, WUE_i is highly and positively correlated to total biomass production (tested only on seedlings) and tree height but only slightly correlated to tree diameter. However, no clear relationships were observed for broadleaved tree species.

Using $\delta^{13}C$ measured in tree rings as a proxy of WUE_i, this study aimed at testing whether WUE_i or its plasticity (based on WUE_i from wet and dry years) could be considered an adaptive trait for environments with prolonged summer droughts. For this purpose, young sessile oak trees originating from 16 populations over Europe and planted in a common garden (Sillegny, France) were examined. In addition, in order to improve the environmental characterization of the original environments, each population was visited to analyze the physico-chemical characteristics of the soil and model the water balance of each population.

- (1) We aimed to characterize the among-population diversity of WUE_i for sessile oak and to link it with the pedoclimatic conditions of the provenance sites. We hypothesized, that, in the common garden of Sillegny, where the pedoclimatic conditions are in average mesic, populations from the driest sites would display the lowest WUE_i, as observed for *Q. ilex* (Ferrio et al., 2003).
- (2) We also sought to assess the plasticity of WUE_i to different soil water conditions (selected years) and to identify any plasticity difference among populations. We hypothesized that populations from dry sites, where annual environmental conditions are more variable, would exhibit larger plasticity in WUE_i than populations from wetter sites, as observed for *Q. suber* (Matías et al., 2019).
- (3) And finally, we wanted to assess the relationship between WUE_i and growth as an estimator of fitness. We hypothesized that trees and populations with higher WUE_i

showed higher radial growth only when the soil water availability was unlimited.

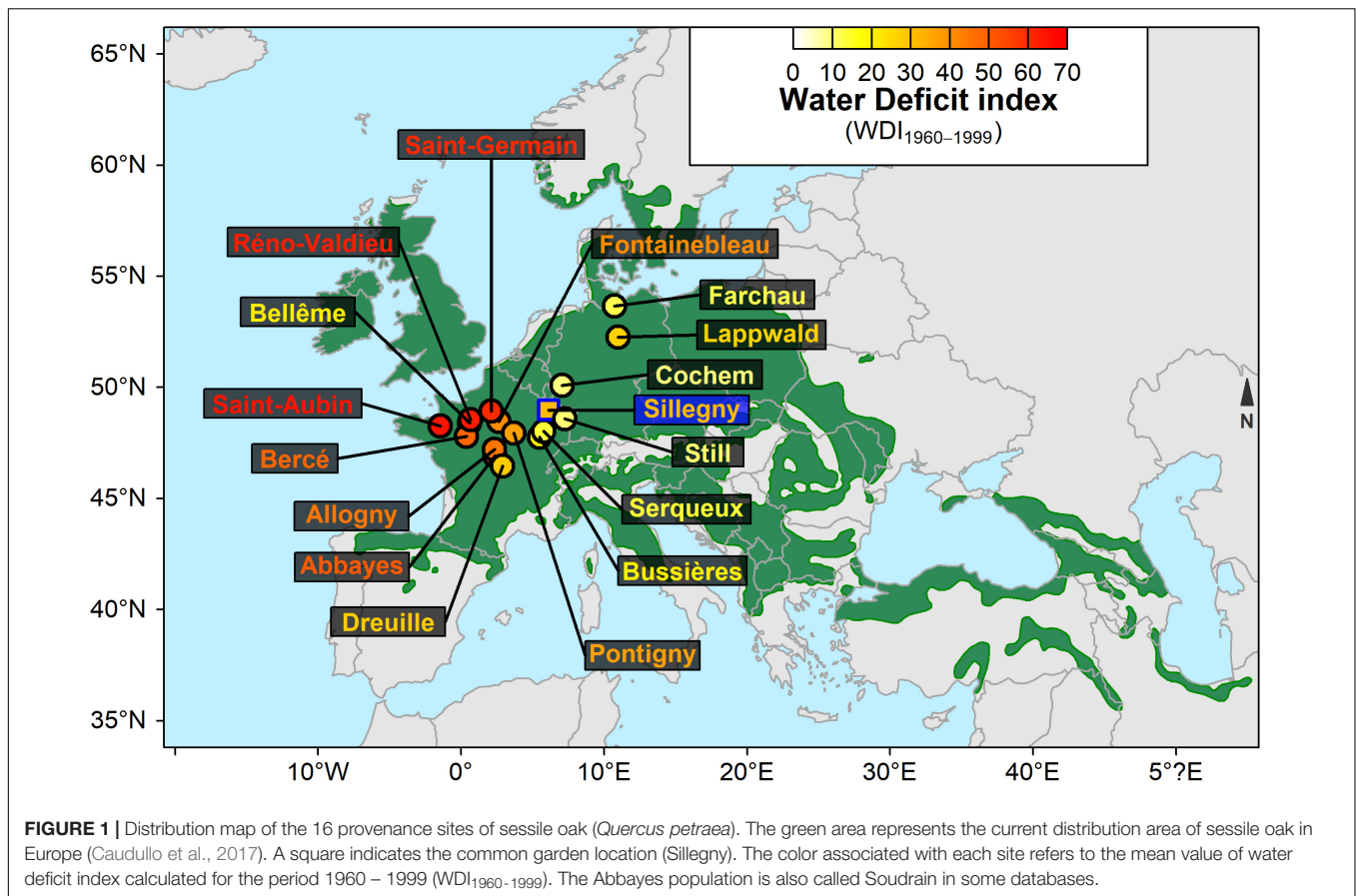## MATERIALS AND METHODS

Trial Description

Open-pollinated seeds were collected in 1989 from one population in each of 64 populations across the distribution area of sessile oak [*Quercus petraea* (Mattuschka) Lieblein, 1784] (Sáenz-Romero et al., 2017; Torres-Ruiz et al., 2019; Bert et al., 2020). After sowing and raising in a nursery, 3-year-old seedlings were planted in March 1993 in a common garden in Sillegny, France (lat. 48° 59' 24" N, long. 6° 7' 56" E, alt. 201 m). A complete randomized block design was used to account for within-site variation, and incomplete micro-blocks were nested in the blocks. Each micro-block consisted of eight plots of 24 oaks from the same population planted 1.75 m × 3 m apart (initial stand density: 1905 trees.ha^{-1}). Survival, height, and diameter at breast height were measured four times between 1993 and 2015. In 2015, the first stand thinning was realized during which trees from 16 among the 64 populations were sampled. The populations were selected according to two criteria: (i) maximizing the variability of pedoclimatic conditions among population sites (**Figure 1** and **Supplementary Table 1**), and (ii) maximizing the variability of growth performances (height and diameter) among transplanted populations at Sillegny. In addition, because genetic variability has been completely reshaped by the last postglacial recolonization, in particular by local selection pressures (Kremer, 2000), the choice of the selected populations was restricted to those belonging to a unique lineage originating from an Iberian refugium (Petit et al., 2002).

Water Deficit Index Calculation

Annual soil moisture in the 16 provenance sites and in the common garden was quantified by Water Deficit Index (WDI, dimensionless) estimated by modeling daily water balance with BILJOU© (Granier et al., 1999[1]). WDI integrates the precocity, the duration, and the intensity of the annual soil water deficit, which is considered to occur when the daily soil relative extractable water (REW) drops below a threshold of 40% (Granier et al., 1999). Daily meteorological data, soil properties, and forest stand characteristics (i.e., evaporative surface) are needed to run BILJOU©.

Each provenance site was visited in 2016–2017 in order to collect soil for a detailed analysis. For both common garden and provenance sites, the soil profile and the rooting depth were described. At least three soil sampling points were taken to verify soil plot homogeneity. Soil samples from each sampling point were then grouped by soil horizon for analysis at the LAS laboratory (INRAE). Particle size distribution analysis (NF X31-107) and organic carbon (ISO 14235) were measured to calculate the plant-available water capacity (PAWC) of the soil using the pedotransfer function of Al Majou et al. (2007). Bulk density was also calculated from organic carbon measurements using the

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[1] https://appgeodb.nancy.inra.fr/biljou/

FIGURE 1 | Distribution map of the 16 provenance sites of sessile oak (*Quercus petraea*). The green area represents the current distribution area of sessile oak in Europe (Caudullo et al., 2017). A square indicates the common garden location (Sillegny). The color associated with each site refers to the mean value of water deficit index calculated for the period 1960 – 1999 (WDI$_{1960-1999}$). The Abbayes population is also called Soudrain in some databases.

pedotransfer function of Manrique and Jones (1991). In addition, pH water and pH KCl (ISO 10390), Cation Exchange Capacity (CEC, ISO 23470), and nitrogen (ISO 13878) were measured to characterize differences in soil fertility among sites.

The different horizon depths and thicknesses were harmonized by applying a spline approach (Bishop et al., 1999) to obtain a topsoil (0–30 cm) and a subsoil (>30 cm-rooting depth) layers. Splines were fitted to the data using the *mpspline* function in the *GSIF* package in R (Hengl et al., 2017). As previously described in Jonard et al. (2017), stocks of organic carbon and nitrogen of topsoil and subsoil were calculated by taking into account dry bulk density, concentrations of organic carbon and nitrogen, the thickness of this layer, and the volume of coarse element (>2 mm).

The daily meteorological data (wind speed at 2 m, precipitation, average temperature, relative humidity, and sunshine duration) were obtained by requesting the SAFRAN meteorological analysis system for French sites (Quintana-Seguí et al., 2008) and Deutscher Wetterdienst (DWD[2]) for German sites, from the 1st January 1960 to the 31th December 1999. A maximum LAI (Leaf Index Area) of 6 m^2 of foliage per m^2 of soil was set for each stand based on visual evaluation in the common garden site and estimation in the provenance sites. For each site, the average days of budburst and leaf fall were

[2]https://www.dwd.de/DE/Home/home_node.html

estimated with the CASTANEA model (Dufrêne et al., 2005) and were inputted into BILJOU© to restrict the calculation of WDI to the leafy period. For each year from 1960, an annual WDI value was modeled, and the average over the 1960–1999 period (WDI$_{1960-1999}$) was used to characterize the long-term mean pedoclimate of each site. Saint-Aubin (WDI$_{1960-1999}$ = 65.75) was the driest site whereas Cochem (WDI$_{1960-1999}$ = 8.90) was the wettest one (**Supplementary Table 1**). The drier sites (i.e., high WDI$_{1960-1999}$ values) appeared to be also those with the largest range of interannual variations in WDI (**Supplementary Figure 1**). In order to compare with other studies, two other drought indices were also used to characterize the sites (**Supplementary Table 1**): aridity index (AI) and summer heat:moisture index (SHM). Both require only meteorological data. AI was calculated as the ratio between mean annual precipitation and mean annual potential evapotranspiration (Torres-Ruiz et al., 2019), and SHM as the ratio between the mean temperature of the warmest month and the mean summer precipitation (May to September) divided by 1,000 (George et al., 2020). In our study, WDI$_{1960-1999}$ appeared only slightly correlated with AI and SHM (R^2 = 0.373, p = 0.012 and R^2 = 0.378, p = 0.112, respectively; n = 16) while AI and SHM were highly correlated (R^2 = 0.804, p < 0.0001, n = 16).

In order to evaluate tree plasticity of WUE$_i$ in response to water availability, three tree rings corresponding to years with contrasted WDI were analyzed. In the common garden of

Sillegny, the canopy started to close after 2007, resulting in a declining trend in radial growth for all trees. As competition for light would strongly affect $\delta^{13}C$ (Stokes et al., 2010), the selection of tree rings was restricted to years before 2007. Based on WDI in Sillegny, the years 2000, 2003, and 2005 were selected (**Figure 2**). In contrast with the wet 2000 year (WDI = 2.7), 2003 was a severe dry year, with a long and strong drought period (130 days) resulting in an annual WDI of 68.7, while 2005 appeared moderately dry with a drought period of similar length (135 days) but less intense (WDI = 49.4).
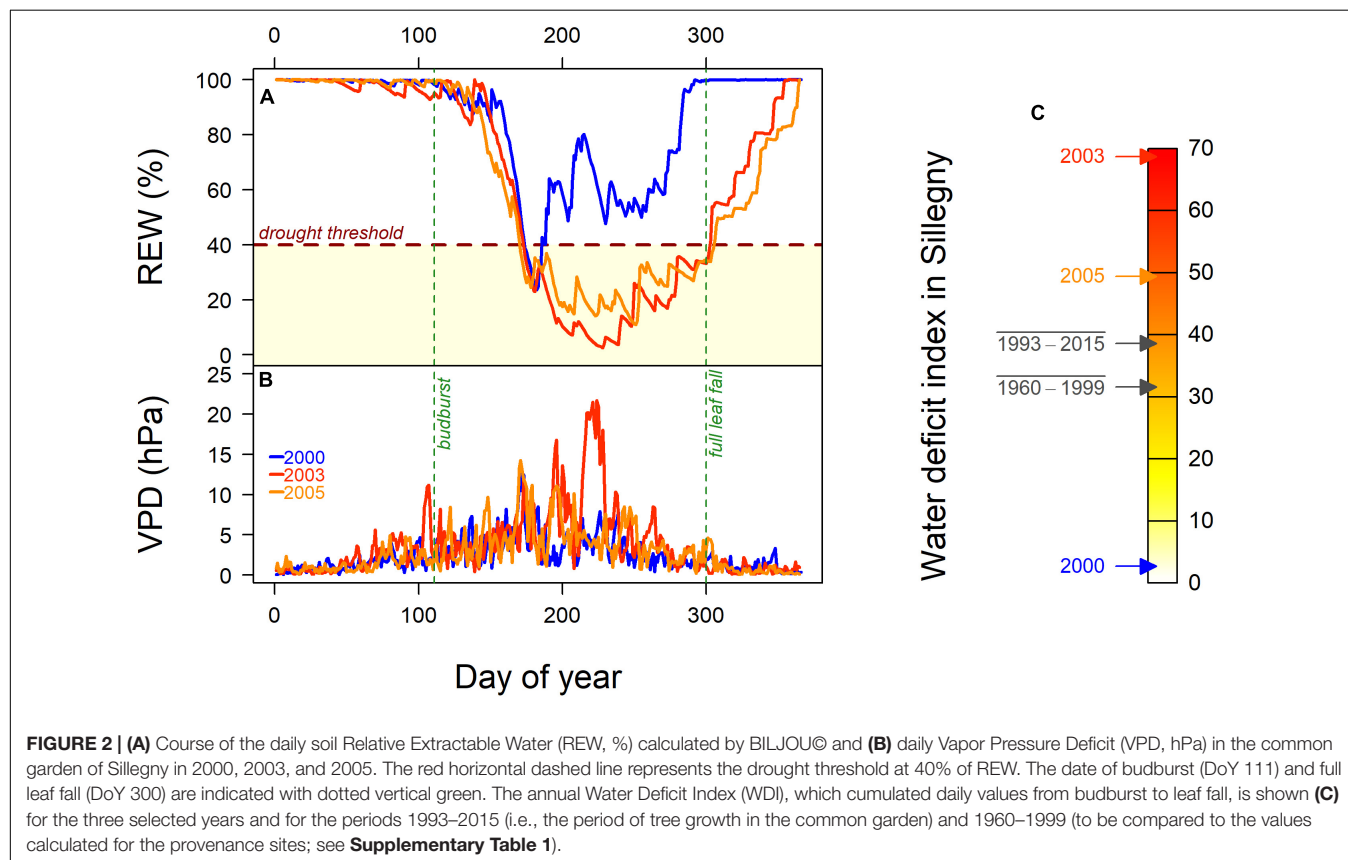
Tree Sampling

The sampling was done during the winter of 2014–2015 when the first thinning operation was planned to remove one in two trees within the common garden plots. Stem disks were collected from a selection of these felled trees. For each population, 30 trees were selected among the different plots, except for four populations (Pontigny, Allogny, Bussières, and Serqueux) where 60 trees were selected to better characterize the diversity within populations (**Supplementary Table 2**). The selection focused primarily on the tree social status, visually assessed before sampling, in 2014 (thus after canopy closure), favoring when possible dominant trees to avoid additional microclimate variability which could affect $\delta^{13}C$ (McDowell et al., 2011) and growth (Trouvé et al., 2015; Alfaro-Sánchez et al., 2020). However, the constraints of systematic thinning forced the selection of some codominant (37%) and suppressed trees (14%)

in order to reach the required sample size for each population (**Supplementary Table 2**). Finally, 595 trees belonging to 16 populations were sampled from 148 single populations plots dispersed over 66 micro-blocks, nested within four large blocks (**Supplementary Figure 2**).

Growth Data

From each stem disk, two opposing laths were cut and shaped with a double-bladed saw. Each lath was used for wood micro-density, radial growth, and carbon isotope composition ($\delta^{13}C$) measurements. Wood micro-density profile was first obtained by exposing the 2 mm-thick laths to X-rays. Ring widths (RW, mm) were measured manually from the obtained wood micro-density profile. The RW series were cross-dated with specific pointer years (i.e., narrow rings in 1995, 1998, and 2003 and wide rings in 2004 and 2007). For a complete description, see Bert et al. (2020). In order to remove any growth trends (mainly due to ontogenic and stand characteristics) and only keep the inter-annual variations, each individual rings series was detrended with a cubic smoothing spline (with a wavelength cutoff of 0.5 and a rigidity of 20 years). The remaining first-order auto-correlation was removed with *dplR* package (Bunn, 2008) to obtain a detrended, dimensionless radial growth index (GI, dimensionless), zero-centered, and normally distributed. In short, RW was the preferred variable for comparison among populations and social status, and GI was retained when comparing years.

FIGURE 2 | (A) Course of the daily soil Relative Extractable Water (REW, %) calculated by BILJOU© and **(B)** daily Vapor Pressure Deficit (VPD, hPa) in the common garden of Sillegny in 2000, 2003, and 2005. The red horizontal dashed line represents the drought threshold at 40% of REW. The date of budburst (DoY 111) and full leaf fall (DoY 300) are indicated with dotted vertical green. The annual Water Deficit Index (WDI), which cumulated daily values from budburst to leaf fall, is shown **(C)** for the three selected years and for the periods 1993–2015 (i.e., the period of tree growth in the common garden) and 1960–1999 (to be compared to the values calculated for the provenance sites; see **Supplementary Table 1**).

Tree-Ring Carbon Isotope Composition

Tree rings corresponding to the years 2000, 2003, and 2005 were cut with a scalpel under a binocular and were milled 1.5 min at 30 Hz in a ball mill (MM200, Retsch GmbH, Haan, Germany). Subsamples of 1 ± 0.2 mg were measured with a continuous-flow elemental analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an isotope ratio mass spectrometer (IsoPrime 100, Isoprime Ltd, Cheadle, United Kingdom). Carbon isotope composition is expressed in delta notation ($\delta^{13}C$, ‰) relative to the Pee Dee Belemnite standard. The precision of the $\delta^{13}C$ measurements, calculated as the standard deviation of 234 repetitions of a laboratory-working standard, was 0.11‰.

In tree-ring isotopes studies, analysis on cellulose was sometimes preferred as compared to whole wood, whose varying composition of cellulose and lignin could affect the $\delta^{13}C$ signal (Weigt et al., 2015). In order to evaluate this potential bias, a preliminary test was run on a subsample of 10 individuals selected for a large range of wood micro-density (as a surrogate for lignin content), including three measurements per tree (i.e., rings 2000, 2003, and 2005). Alpha-cellulose was extracted from whole wood using a variant of the Jayme/Wise methods, as described in Richard et al. (2014), which uses successive steps: solvents and boiled water to remove extractives (extractives-free wood), then acidified sodium chlorite to digest the lignin, and finally alkaline solution to remove the hemicelluloses and produce the "analytical α-cellulose." The lignin content was carried out on dry extractives-free wood sample and determined by a gravimetric analysis of 72% sulfuric acid-insoluble lignin (Klason lignin), according to the ASTM D1106-96(2007), Standard Test Method for Acid-Insoluble Lignin in Wood (ASTM International, West Conshohocken, PA, 2007, United States[3]). $\delta^{13}C$ was measured on whole wood, α-cellulose and lignin. Compared to α-cellulose, an average depletion in ^{13}C of 0.83‰ and 2.77‰ were observed in whole wood and Klason lignin, respectively. However, differences between (i) wood and α-cellulose and (ii) lignin and α-cellulose were constant (i.e., the slope of their relationship was not significantly different from 1: $p = 0.730$ and $p = 0.975$, respectively) and not significantly related to the lignin content of the samples (**Supplementary Figure 3**). Accordingly, we decided to perform the $\delta^{13}C$ analyses on whole wood.

Plasticity Index

For both $\delta^{13}C$ and GI, a plasticity index was calculated to quantify the change in $\delta^{13}C$ and GI between the wet year and the moderate or severe dry years. The difference of $\delta^{13}C$ (GI) values between 2005 and 2000, hereafter named $\delta^{13}C_{2005-2000}$ ($GI_{2005-2000}$), characterized the plasticity of $\delta^{13}C$ (GI) to moderate drought, whereas the plasticity of $\delta^{13}C$ (GI) to severe drought was calculated as the difference between $\delta^{13}C$ (GI) values in 2003 and 2000, hereafter named $\delta^{13}C_{2003-2000}$ ($GI_{2003-2000}$). The term "drought intensity," used in this paper, refers to these two responses (to moderate and severe drought compared to the control year). The larger the plasticity index of $\delta^{13}C$ or of GI, the

more $\delta^{13}C$ increased or GI decreased in response to the drought compared to the wet year. It is then expected that the plasticity index of $\delta^{13}C$ in response to drought will be positive, whereas the plasticity index of GI will be negative.

Data Analysis

All statistical analyses were performed with R-environment (R Core Team, 2022[4]). Variations in trait expressions and plasticity were tested with a linear mixed model using the *nlme* package (Pinheiro et al., 2020). The interactions between factors were first included in the model, which was later simplified by minimizing AIC (Akaike Information Criteria) to select the most parsimonious model:

$$
\begin{aligned}
Y_{ijklm} = \mu + P_i + T_j + \left(P_i {}^* T_j\right) &+ S_m \\
&+ B_k + M_{kl} + I_{klm} + \varepsilon_{ijklm}
\end{aligned} \tag{1}
$$

With:

- Y_{ijklm} = observed trait or trait plasticity index of the tree m from the population i, block k, and micro-block l for the year j or in response to the drought intensity j compared to the control year (2000);
- μ = overall mean;
- P_i = population effect of the ith population;
- T_j = effect of the jth year (2000, 2003, 2005) or of the jth pair (2000–2003, 2000–2005);
- $(P_i {}^* T_j)$ = effect of the interaction between population and year or between population and drought intensity;
- S_m = social status in 2014 effect of the mth tree;
- B_k = block random effect of the kth block;
- M_{kl} = micro-block random effect at the lth micro-block nested within the kth block;
- I_{klm} = tree random effect of the mth tree nested in the lth micro-block nested within the kth block;
- ε_{ijklm} = error term.

The contribution of fixed and random factors in the model was, respectively, evaluated by marginal and conditional r-squared (Nakagawa et al., 2017), computed with the *MuMIn* package (Barton, 2020). Because the design of this study is unbalanced (i.e., different proportions of dominant, co-dominant, and suppressed trees among populations), the Tukey *post-hoc* test was done on the estimated marginal means (Searle et al., 1980) obtained by using the *emmeans* package. All mean values of traits and plasticity indices hereafter are therefore estimated marginal means (emmeans). These marginal mean values of traits and plasticity indices per population were correlated with the average $WDI_{1960-1999}$ and pedoclimatic parameters of provenance sites over the period 1960–1999 (summarized in **Supplementary Table 1**). The correlations between $\delta^{13}C$ and growth index and between their plasticity indices were tested at both population and individual levels (for each population separately).

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[3]www.astm.org

[4]https://www.R-project.org/

RESULTS

Social Status Effects on the Traits and Their Plasticity

Overall, the social status had a significant effect on both $\delta^{13}C$ and RW (**Table 1**), with no significant interaction with the year (not shown). The dominant trees displayed a significantly 0.21‰ less negative $\delta^{13}C$ than the codominant trees that were not significantly different from suppressed trees (**Table 2**). The dominant trees also had a higher RW than the codominant trees, which in turn had significantly higher values than the suppressed trees. In contrast, $\delta^{13}C$ and GI plasticity indices (i.e., the variation of trait expression between dry and wet years) were not significantly affected by social status (**Table 1**).

Among-Year Trait Variation

The year effect was significant for $\delta^{13}C$ (**Table 1**). The least negative $\delta^{13}C$ values were observed in 2003, corresponding to the driest year (WDI = 68.7; **Figure 2**), and the most negative values in 2000, when WDI was the lowest, i.e., 2.7 (with an average difference of 1.08‰; **Table 2**). The moderately dry year 2005 (WDI = 49.4) led to $\delta^{13}C$ values closer to those of 2000 (+0.16‰), although significantly different (**Table 2**). The plasticity index of $\delta^{13}C$ was significantly higher when the drought intensity was severe than moderate (**Table 2**).

The year effect also influenced RW (**Table 1**), whose values showed an overall increase until 2007 (**Table 2** and **Supplementary Figure 4**). GI, which by construction showed interannual variations from which longer-term trends were

removed, showed the lowest mean value in 2003 and the highest in 2000 (with a difference of 0.36; **Table 2**). In 2005, GI mean was just slightly negative (–0.01; **Table 2**) and significantly different from 2003 and 2000. The plasticity index of GI was significantly higher when the drought intensity was severe than moderate (**Table 2**).

Among-Population Trait Variation

The population effect on $\delta^{13}C$ was significant, although moderate, and there was only a weak evidence for an effect of the interaction with the year ($p = 0.024$; **Table 1**). In 2000, when the water deficit was almost non-existent, the trees from Fontainebleau displayed significantly less negative $\delta^{13}C$ than those from Dreuille and Farchau (with a difference of 0.61–0.63‰; **Supplementary Table 3**). In 2003, during the driest studied year, only the trees from Farchau had significantly more negative $\delta^{13}C$ than those from Pontigny and Bercé (a difference of 0.58–0.62‰; **Supplementary Table 3** and **Figure 3**). In the moderately dry year 2005, the trees from Saint-Germain and Farchau displayed significantly more negative $\delta^{13}C$ values than those from Still (a difference of 0.61–0.64‰; **Supplementary Table 3**). Overall, Farchau showed consistently the most negative $\delta^{13}C$. The $\delta^{13}C$ values observed in 2003 were strongly and positively correlated with those observed in 2005 ($R = 0.84$; **Figure 4**) whereas correlations between 2000 values and 2003 and 2005 appeared lower, although significant ($R = 0.68$ and $R = 0.55$, respectively).

The population effect was low, yet significant, on RW but not on GI (**Table 1**). A significant interaction with the

TABLE 1 | Variable significance and model performance for $\delta^{13}C$, ring width (RW), growth index (GI), $\delta^{13}C$ plasticity index, and GI plasticity index.

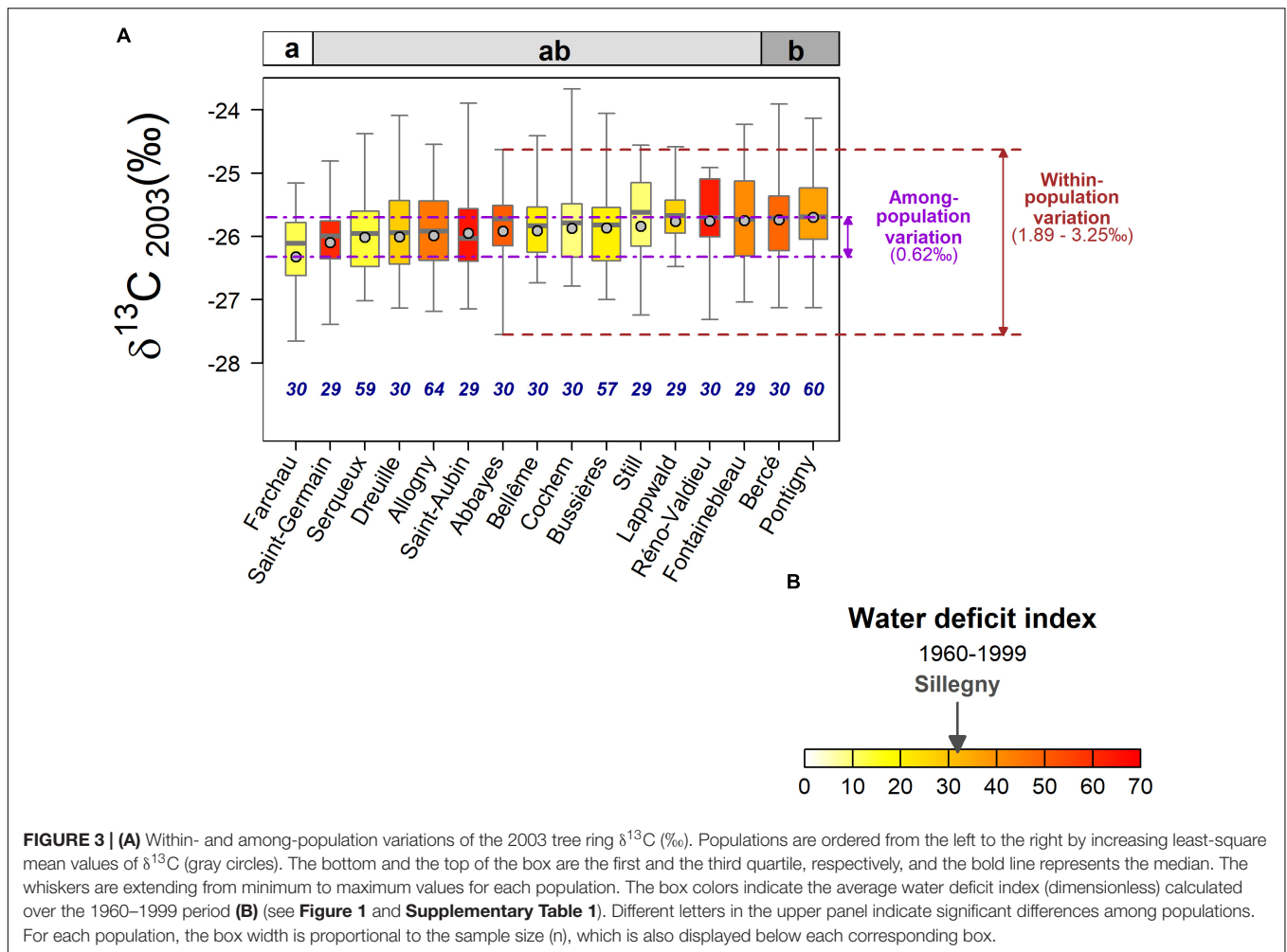|	δ^{13}C			RW			GI			δ^{13}C plasticity index			GI plasticity index		
Population (P)	2.4	**	(15, 510)	1.9	*	(15, 511)	1.0	ns	(15, 511)	1.4	ns	(15, 509)	1.4	ns	(15, 515)
Year/Drought intensity (T)	1058.2	***	(2, 1152)	131.8	***	(2, 1156)	50.8	***	(2, 1156)	1806.6	***	(1, 575)	20.3	***	(1, 582)
P*T	1.6	*	(30, 1152)	2.3	***	(30, 1156)	2.7	***	(30, 1156)	1.2	ns	(15, 575)	3.7	***	(15, 582)
Social status in 2014 (S)	12.2	***	(2, 510)	81.7	***	(2, 511)	0.4	ns	(2, 511)	2.1	ns	(2, 509)	0.3	ns	(2, 515)
Marginal R^2	0.389			0.259			0.099			0.371			0.049		
Conditional R^2	0.750			0.650			0.162			0.800			0.689		
SD_{Block}	0.013			0.168			0.090			0.045			0.160		
$SD_{Micro-block(Block)}$	0.000			0.178			0.134			0.187			0.296		
$SD_{Tree[Micro-block(Block)]}$	0.492			0.764			0.000			0.472			0.707		

*For each variable, F-value, p-value and degrees of freedom in the numerator (numDF) and denominator (DenDF) are provided. For p-values, ns : p > 0.05; * : 0.01 < p < 0.05; ** : 0.001 < p < 0.01 ; *** : p < 0.001.*

TABLE 2 | Estimated marginal means (emmeans ± SE) and Tukey test group by year and by social status in 2014 for $\delta^{13}C$, ring width (RW), and growth index (GI); by drought intensity and by social status in 2014 for the plasticity indices of $\delta^{13}C$ and GI.

		δ^{13}C (‰)	RW (mm)	GI	δ^{13}C plasticity index (‰)	GI plasticity index
Year	2000	–26.98 ± 0.03[a]	3.35 ± 0.10[a]	0.20 ± 0.06[c]	–	–
	2003	–25.90 ± 0.03[c]	3.72 ± 0.10[b]	–0.16 ± 0.06[a]	–	–
	2005	–26.82 ± 0.03[b]	4.11 ± 0.10[c]	–0.01 ± 0.06[b]	–	–
Drought intensity	2003–2000	–	–	–	1.05 ± 0.05[a]	–0.34 ± 0.10[a]
	2005–2000	–	–	–	0.13 ± 0.05[b]	–0.19 ± 0.10[b]
Social status in 2014	Suppressed	–26.68 ± 0.07[a]	3.10 ± 0.14[a]	0.01 ± 0.06[a]	0.56 ± 0.07[a]	–0.22 ± 0.13[a]
	Codominant	–26.62 ± 0.04[a]	3.64 ± 0.11[b]	0.03 ± 0.06[a]	0.56 ± 0.05[a]	–0.27 ± 0.11[a]
	Dominant	–26.41 ± 0.03[b]	4.43 ± 0.10[c]	0.00 ± 0.05[a]	0.65 ± 0.05[a]	–0.30 ± 0.10[a]

Different letters indicate significant differences.

FIGURE 3 | (A) Within- and among-population variations of the 2003 tree ring δ^{13}C (‰). Populations are ordered from the left to the right by increasing least-square mean values of δ^{13}C (gray circles). The bottom and the top of the box are the first and the third quartile, respectively, and the bold line represents the median. The whiskers are extending from minimum to maximum values for each population. The box colors indicate the average water deficit index (dimensionless) calculated over the 1960–1999 period **(B)** (see **Figure 1** and **Supplementary Table 1**). Different letters in the upper panel indicate significant differences among populations. For each population, the box width is proportional to the sample size (n), which is also displayed below each corresponding box.

year effect was observed for both RW and GI (**Table 1**). Particularly, if no significant difference in GI was detected among populations in 2000, trees from Fontainebleau had significantly lower GI in 2003 compared to ten other populations and higher GI in 2005 than those from Dreuille (**Supplementary Table 3**). For all traits, the within-population variations were always higher than the among-population variations (**Supplementary Table 4**).
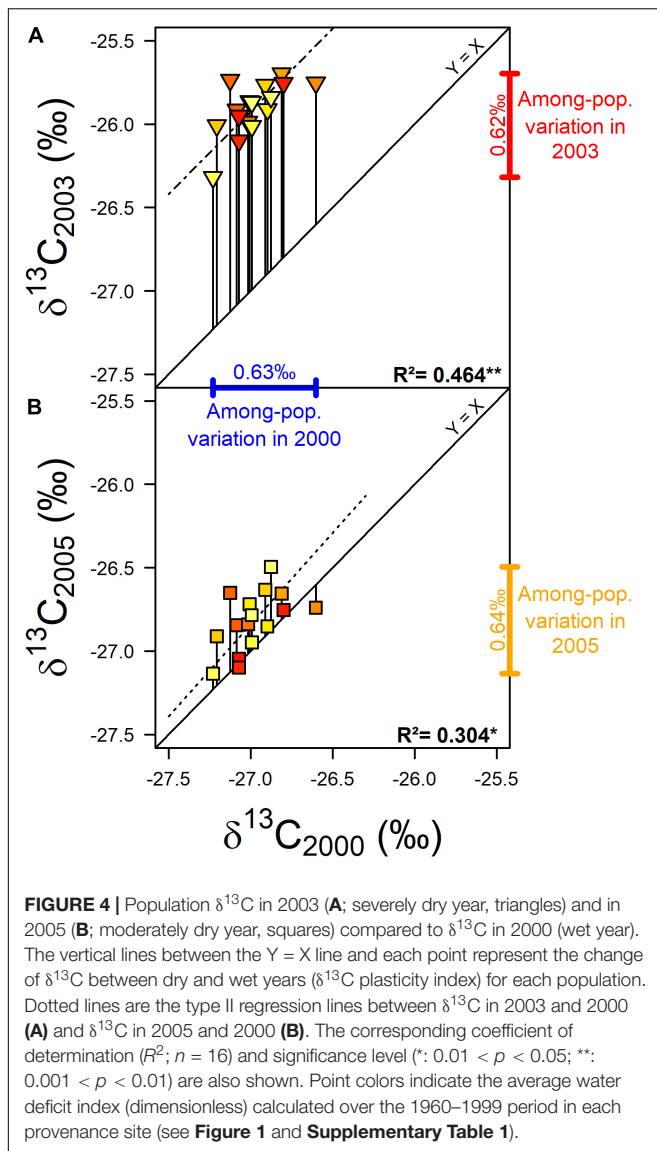
Among-Population Variation in Plasticity Indices

No statistically significant differences of the δ^{13}C plasticity indices were observed among populations (**Table 1** and **Supplementary Table 3**), and the drought intensity × population interaction was also not significant (**Table 1**). Regarding GI plasticity indices, there was globally no significant effect of the population but its interaction with drought intensity effect appeared significant (**Table 1**). Indeed, significant population differences in GI plasticity were detected in response to the severe drought while the response to the moderate drought proved to be uniform among populations. In response to the severe drought, trees from Fontainebleau displayed a larger increase

in GI compared to those from Abbayes, Bercé, and Lappwald (**Supplementary Table 3**).

Relationship Between Among-Population Trait Variation and Provenance Sites Characteristics

Based on $WDI_{1960-1999}$, the common garden of Sillegny appeared in a median position with eight drier and eight wetter provenance sites (**Figure 1**). More negative δ^{13}C values were observed on populations with both lower and higher $WDI_{1960-1999}$ values than Sillegny (**Figure 3**). Regardless of the year or drought intensity considered, no significant relationship was observed between δ^{13}C – or δ^{13}C plasticity – and the $WDI_{1960-1999}$ of the provenance sites ($p > 0.3$). No other pedoclimatic parameters described in **Supplementary Table 1**, including AI and SHM, were significantly related to δ^{13}C. The plasticity in δ^{13}C between the wet and the moderately dry year ($\delta^{13}C_{2005-2000}$) was also not significantly correlated to any pedoclimatic parameters. However, the increase in population mean δ^{13}C between the wet and the severely dry year ($\delta^{13}C_{2003-2000}$) was positively correlated to the stock of organic carbon (C_{org}) in the topsoil (the first 30 cm of depth, see **Supplementary Table 5**) at their provenance sites

FIGURE 4 | Population $\delta^{13}C$ in 2003 (**A**; severely dry year, triangles) and in 2005 (**B**; moderately dry year, squares) compared to $\delta^{13}C$ in 2000 (wet year). The vertical lines between the Y = X line and each point represent the change of $\delta^{13}C$ between dry and wet years ($\delta^{13}C$ plasticity index) for each population. Dotted lines are the type II regression lines between $\delta^{13}C$ in 2003 and 2000 (**A**) and $\delta^{13}C$ in 2005 and 2000 (**B**). The corresponding coefficient of determination (R^2; n = 16) and significance level (*: 0.01 < p < 0.05; **: 0.001 < p < 0.01) are also shown. Point colors indicate the average water deficit index (dimensionless) calculated over the 1960–1999 period in each provenance site (see **Figure 1** and **Supplementary Table 1**).

parameters described in **Supplementary Table 5** (Root, C/N, pH_{H2O}, pH_{KCl}, CEC, N stock, and PAWC).

Within-Population Trait Variation

When analyzing variations in traits and plasticity indices with the mixed model, the conditional R^2 was always approximately twice the marginal R^2 (**Table 1**), which suggests that random effects explained as much variability as fixed effects. Among random effects, the tree effect (in the micro-block nested in the block) had the largest standard deviation for $\delta^{13}C$, RW, $\delta^{13}C$ plasticity index, and GI plasticity index (**Table 1**). Because the detrending process included the centering of the data for each tree independently, the standard deviation due to tree effect was, as expected, zero for GI (**Table 1**).

Growth – $\delta^{13}C$ Relationship

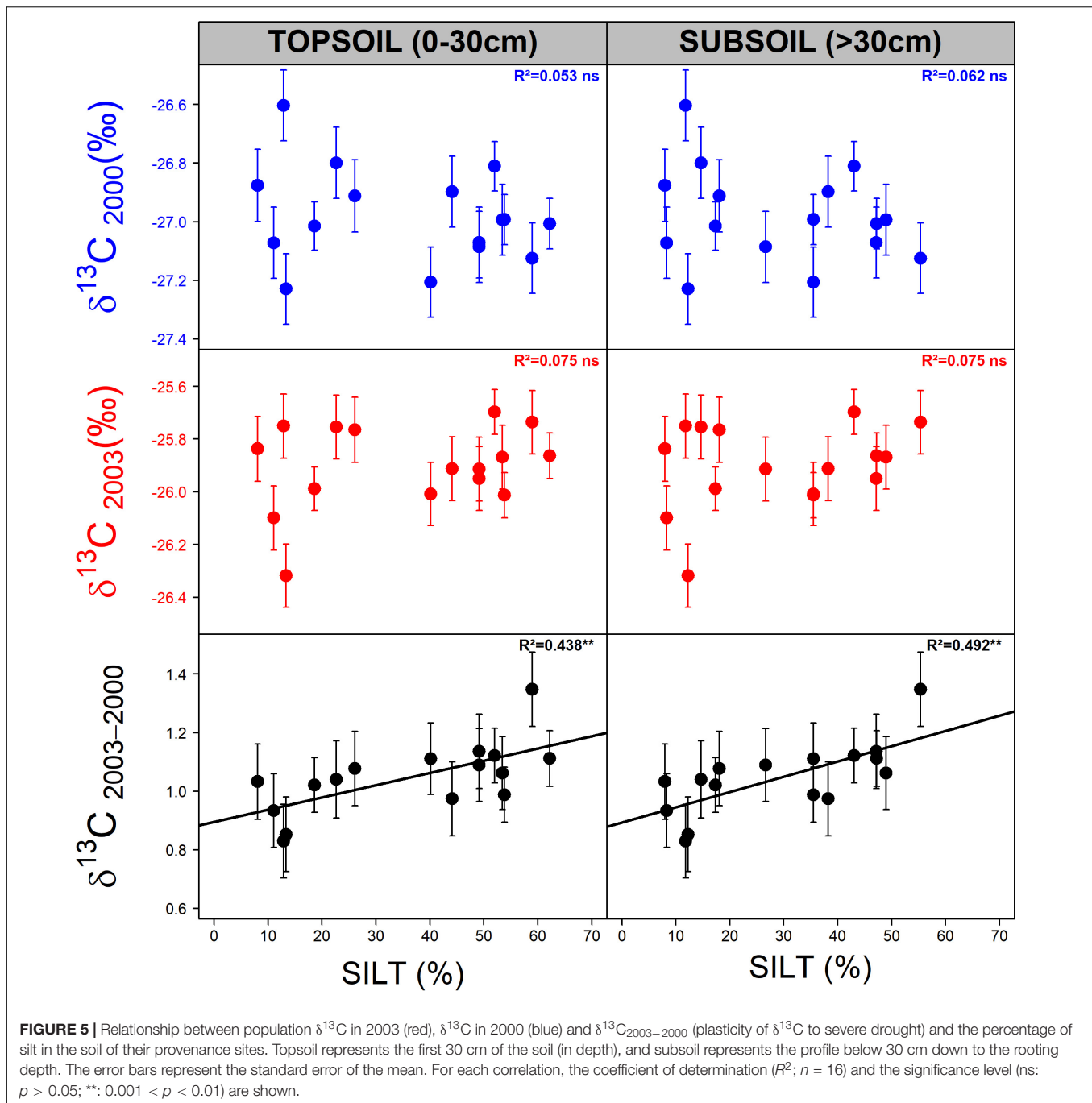During the wet 2000 year, the populations with the highest growth index also displayed the less negative $\delta^{13}C$ (R^2 = 0.343; p = 0.0171; **Figure 6**). In 2000, even if no significant difference was detected among populations for GI, the trees from Dreuille, which showed the most negative $\delta^{13}C$ mean value, showed a slightly negative GI, and the trees from Fontainebleau, which presented the least negative $\delta^{13}C$ mean value, showed the highest GI mean value (**Supplementary Table 2**). Especially, trees from Fontainebleau, which showed the less negative $\delta^{13}C$ mean value in 2000, showed the lowest GI in 2003. During dry years, in 2003 and 2005, the among-population relationships between $\delta^{13}C$ and GI were not significant (p > 0.65). However, a positive significant correlation was found among populations between the plasticity indices of $\delta^{13}C_{2003-2000}$ and $GI_{2003-2000}$ (R^2 = 0.429; p = 0.0059). It is also noticeable that populations with high $\delta^{13}C$ in the wet 2000 year tended to have low GI in the dry 2003 years (R^2 = 0.293; p = 0.0303).

At the within-population level, correlations between $\delta^{13}C$ and GI in 2000 were significant for the four populations where 60 trees were sampled (instead of 30 for the other populations) as well as the Lappwald population (0.103 < R^2 < 0.295, 0.0004 < p < 0.0166). A positive correlation between $\delta^{13}C_{2003-2000}$ and $GI_{2003-2000}$ was observed within 10 out of 16 populations (including all populations with n ≈ 60, 0.118 < R^2 < 0.379, 0.000001 < p < 0.0219).

DISCUSSION

Oaks Increased Intrinsic Water-Use Efficiency in Response to Low Water Soil Availability

Trees, as long-lived organisms, need to be able to respond to their environment by adjusting their physiology and their development through plasticity (Scheiner, 1993). By measuring functional traits on tree rings, one is able to observe retrospectively the plastic responses of trees over the years and relate them to environmental variables. A significant relationship between wood carbon isotope composition ($\delta^{13}C$) and WUE$_i$ was

(respectively, R^2 = 0.464, p = 0.0037). Whether in topsoil or subsoil (**Supplementary Table 5**), population $\delta^{13}C_{2003-2000}$ was also positively correlated to proportion of silt (**Figure 5**; topsoil: R^2 = 0.438, p = 0.0052; subsoil: R^2 = 0.492, p = 0.0025) and negatively correlated to the proportion of sand in the soil at their provenance sites (topsoil: R^2 = 0.335, p = 0.0189; subsoil: R^2 = 0.300, p = 0.0279). No significant relationship was found between the pedoclimate of the provenance sites and the radial growth (i.e., RW and GI) of the populations in the common garden. However, positive correlations were found between the mean population plasticity indices of GI to drought ($GI_{2003-2000}$ and $GI_{2005-2000}$) and the average air vapor pressure deficit from May to July for the period 1960–1999 (D0507) of the provenance sites (respectively, R^2 = 0.289, p = 0.0318 and R^2 = 0.338, p = 0.0182). No significant relationship was found between the population means of the measured traits (i.e., $\delta^{13}C$, GI, and their plasticity indices) and the remaining soil characteristic

FIGURE 5 | Relationship between population $\delta^{13}C$ in 2003 (red), $\delta^{13}C$ in 2000 (blue) and $\delta^{13}C_{2003-2000}$ (plasticity of $\delta^{13}C$ to severe drought) and the percentage of silt in the soil of their provenance sites. Topsoil represents the first 30 cm of the soil (in depth), and subsoil represents the profile below 30 cm down to the rooting depth. The error bars represent the standard error of the mean. For each correlation, the coefficient of determination (R^2; $n = 16$) and the significance level (ns: $p > 0.05$; **: $0.001 < p < 0.01$) are shown.

demonstrated for white oak species (Ponton et al., 2002; Roussel et al., 2009).

In our study, the moist year 2000 was considered as a control compared to the moderately dry year 2005 and the severely dry year 2003. $\delta^{13}C_{2003-2000}$ and $\delta^{13}C_{2005-2000}$, used as plasticity indices of $\delta^{13}C$ in response to severe and moderate drought, respectively, were as expected positive (**Table 2**). Indeed, for most plants and under most circumstances, a decrease in soil water availability is immediately followed by stomatal closure, resulting in an increase in WUE$_i$ and $\delta^{13}C$ (Farquhar and Sharkey, 1982;

Farquhar et al., 1989; Brendel and Epron, 2022), due to the non-linear relationship between A and g_{sw} (**Supplementary Figure 5**). However, the $\delta^{13}C$ values observed in 2005 were much closer (although significantly higher) to those of the wet year 2000 than those of the dry year 2003. It has been demonstrated, especially for sessile oak, that the stomatal closure occurs gradually below a drought threshold of 40% REW (Bréda et al., 1993, 1995; Triboulot et al., 1996). In 2005, the drought lasted longer than in 2003 but the daily REW never dropped below 10% contrary to 2003 with 33 consecutive days below 10% (**Figure 2**). In

FIGURE 6 | Correlation between the least-square means of $\delta^{13}C$ and growth index (GI) in 2000 (blue circles), 2003 (red triangles), and 2005 (orange squares). The error bars represent the standard error of the mean. The blue line indicates the significant among-population relationship between the two traits in 2000 ($n = 16$) with its coefficient of determination (R^2) and significance level (*: $0.01 < p < 0.05$). The green arrow represents the direction of $\delta^{13}C$ and growth index variations in response to drought. The type II regression between the two traits in 2003 and 2005 is not shown because not significant. Symbol fill colors indicate the average water deficit index (dimensionless) calculated over the 1960 – 1999 period (**Figures 1**, **3**).

addition, air vapor pressure deficit (VPD) reached very high values in August 2003 (>15 hPa) whereas much lower ones were observed at the same period in both 2005 and 2000 (**Figure 2**). A less negative $\delta^{13}C$ in 2003 was therefore expected but the relatively low value observed in 2005, although clearly marked by a water deficit, remained surprising. It could suggest that for these young oak trees, REW needs to decrease below 10% for a strong stomatal reaction.

Compared to 2000, the growth index in 2003 was reduced. The concomitant increase in $\delta^{13}C$ in 2003 could indicate either a stomatal closure or an increase in A, the latter being not likely to happen under the estimated soil water deficit. Thus, although a slight decrease in A (hidden by a much larger decrease in g_{sw}) cannot be ruled out, the main reason for the decrease in radial growth might be growth inhibition at low water potentials (Fatichi et al., 2014).

Differentiation in Intrinsic Water-Use Efficiency Among Sessile Oak Populations Was Low and Not Related to the Pedoclimates of the Provenance Sites

Using a common garden, with the assumption that all trees grow in a homogeneous environment, allows separating the effects of genetic diversity from those of the environment among the

studied populations (Wang et al., 2010). Although significant differentiations in $\delta^{13}C$ were detected among populations for the three studied years (**Table 1**), only a few populations differed significantly from the others, with only one (i.e., Farchau) being remarkable for three years with the lowest WUE_i (**Supplementary Table 3**). The $\delta^{13}C$ range of 0.6‰ observed among the studied populations was remarkably constant over the three years, despite their different drought intensities. This variation of 0.6‰ among $\delta^{13}C$ populations found in sessile oak seems to be low compared to the 2‰ observed in *Castanea sativa* (Lauteri et al., 2004). However, such small but significant differences among populations have also been observed in other oak species (0.2‰ for *Quercus suber*, Matías et al., 2019; 0.6‰ for *Quercus variabilis*, Sun et al., 2016; 0.8‰ for *Quercus douglasii*, Rice et al., 1993) and for *Fagus sylvatica* (0.2–1‰, Rose et al., 2009; Robson et al., 2012; Knutzen et al., 2015). In contrast to these studies where $\delta^{13}C$ was measured in leaves, our study is, to our knowledge, the only one to use wood $\delta^{13}C$ to assess WUE_i diversity among populations in the Fagaceae family. While measurements in leaves introduce variability due to the position of the harvested leaves (Le Roux et al., 2001), measuring $\delta^{13}C$ in wood has the advantage of integrating the functioning of the entire canopy (Ponton et al., 2002; Roussel et al., 2009).

Because the selection was restricted to populations from the Iberian post-glaciation recolonization lineage (lineage B, Petit et al., 2002), our population selection did not cover the entire distribution area of sessile oak and excluded the more drought-exposed southern populations. However, Torres-Ruiz et al. (2019) who compared a different selection of populations from the same common garden of Sillegny, including different lineages and populations from Ireland and southern France, did not detect any significant differences in $\delta^{13}C$ among populations. This supports Kremer's (2016) statement that there is no difference in local adaptation between white oak lineages from different glacial refugia.

Detecting a relationship between variations in functional traits among populations and variations in the average environmental conditions at their site of origin would support the hypothesis that variations in these traits have evolved under different local selection pressures. Of all the studies detecting significant population differences for $\delta^{13}C$ or A/g_{sw} on trees, negative (Li et al., 2000; Cregg and Zhang, 2001; Bekessy et al., 2002; Zhang et al., 2005; Duan et al., 2009) as well as positive (Aitken et al., 1995; Guehl et al., 1996; Nguyen-Queyrens et al., 1998; Ferrio et al., 2003; Lauteri et al., 2004; Eriksson et al., 2005; Fan et al., 2008) correlations have been detected between drought indices and population $\delta^{13}C$. This might suggest that there is not a simple relationship between the mean WUE_i of a population and its adaptation to a seasonal dry environment (Brendel and Epron, 2022). In the current study, the pedoclimate of each provenance site was characterized in detail by using the BILJOU© water balance model (Granier et al., 1999), which includes soil features in addition to climatic parameters. The lack of significant correlation between the $\delta^{13}C$ of the 16 populations and the pedoclimatic indices calculated by the model, as well as the raw atmospheric variables and soil characteristics, leads to rejection of our first hypothesis, stipulating that populations

from the driest origins would display the lowest WUE_i. Similar observations were made for *Quercus ilex* (Gimeno et al., 2009) and *Quercus robur* (George et al., 2020) and for conifer species in the *Pinaceae* and *Cupressaceae* families (Zhang and Cregg, 1996).

The estimation of the environmental constraints in the populations based on meteorological data from a relatively recent period (1960–1999) might be temporally disconnected from the actual genetic differentiation, which would have been ongoing over several generations, thus probably several centuries earlier (Saleh et al., 2021). Nevertheless, significant relationships were established for sessile oak between soil water availability at provenance sites and other traits such as height (Bruschi, 2010; Torres-Ruiz et al., 2019; but also see Arend et al., 2011), root–shoot ratio, leaf size, and thickness (Bruschi, 2010) or leaf unfolding and specific leaf area (Torres-Ruiz et al., 2019), demonstrating that sessile oak populations show differentiation in functional traits related to drought adaptation. Bert et al. (2020), in a study partly based on the same experimental design as our study, found that the correlation between radial growth of sessile oak populations and water balance was lower at Sillegny than at the other two common gardens studied, exposed to drier conditions. Therefore, the lack of relationship between populations WUE_i and pedoclimatic conditions at the provenance sites might be related to the relatively low-stress environment of the Sillegny common garden.

The Plasticity of Water-Use Efficiency Is Related to Soil Texture Rather Than WDI$_{1960-1999}$

The phenotypic plasticity of a trait to an environmental change can also be subject to selection and considered as an adaptive trait (Via et al., 1995), resulting in population differences in plasticity, related to environmental differences among provenance sites. In our study, no significant population effect was detected for the plasticity indices of $\delta^{13}C$ to drought (**Table 1** and **Supplementary Table 3**), suggesting that the within-population variance was larger than the among-population differences. However, a significant interaction between drought and population effects was observed for $\delta^{13}C$. Moreover, the population means of $\delta^{13}C_{2003-2000}$ plasticity were correlated to soil texture. No such correlation was detected for the modeled population WDI$_{1960-1999}$, which is based on relatively recent meteorological data. Soil texture is constant over a much longer time period, and might better reflect past selection pressures, which might have resulted in population differences. Populations with a lower $\delta^{13}C_{2003-2000}$ plasticity were originating from sites with a lower proportion of silt (**Figure 6**) and organic carbon (in the topsoil) and a higher proportion of sand. These results are consistent with observations made by Rellstab et al. (2016) who showed a significant association between genetic variation within and across three oak species (including sessile oak) and soil characteristics related to soil aeration and clay content. To our knowledge, there are only few publications that have investigated among-population differences in plasticity of WUE_i to drought. A significant among-population difference in WUE_i plasticity to drought was found for *Quercus suber* (Matías et al., 2019),

where only the southern population had shown a significant $\delta^{13}C$ increase to drought, whereas the northern population did not. However, Gimeno et al. (2009) did not detect a significant population x drought interaction on direct estimates of WUE_i on *Quercus ilex* leaves, suggesting no among-population difference in WUE_i plasticity, whereas significant population differences were shown for absolute values of WUE_i.

Our results suggest that populations from provenance sites on soils with more draining soil texture (i.e., more sand/less silt and soil carbon) showed a less plastic response of WUE_i to the severe 2003 drought at Sillegny, presumably by maintaining their stomata more open. Maintaining stomata open during drought could indicate either higher tolerance for low water potentials, or a larger root system with a lower leaf surface/root surface ratio maintaining the soil water supply. The populations from the provenance sites with more sandy soils might well have evolved toward larger root systems [as for example shown by Matías et al. (2019) for more Southern populations of *Q. suber*] and thereby acquired a different response strategy to soil water deficit compared to populations from provenance sites with a high plant-available water capacity of the soil.

Further, populations originating from provenance sites with the driest atmosphere, based on May-July mean values, decreased less their growth (GI) in the dry years 2003 and 2005 at Sillegny compared to the wet year (2000). This, again, suggests that populations originating from drier sites showed less response to drought in the mesic conditions of Sillegny. Such an among-population variation in the plasticity to VDP provides an interesting outlook, considering the predicted increase in VPD with the ongoing climate change and the concurrently increasing risk of mortality (Grossiord et al., 2020).

Both results, the correlation of mean population plasticity of $\delta^{13}C$ with soil texture and of mean population plasticity GI with atmospheric humidity, suggest that populations from drier environments have evolved different drought response strategies than populations from wetter environments. These differences resulted in a similar variation in WUE_i and growth plasticity for the severe drought year, as GI$_{2003-2000}$ and $\delta^{13}C_{2003-2000}$ were significantly correlated. Whereas during the moderate drought year 2005, a more pronounced reduction in GI was observed compared to the smaller increase in $\delta^{13}C$ (**Table 2** and **Figure 6**). It is likely that under this moderate drought level, leaf gas exchanges were maintained whereas stem growth was decreased (Bogeat-Triboulot et al., 2007).

High Within-Population Variability in Intrinsic Water-Use Efficiency

For woody species, within-population variation in traits is generally larger than among-population variation (Hamrick et al., 1992; Bresson et al., 2011), as also found in this study for $\delta^{13}C$ as an estimator of WUE_i. The experimental design of the common garden in blocks and micro-blocks was made to minimize as much as possible the variation in environmental conditions among trees to improve the detection of genetic variations. However, in addition to the influence of genetic factors on WUE_i, that of variations in the microenvironment, including

those generated by differences in social status, cannot be excluded (McDowell et al., 2003; Niccoli et al., 2020).

In our study, dominant trees expectedly expressed slightly less negative $\delta^{13}C$ (higher WUE_i) values than co-dominant and suppressed trees, probably due to higher overall assimilation rates (Forrester, 2019; Vitali et al., 2021). The attribution of the social status was done in 2014, when the canopy of the plantation was closed, whereas the $\delta^{13}C$ measurements were done on annual rings before canopy closure. However, height measurements taken in 2002 showed that the trees identified as dominant in 2014 were already taller in 2002 (data not shown). Overall, this could suggest that the higher WUE_i of dominant trees is not only due to the direct physiological impacts of competition for light, but might also indicate that the stronger growth of dominant trees might be related to higher photosynthetic capacity. However, no significant social status effect (**Table 1**) and no interaction with drought intensity were found for the plasticity index of $\delta^{13}C$ to drought, supporting the idea that trees with different social status reacted similarly to the studied drought intensities.

In our study, more phenotypic variability in sessile oak $\delta^{13}C$ (thus WUE_i) was found among individuals within the same population than among populations. The among-sibling variation in $\delta^{13}C$ in one full-sib family of *Quercus robur* was more than 3‰ (similar to the range observed within populations in our study, **Supplementary Table 3**), and was strongly genetically controlled (Brendel et al., 2008). Large within-population variability in WUE_i was also reported for *Fagus sylvatica* (Aranda et al., 2017) and *Quercus suber* (Ramirez-Valiente et al., 2010). One reason for this large within-population variability in WUE_i may be the low heritability of WUE_i, demonstrated by Alexandre et al. (2020a) for sessile oak. Alexandre et al. (2020b) found that $\delta^{13}C$, unlike tree growth and some leaf morphological traits, was unresponsive to contemporary selection in sessile oak and attributed the considerable variations among individuals to adaptive divergence to drought driven by diversifying selection. This diversifying selection of WUE_i for sessile oak may explain why no linear relationship was found between populations WUE_i and the pedoclimatic conditions at their provenance sites.

Among-Population Diversity of Radial Growth and Intrinsic Water-Use Efficiency Are Only Linked During Wet Conditions

Based on the hypothesis that during the wet year (i.e., in 2000), the stomata were overall more open than during the dry years and did therefore restrict *A* less, and if light resources were not limiting, the observed among-population variation in WUE_i would have more likely resulted from a variation in photosynthetic capacity, rather than from variations in stomatal conductance (**Supplementary Figure 5**) as suggested by Aranda et al. (2017) for *Fagus sylvatica*. There was no significant effect of population on GI, however, the observed significant population/year interaction would suggest a diversity of growth plasticity for drought among populations. A similar result was

observed in a much larger study, in which Sillegny was one of the common gardens studied (Bert et al., 2020). In 2000, populations with high $\delta^{13}C$ also displayed a high growth index (**Figure 6**). A similar relationship was also observed at the within-population level and was statistically significant for populations with 60 individuals sampled, suggesting diversity among but also within populations for photosynthetic capacity. Establishing a relation between WUE_i and radial growth appears complex because carbon from leaf photosynthetic assimilation (*A*) is redistributed into different compartments of the tree and only a portion is used to build tree rings (Hartmann et al., 2018a). In addition, ring width and $\delta^{13}C$ are the final results of different dynamic processes, including post-photosynthetic fractionations between leaf assimilates and wood (Gessler et al., 2014), and the use of assimilates from previous years to build earlywood in oak species (Vincent-Barbaroux et al., 2019).

The relationship between $\delta^{13}C$ and growth index disappeared during dry years (**Figure 6**), likely because carbon assimilation is restricted by stomatal closure, and therefore masking any population differences in photosynthetic capacity. It has also been shown that during dry conditions, wood growth can be disconnected from carbon assimilation due to carbon storage processes, allocation, and remobilization (Pflug et al., 2015). Our third hypothesis, stipulating that trees and populations with a higher WUE_i only showed a higher radial growth when the soil water availability was unlimited, is confirmed.

CONCLUSION

In this study, the within-species variability in sessile oak WUE_i was evaluated by comparing the $\delta^{13}C$ values of 16 populations growing in the common garden of Sillegny. The among-population variation in $\delta^{13}C$ (0.6‰) was low compared to the inter-annual variation in $\delta^{13}C$ (1‰), and especially compared to the within-population variation in $\delta^{13}C$ (2–4‰). The $\delta^{13}C$ measurements over three contrasted years with different soil drought levels showed similar plasticity of WUE_i to drought among populations. Nevertheless, it was found that the among-population variation in WUE_i plasticity correlated with soil characteristics at the provenance sites. In addition, the plasticity in the growth index correlated with summer atmospheric humidity. Both results could suggest a local adaptation of sessile oak in terms of drought response strategies. Moreover, we observed a large variability in WUE_i within populations. This large variability, observed in a common environment, could suggest a large underlying genetic diversity, which could facilitate the adaptation of sessile oak to future climate changes. However, to substantiate this conclusion, it will be necessary for future research programs to partition observed variation into genetic and environmental causes.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AR: data curation, formal analysis, investigation, methodology, and writing—original draft. SP: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, and writing—original draft. DB: investigation, validation, and writing—original draft. AD: resources. BR: investigation, methodology, resources, validation, and writing—original draft. JL: investigation, methodology, resources, validation, and writing—original draft. OB: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, and writing—original draft. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.914199/full#supplementary-material

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