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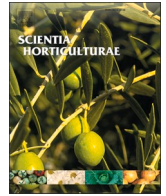
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## Research Paper

# The potential of sap conduction in the olive tree is linked to aridity conditions of the main cultivation area of varieties and allow to uncover their sensitivity to ongoing climate change.

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## ABSTRACT

This study examines the impact of drought, and by extension potential water scarcity, on the potential of sap conduction in the olive tree, the emblematic fruit tree of the Mediterranean Basin. To understand adaptation of sap conduction potential of varieties concerning drought, we focus on wood anatomical traits in trees cultivated in the conservatory orchard of the 'Conservatoire Botanique National Méditerranéen' (Porquerolles, France) and others from their main cultivation area. Leveraging branch diameter as a key factor influencing anatomical traits, we model density of vessels (DVS) and lumen area of vessels in transverse section (LAV) variation based on branch diameter using regression analyses. Our results show that the pattern of increase in LAV cannot be considered to be dependent on the biogeography and evolutionary history of varieties. But, it is significantly linked to the aridity conditions of the main cultivation area of these varieties. In the perspective of a future drastic increase in aridity, results point to the potential incapacity of varieties from non-irrigated semi-arid zones, to produce vessels large enough to transport sap to the leafy parts of branches, and other varieties from the northern margins of olive distribution area, to modulate conduction in terms of efficiency – safety balance. While some varieties exhibit a robust or moderately plastic phenotype, showing negligible variations in conduction potential with changing aridity in growing conditions, these results concern about the sustainability and future viability of some varieties. More broadly, they raise questions about the olive cultivation sector's resilience in the face of intensifying water stress.

## 1. Introduction

The olive tree (*Olea europaea* L. subsp. *europaea*) stands as an iconic tree crop within the Mediterranean Basin, where it has played a pivotal role in the cultural, socio-economic and ecological history of the region for millennia (Kaniewski et al., 2012). The olive tree is estimated to

comprise more than 2000 varieties, yet a mere 5–10% of these contribute to a staggering 99% of global olive production (IOC, 2022), most of which taking place in the Mediterranean Region. However, the harsh heat waves and the erratic, low rainfall experienced during the summers of 2020 and 2021 have induced a significant decline in yields, particularly pronounced in Spain, the main olive producer worldwide

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(FranceAgriMer, 2022).

All olive varieties derive from a unique ancestor, the wild olive tree or oleaster (*O. e. subsp. sylvestris*), which was domesticated almost 7000 years ago in the Levantine region (Eastern Mediterranean) (Zohary et al., 2012; Besnard et al., 2013; Besnard et al., 2018; Galili et al., 2021; Terral et al., 2021). From the primary domestication centre, humans have played a significant role in shaping the varietal diversity of olive tree through selection, propagation throughout the Mediterranean, hybridization and adaptation to various environmental / climatic conditions (Besnard et al., 2018). Thus, maternally (plastid DNAs) and biparentally (nuclear markers) inherited genomes defining different genetic profiles indicates varied biogeographical and evolutionary histories. Olive varieties are categorized into East or West maternal lineages, as determined by cytoplasmic genetic markers (Besnard et al., 2013; Besnard et al., 2018), and East, West, or Centre genepools, based on nuclear genetic markers (Díez et al., 2015; Bakkali et al., 2013; Khadari et al., 2019).

As outlined in the latest report from the Intergovernmental Panel on Climate Change (IPCC, 2022), the Mediterranean Basin stands out as one of the most vulnerable regions to climate change impacts. Projections for the region include an anticipated temperature rise, reduced precipitation, and an increase in the frequency and intensity of extreme meteorological events, such as prolonged drought periods. These changes will exert profound impacts on the distribution of species, ecosystems, water resources and agriculture (Thornes, 2002; Allen et al., 2010; Xu et al., 2019; Berdugo et al., 2020; Kassout et al., 2022; Kassout et al., 2023), and olive cultivation in particular (e.g. Ponti et al., 2014; Fraga et al., 2021; Kaniewski et al., 2023). In this context, improving our understanding of the mechanisms enabling the olive tree to cope with drought becomes imperative.

The olive tree is well-adapted to the Mediterranean climate, characterized by high summer temperatures and water deficits. During this period, a combination of morpho-anatomical traits and ecophysiological mechanisms allows the olive tree to thrive under high temperatures and drought stresses (Sofo et al., 2008; Fernández, 2014; Brito et al., 2019; Calvo-Polanco et al., 2019). Water stress is recognized to increase the susceptibility to cavitation: the air trapped in xylem vessels impedes sap conduction and causes substantial damage to plant parts that are no

longer supplied with water. Wood density ( $\text{g}/\text{cm}^3$ ) emerges as a reliable predictor of vulnerability and resistance to cavitation (Anderegg et al., 2016; Rosner et al., 2017). In trees from spontaneous olive populations (wild olive hereafter), the adjustment of the hydraulic system to cope with water stress seems also to involve the number of vessels grouped by radial line (Terral and Arnold-Simard, 1996; Heinz et al., 2004; Marguerie et al., 2010). In regions with limited water resources, the wood of wild olive tree exhibits a higher number of clustered vessels compared to the wood of olive trees from areas with ample water availability (Terral et al., 2004). These anatomical characteristics contribute to the trade-off between sap conduction safety and efficiency, which can be assessed through the relationship between vessel density (DVS, number/ $\text{mm}^2$ ) and vessel diameter or lumen area of vessels in transverse section (LAV,  $\mu\text{m}^2$ ) (Terral et al., 2004; Kassout et al., 2021).

A recent study on wild olive trees in Morocco revealed a log-linear relationship between branch diameter and the lumen area of vessels (Kassout et al., 2021: Fig. 1) in which the y-intercept represents the inferred vessel lumen area at the onset of branch growth and secondary xylem development. The slope, correlated with the y-intercept, reflects the potential increase in sap conductivity during the course of branch development. From a functional point of view, this increase in sap conductivity corresponds to an increase in water flow required to sustain transpiration during photosynthesis, as more leaves are produced higher up the branch. The pattern of increase in lumen area of vessels against branch diameter appears to be modulated by environmental conditions, particularly water availability (Kassout et al., 2021). In regions where water supply is adequate for wild olive trees, the slope of the log-linear model is high, while y-intercept is low, contrary to regions where olive trees face water stress (Fig. 1).

Building on these findings, this study tests whether this model holds for olive varieties from different countries or regions of origin, using samples from individuals growing under comparable environmental conditions (germplasm collection from the Porquerolles island, Southern France) and individuals from trees growing in their region of origin.

We therefore hypothesize that anatomical traits and associated sap conduction strategies may be intricately linked to the biogeographical and evolutionary history of these varieties, as well as to the climatic conditions prevailing in their main cultivation area.

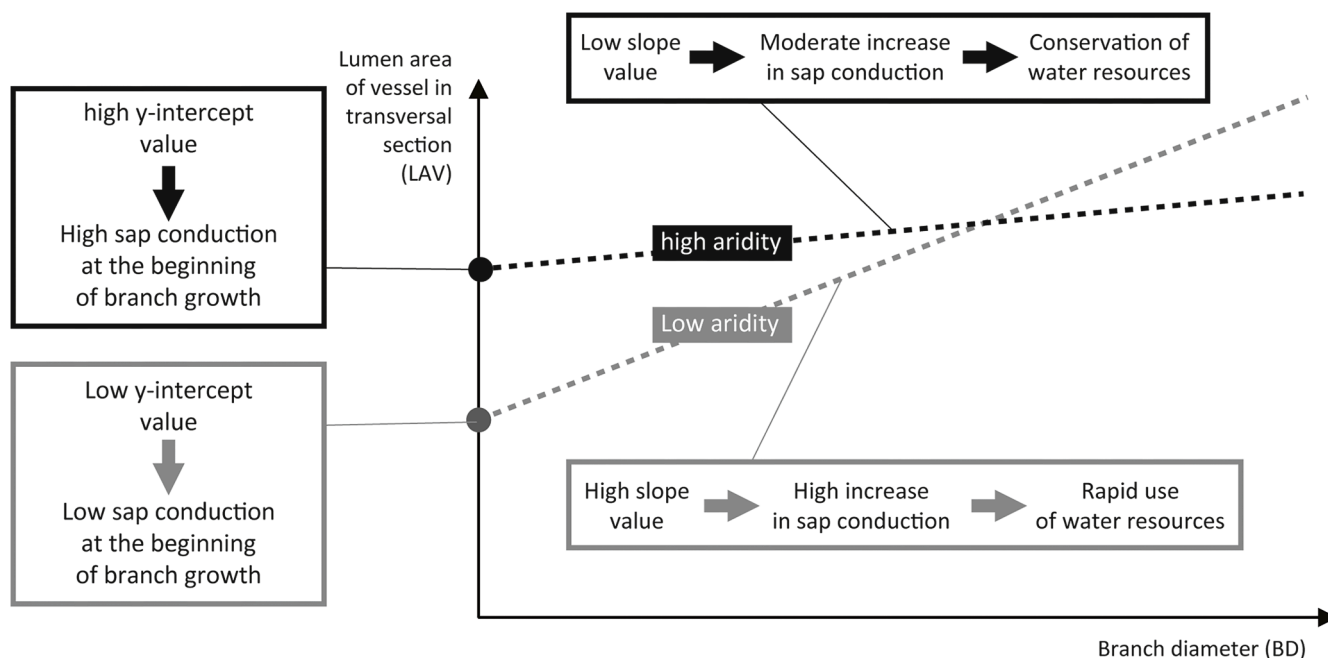


Fig. 1. Theoretical functional significance of the Lumen area of vessels (LAV) variation in relation to branch diameter (after Kassout et al., 2021 on the wild olive tree).

The objectives of this study are threefold: (1) tests the relationship between wood anatomical traits and branch diameter, for several cultivated varieties growing under identical conditions in the Porquerolles Island orchard, (2) assess the variation in the anatomical trait – branch diameter relationships across varieties, in particular to understand whether they are linked to a particular genetic profile or to the climatic conditions of their main cultivation area, (3) explore the plasticity in wood anatomical traits, by comparing trait values measured in trees from the Porquerolles orchard with those collected from trees growing in their main cultivation area.

Finally, through wood anatomical trait variation, this investigation serves two primary purposes: firstly, to assess the capacity of these trees to adapt their sap conduction potential and secondly, to identify potentially resistant and vulnerable varieties in the face of increasing drought conditions.

## 2. Material and methods

### 2.1. Study locations and sampling

Some of the trees studied come from the olive germplasm collection of the “Conservatoire Botanique National Méditerranéen de Porquerolles” (CBNMed) on Porquerolles Island (42.9917° N, 6.2039° E - Var department, France; Fig. 2). Mean annual temperature and rainfall are 16.8 °C and 615 mm, respectively (1990–2019 period, record of the Porquerolles meteorological station). Other trees were sampled in the main cultivation area of the corresponding varieties (see below). We studied 30 varieties from diverse main cultivation areas (Figure S1 and Figure S2) and distinct genetic profiles defined by the maternal lineage (East or West; after Besnard et al., 2013; Besnard et al., 2018) on the one hand, and the nuclear genepool (West (Q1), Central (Q2) and East (Q3), after Bakkali et al., 2013; Díez et al., 2015; Khadari et al., 2019) on the other hand (Table S1). Additionally, a genetic pool termed “Admixed” has been introduced for highly admixed varieties without a clear affiliation to a distinct geographical nuclear genepool (Table S1).

Wood samples were collected from 2 to 3 trees for each variety (total of 506 samples from 85 trees). Branch sections, with diameters ranging from 1.98 to 19.4 mm, were randomly collected at varying heights and orientations (half in South-Southwest, half in East-Northeast) to account for potential variations linked to exposure.

To assess intra-variety plasticity in wood traits, we collected samples (N=140) from 33 trees (8 varieties overlapping with those on Porquerolles) grown in their main cultivation area (Figure S1; Figure S2; Table S2). Branch samples were collected between 2005 and 2015 from non-irrigated trees.

### 2.2. Preparation of samples and data acquisition

A sliding microtome (G.S.L.1, Microm International GmbH, Wall-dorf, Germany) was used to obtain thin transverse sections, approximately 13 µm in thickness, from the wood samples. The histological preparations involved staining the transverse sections with a one-to-one mixture of Fast Green (2%) and Safranin (1%) solutions. Subsequently, the sections underwent dehydration using a sequence of ethanol solutions (96%, 70% and 40%), followed by washing with xylene. Finally, the sections were embedded in Canada balsam to produce permanent slides for observations (Kassout et al., 2021). An eco-anatomical approach was employed for the measurement of selected wood traits under a light transmission microscope connected to an image analysis system (Terral and Mengüal, 1999; Terral et al., 2004; Limier et al., 2018; Kassout et al., 2021). This methodology involves the measurement of anatomical wood traits, followed by subsequent statistical analyses of the collected data. For each wood sample, we measured branch diameter with bark (BD, mm), and three anatomical characters relevant to sap conduction: vessel density (DVS, number of vessels/mm<sup>2</sup>), the number of vessels grouped in radial files (NVS, N/group of vessels), and the Lumen area of vessels (LAV, µm<sup>2</sup>). Measurements were conducted on the youngest (peripheral) wood section (1 to 3 years old) to link functional anatomical traits to branch diameter, under magnifications of 100 ×, 200 ×, and 500 × for DVS, NVS, and LAV, respectively (Fig. 3).

Based on previous methodological development (Kassout et al., 2021), we performed 35 measurements per sample at different places of the transverse sections for both LAV and NVS, and 20 measurements for DVS. To measure the last two traits, the widest possible window of microscopic observation of the wood was used.

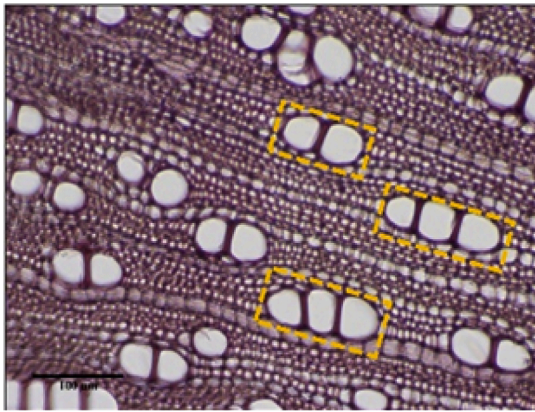
### 2.3. Data analysis

In order to assess the variability of wood anatomical traits according to the branch age assessed by the branch diameter (BD), a Principal Component Analysis (PCA) was conducted on the dataset obtained from the measurement of anatomical traits (LAV, DVS, and NVS) carried out on 506 olive wood samples from trees within the CBNMed collection. The corresponding branch diameter of the samples was integrated into the PCA as a supplementary (passive) variable. Given that the branch diameter is probably the major parameter of anatomical variation (after Kassout, 2019; Kassout et al., 2021), a correlation matrix showing correlations coefficients between BD and anatomical traits was established.

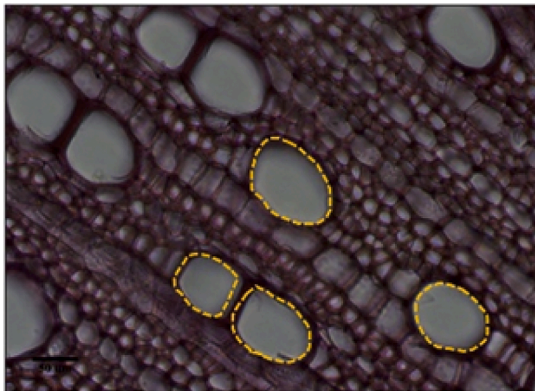
Once the impact of branch diameter was evidenced and the anatomical traits more significantly linked to BD determined, we tested the hypothesis that anatomical trait – branch diameter relationships vary according to the biogeographical and evolutionary history of these



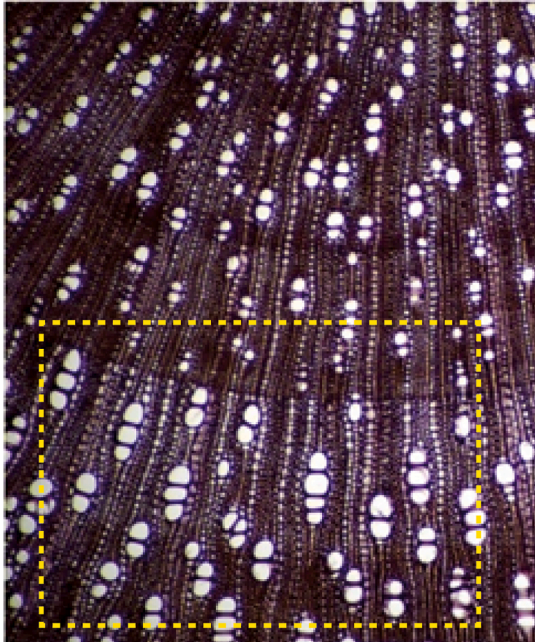
Fig. 2. Geographical location of the olive collection orchard of the CBNMed Porquerolles.



Number of vessels joined in radial files  
(NVS, N/group of vessels),  
200x



Lumen area of vessels in transverse  
section (LAV,  $\mu\text{m}^2$ ),  
500x



Vessel density (DVS, number of vessels/ $\text{mm}^2$ ),  
100x

Fig. 3. Measured anatomical traits of olive wood.

varieties. To achieve this, a standardized major axis (SMA) regression was carried out to compare the different groups of maternal lineages (East and West) on the one hand, and the different nuclear genetic profiles (East (Q3), Central (Q2), West (Q1), and Admixed) (Besnard et al., 2013; Díez et al., 2015) on the other hand. Differences in slopes and y-intercepts of SMA fitted for these different groups were tested using likelihood ratio statistic and Wald statistic, respectively (Warton

et al., 2012). SMA regressions were carried out on Log-transformed data (natural logarithm) to meet normality requirements and minimize heterogeneity of residuals. The related statistical analyses were performed using the R software (R 3.3.3; R Development Core Team, 2015) and the *smatr* package version 3 (Warton et al., 2012).

To test the relationship between wood anatomy and climate, a different approach was used. For the anatomical traits of interest whose

variation is related to BD, we carried out linear regression analyses, variety by variety, using Log-transformed (natural logarithm) data. The parameters of the linear models (y-intercept and slope) established for each variety were regressed against the aridity index (AI=Mean annual precipitation/Potential Evapotranspiration – reference data of the 1970-2000: Cherlet et al., 2018) of their main cultivation area. For varieties growing in the Porquerolles and for the 8 varieties sampled in their main cultivated area. The AI was calculated using data extracted from Worldclim database, version 2.1 (Fick and Hijmans, 2017) and the CGIAR Global aridity and PET database, version 3 (Zomer et al., 2022). For each variety, the reference AI corresponds to the mean value of several climate recording points (Table S3), representative of its main cultivation area (including altitude, geomorphological and soil characteristics, insolation, slopes, and water resources) (Figures S1, S2).

Finally, following the guidelines of Valladares et al. (2006), the anatomical plasticity or adaptation of sap conduction potential of concerned varieties was assessed by calculating the intra-varietal range in y-intercept and slope between Porquerolles and the main cultivation area (MCA):  $\Delta y\text{-intercept (variety)} = y\text{-intercept (Porquerolles)} - y\text{-intercept (MCA)}$  and  $\Delta \text{slope (variety)} = \text{slope (Porquerolles)} - \text{slope (MCA)}$ . In addition to comparing varieties in terms of level of plasticity as carried out previously, the importance of variety-by-variety plasticity in relation to the maximum range of regression parameters in cultivated olive trees was assessed. To do this, we calculated a rate of variation based on the maximum inter-variety variation in y-intercept and slope (rate =  $100 * (\Delta \text{intra-variety} / \Delta \text{max inter-variety})$ ). This approach made it possible to better quantify the extent to adaptation of sap conduction potential in the cultivated olive tree.

### 3. Results

#### 3.1. Variability in wood anatomical traits in olive varieties

The first two axes of the PCA conducted on data from trees of the CBNMed collection account for 82.9% of the variation in the phenotypic space defined using the three anatomical traits (Figure S3); BD is plotted as a supplementary inactive variable). The distribution of individuals along the first axis, explaining 49.5% of variance, is primarily driven by differences in LAV and DVS, exhibiting significant correlations with BD (Table 1). The second axis (33.4% of variance explained) is associated with NVS. Given that LAV and DVS are significantly correlated with BD (Table 1), these two anatomical traits were selected for SMA regressions (Warton et al., 2012).

**Table 1**

Correlation matrix showing Pearson correlation scores among variables used in the PCA (A) and associated p-values (B) (please refer to Fig. S3). The most significant scores are indicated in bold. BD (branch diameter, mm), NVS (number of vessels joined in radial file, N / group of vessels), DVS (vessel density, N / mm<sup>2</sup>), LAV (Lumen area of vessels,  $\mu\text{m}^2$ ).

A.				
Variables	BD	NVS	DVS	LAV
BD	1	-	-	-
NVS	0.127	1	-	-
DVS	<b>-0.489</b>	-0.003	1	-
SVS	<b>0.543</b>	0.079	-0.491	1
B.				
Variables	BD	NVS	DVS	LAV
BD	0	-	-	-
NVS	0.004	1	-	-
DVS	<b>&lt;0.0001</b>	-0.003	1	-
SVS	<b>&lt;0.0001</b>	0.079	-0.491	1

#### 3.2. Relationships between anatomical traits and branch diameter according to the genetic profile

SMA regressions fitted between DVS and BD for the different groups according to maternal lineages and nuclear pools did not reveal any differences, either in slope or y-intercept among these groups (Fig. 4A, 4B; Table S4). Between LAV and BD, this approach showed significant differences in y-intercepts according to maternal lineages (Wald statistic = 5.756, df = 1, p = 0.016), but did not in slopes (likelihood ratio statistic = 0.56, df = 1, p > 0.05) (Fig. 4C; Table S5). When testing divergences according to nuclear pools, SMAs showed differences in slope (likelihood ratio statistic = 37.52, df = 3, p < 0.0001) and y-intercept (Wald statistic = 45.37, df = 3, p < 0.0001) (Fig. 4D; Table S5).

Varieties belonging to the West nuclear pool (mainly) and varieties from the Centre nuclear pool contribute to the differences in y-intercept (Table S6). For slopes, all varieties seem to differ from each other with the exception of the East-West-Center and West-Admixed groups (Table S6).

#### 3.3. Relationship between climate and patterns of anatomical trait variation depending on branch diameter

The slope and y-intercept of the log-transformed linear DVS – BD relationship on the one hand and the LAV – BD relationship on the other hand were calculated for each variety, both for trees from the Porquerolles collection and grown in their main cultivation area (Table S7). We then tested the relationships between each of these 3 parameters and the aridity index (AI) of the main cultivation area for each variety, both for trees in Porquerolles and for trees growing in their main cultivation area. We did not find any significant correlations between either the slope ( $R^2 = 0.013$ , p = 0.52 for trees in Porquerolles;  $R^2 = 0.158$ , p = 0.33 for trees from their main cultivation area) or the y-intercept ( $R^2 = 0.008$ , p = 0.61;  $R^2 = 0.002$ ; p = 0.91) of the DVS – BD relationships. By contrast, both correlations were found to be significant for the coefficients of the LAV – BD linear models, as previously found for the Moroccan wild olives (Kassout et al., 2021) (Fig. 5).

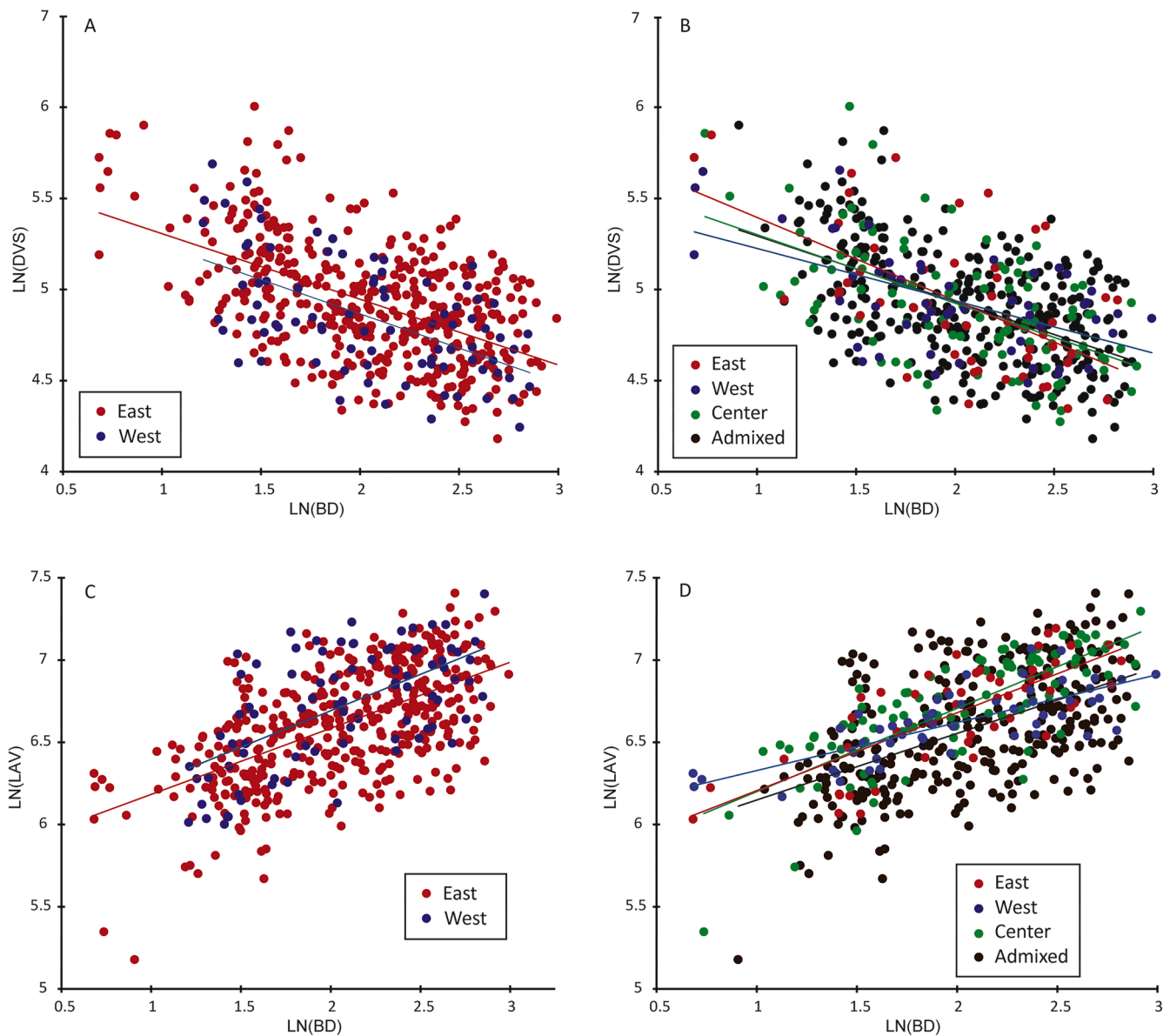
Three distinct groups could be identified on the basis of these relationships (Fig. 5):

- (1) Group 1A comprises the majority of varieties (individuals from Porquerolles and from their main cultivation area) for which the y-intercept decreases linearly with the AI of the main cultivation area;
- (2) Group 1B corresponds to varieties (individuals from Porquerolles and from their main cultivation area) for which the slope increases linearly with AI: these are the same as those from group 1A, except varieties 'Baguet' (BAGU), 'Négrette des Vans' (NEVA), 'Grossane' (GROS) and 'Tanche' (TANC). These last four varieties make up Group 3. They originate from areas with bioclimatic conditions ranging from subhumid to humid, and are characterized by an exceptionally low slope value (Fig. 5B).
- (3) Group 2 comprises two varieties ('Amigdalolia' (AMIG), Greece and 'Ecijano' (ECLJ), Spain) with an exceptionally low y-intercept and high slope compared to varieties from the semi-arid area of Group 1A and Group 1B, respectively.

#### 3.4. Anatomical plasticity

Fig. 6 provides an overview of the variation in y-intercept and slope of the LAV-BD relationships for the eight varieties measured both in Porquerolles and in their main cultivation area (MCA). We also assessed the extent of anatomical plasticity through the rate of variation of the y-intercept and slope parameters, which is based on the ratio of intra-varietal variation to inter-varietal variation (Fig. 6).

In relation to the maximum variation in cultivated olive trees, the extent of anatomical plasticity has been categorized into 4 classes: low if



**Fig. 4.** Standardized major axis (SMA) regressions used to test differences in density of vessels (DVS) – Branch diameter (BD) (A, B) and Lumen area of vessels (LAV) – BD (C, D) (Log-transformed data) relationships according to various genetic profiles (maternal lineages (A, C) and nuclear gene pools (B, D)).

the rate is between 0 and 25% of the total variation, moderate if the variation varies between 25 and 50%, high if the variation reaches a value between 50 and 75% and very high if the variation is greater than 75% (Fig. 6). As a result, anatomical plasticity may be considered low for the ‘Arbequina’ (moderate in terms of slope difference), ‘Blanc de Payzac’, ‘Chemlali’, ‘Menara’ – ‘Picholine Marocaine’ and ‘Meski’ varieties for which the rate of y-intercept parameter variation. On the other hand, the ‘Négrette des Vans’, ‘Tanche’ and ‘Grossane’ varieties are characterized by a very high rate of slope, while their y-intercept rate ranges from moderate (‘Tanche’ and ‘Grossane’) to high (‘Négrette des Vans’).

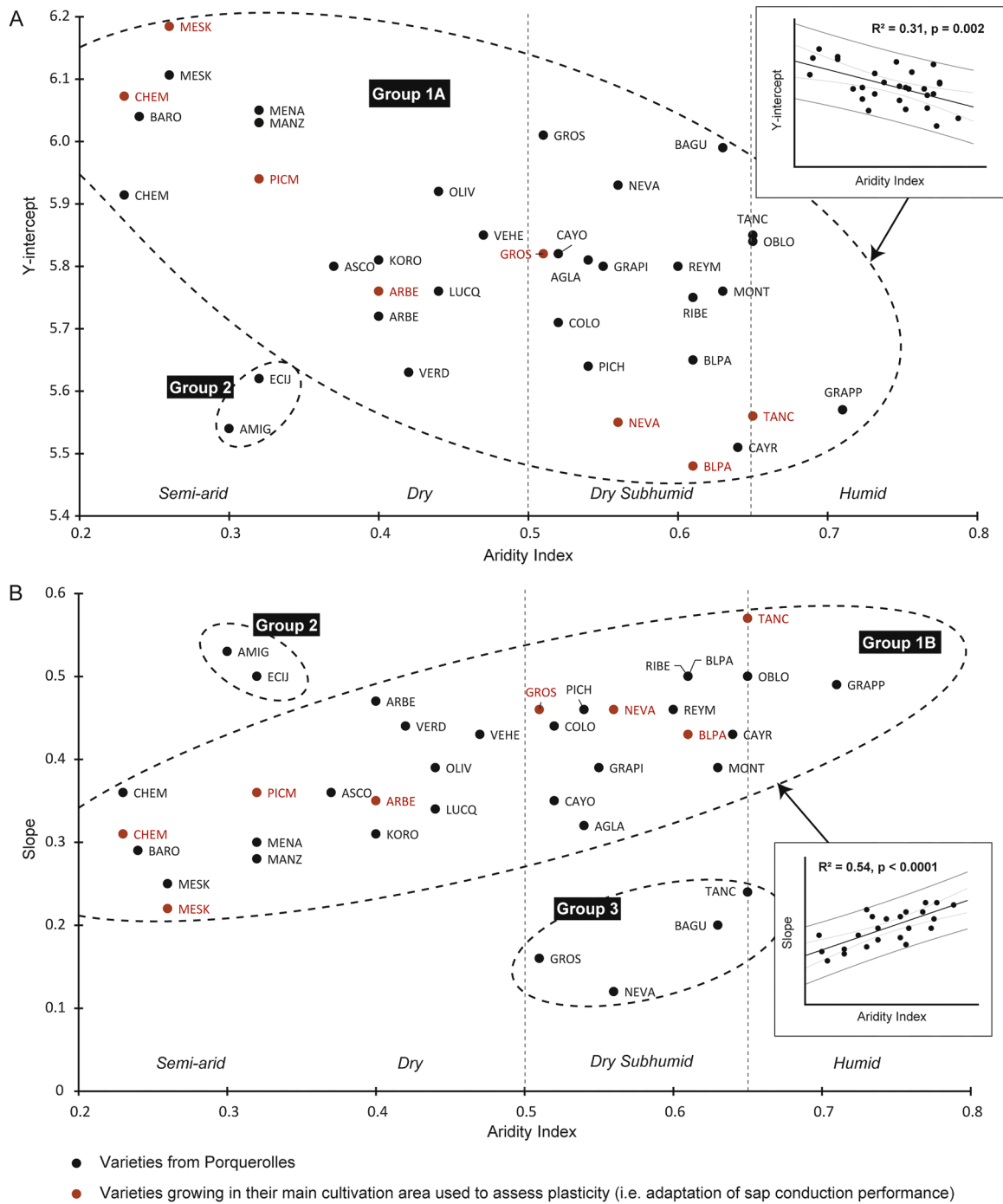
Specifically, we can notice that for the varieties Chemlali, Meski and Arbequina, the  $\Delta$  y-intercept is negative, which means that this parameter is higher in MCA than in Porquerolles. Conversely, for the Blanc de Payzac, Grossane, Négrette des Vans, Menara - Picholine Marocaine and Tanche varieties, the y-intercept is higher in Porquerolles than in MCA (Table S7). Similarly, there was an increase in slope between Porquerolles and MCA for the varieties ‘Grossane’, ‘Négrette des Vans’, ‘Menara’ – ‘Picholine Marocaine’ and ‘Tanche’ ( $\Delta$  slope < 0).

On the other hand, for the varieties ‘Arbequina’, ‘Blanc de Payzac’, ‘Chemlali’ and ‘Meski’, the slope parameter decreased between Porquerolles and MCA ( $\Delta$  slope > 0).

#### 4. Discussion

##### 4.1. Sap conduction is linked to branch size

We show that the density of vessels and the lumen area of vessels depend on branch diameter (BD) in cultivated olive trees, as previously observed in young stems of wild olive not yet subjected to mechanical constraints linked to an oblique growth direction, which can lead to the production of tension wood (Kassout et al., 2021). Both DVS and LAV are expected to vary in relation with the circumference of the vascular cambium and, consequently, with the size of the cauline part (stem and leaves) located above the studied cross-section, on which the transpiration stream depends. The negative correlation between the two anatomical traits suggests a trade-off between conduction efficiency (potential volume of sap transported), represented by LAV, and



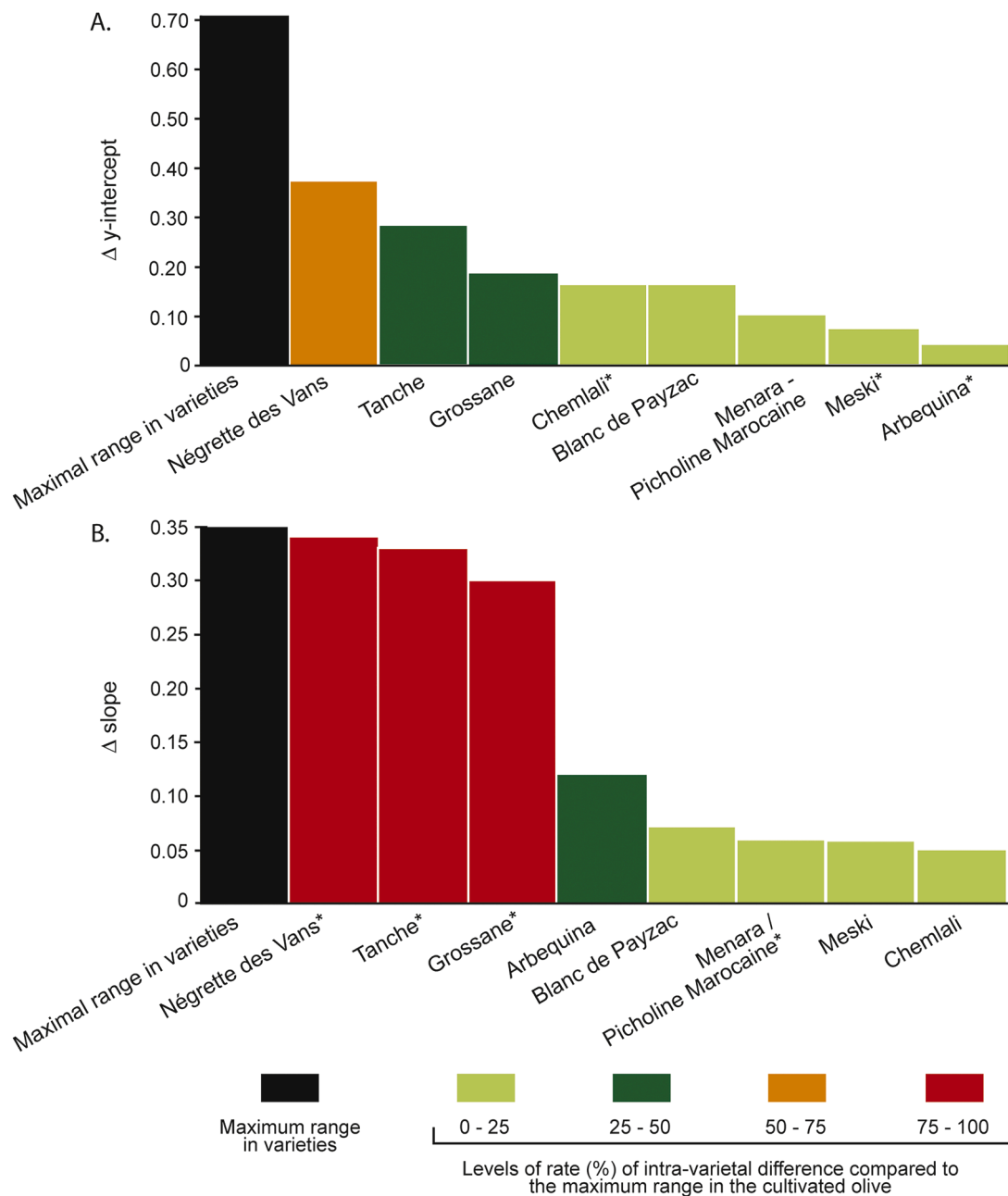
**Fig. 5.** Biplots showing relationships between the aridity index of the main cultivation area of each variety and (A) the y-intercept, and (B) the slope of linear regressions relating log transformed vessel surface area (LN(LAV)) and branch diameter (LN(BD)). Insets show the respective linear regression models for group 1A and 1B varieties. Black and red points and letters are for trees of the Porquerolles collection and trees growing in their main cultivation area, respectively. Please refer to Table S1 for abbreviations. Bioclimates (from semi-arid to humid) are categorised according to Cherlet et al., 2018. For information, AI<sub>Porquerolles</sub>=0.51.

conduction safety as assessed by DVS. The latter indeed reflects the vessels' capacity to resist cavitation in olive, also call gaseous embolism (Terral and Mengüal, 1999; Terral et al., 2004; Choat et al., 2012).

As trees growing in the Porquerolles collection grow in homogeneous environmental conditions, the variations in DVS and LAV could be explained by the biogeographical and evolutionary history of the varieties, traced by plastid haplotypes (maternal lines) and nuclear microsatellite markers, as a result of adaptive processes. In terms of variation in DVS as a function of BD, we did not find any differences regardless of the genetic profile. From the point of view of LAV, how much credibility

should be given to differences in y-intercept according to maternal lineage and differences in y-intercept and slope in relation to the nuclear pool? Indeed, the regression line for varieties belonging to the Eastern maternal lineage appears to have a slope greater than that of varieties belonging to the Western lineage. However, the two maternal lineages are represented in this study by 20 varieties of various origins in the Mediterranean for the Eastern lineage, and by only 4 French varieties (subhumid-humid bioclimatic areas) for the Western lineage. This imbalance in terms of variety number and biogeographical origin does not allow us to draw any relevant conclusions. Regarding the differences





**Fig. 6.** Anatomical plasticity i.e. adaptation of sap conduction performance assessed by calculating the intra-variety range ( $\Delta$  expressed in absolute value) in y-intercept (A) and slope (B) between Porquerolles and the main growing area (MCA) following the requirements of Valladares et al. (2006). Varieties marked with an \* are characterized by a negative  $\Delta$ . The colour codes indicate different levels of rate (%) of intra-variety variation in relation to the maximal range in the varieties studied [Rate =  $100 * (\Delta \text{ intra-variety} / \Delta \text{ max in varieties})$ ] in y-intercept (A) and slope (B).

among nuclear gene pools, for the same reasons, we cannot conclusively interpret the results obtained. The regression lines of varieties belonging to the western pool (Q1) seem to decline more rapidly (lower model slope) than the other gene pools. Nonetheless, this result appears to be influenced by the fact that the 3 varieties of the western gene pool (Q1) are all cultivated in dry or semi-arid regions. In addition, "admixed" varieties make up the vast majority (15 varieties), whereas the Q2 (Center) and Q3 (East) pools only have 5 and 1, respectively.

#### 4.2. Wood anatomy and climate

Variations in the y-intercept and slope of the linear relationships between LAV with BD were found to be modulated by the aridity conditions of the variety's main cultivation area, while this was not the case

for DVS.

The differences in the patterns of LAV variation against BD between varieties adapted to different drought conditions reflect, from a functional point of view, variations in hydraulic conductivity and thus different levels of resistance to water-stress-induced vessel cavitation (Maherali et al., 2004; Terral et al., 2004; Anderegg et al., 2016). It has in particular been shown that the size of vessels in wild olive forms of the 6 subspecies of the *Olea europaea* complex was linked to mean annual precipitations as a consequence of adaptation to various environmental conditions, from Mediterranean to tropical (Terral et al., 2004). Similarly, it has also been demonstrated in *O. e. subsp. europaea* var. *sylvestris* that the density of vessels varies according to mean annual temperature, allowing one to distinguish wild olive trees thriving in the thermomediterranean bioclimatic area from those growing under

mesomediterranean conditions (Terral and Arnold-Simard, 1996; Terral and Mengüal, 1999; Terral et al., 2004). The results presented here on cultivated olive trees, show that the adjustment of the hydraulic system in relation to drought involves only a reduction in the trend of increasing vessel size as a function of branch diameter to cope with water stress. At a constant overall vessel density, the ability of cultivated olive trees to resist cavitation must take into account not only the size of vessels but also other anatomical traits such as the quantity of vertical and horizontal fibers and parenchyma, which contribute to a decrease in porosity and correlatively to an increase in wood density, as shown by Anderegg et al. (2016) and Rosner et al. (2017).

Therefore, the higher the aridity (low value of AI), the lower the slope value (Fig. 5) and, consequently, the higher the intercept value. At the inter-varietal level, the increase in conduction efficiency inferred by the lumen area of vessels (LAV) linked to the growing need for water resources of innervated organs, particularly leaves, appears to be modulated by the aridity of the environment.

Varieties common to groups 1A and 1B adapted to semi-arid and dry conditions ('Barouni' (Tunisia), 'Chemlali' (Tunisia), 'Manzanilla' (Spain), 'Menara' (Morocco) and 'Meski' (Tunisia)) exhibit a low slope with a high value of y-intercept, while varieties adapted to sub-humid and humid regions are characterized by a steeper increase in LAV, with the initially produced elements generally being narrower (Fig. 5). Two varieties defining the group 2 ('Amigdalolia' and 'Ecijano') seem to be an exception to the rule, displaying traits of varieties from subhumid and humid areas. In the current state of research, we cannot explain this behaviour, which is atypical on the face of it. Furthermore, the French varieties 'Baguet', 'Grossane', 'Négrette des Vans' and 'Tanche' from subhumid and humid conditions, comprising the group 3, show lower slope values than the semi-arid varieties. Their inability to modulate vessel size seems to indicate a failure of hydraulic conductivity and reflect the suffering of these varieties, which seem unable to acclimatize to the environmental conditions of Porquerolles. To verify this hypothesis based on anatomical traits, it would be very interesting to test osmotic potential shoot growth unit, a reduction in which would be linked to a leaf area decrease and stomatal regulation to conserve water.

Drawing on studies conducted on leaf traits of wild olive trees from Moroccan populations distributed along an aridity gradient (Kassout, 2019; Kassout et al., 2019, 2024), the established models underscore the significance of adaptation, particularly of varieties originating from regions with the most arid conditions. In these regions characterized by prolonged periods without precipitation, olive trees would rely on a high acquisition of water resources at the beginning of growth (high y-intercept value) and subsequently adopt a strategy of resource conservation (low slope value) (see Fig. 1). This strategy is associated with a slower growth rate and metabolism, as well as sclerophyllous and thick leaves (Kassout, 2019; Kassout et al., 2019, 2024). In contrast, varieties adapted to subhumid to humid conditions in regions with higher and more evenly distributed precipitation throughout the tree's development cycle seem to be distinguished by a lower acquisition of water resources at the beginning of branch growth (low y-intercept value) and a more pronounced increase in conduction efficiency throughout growth and branch development (high slope value) (Fig. 1). Functionally, this strategy relies on the rapid use of water resources, necessitating a more significant increase in conduction efficiency as the branch develops. These hydraulic characteristics are linked to faster growth and metabolism, as well as thinner leaves with lower water content (Kassout, 2019; Kassout et al., 2019, 2024).

Our results represent the first attempt to characterize and quantify differences among olive varieties in terms of sap conduction potential and drought conditions. This classification extends beyond the traditional categories (high, intermediate, and low susceptibility to drought) used in olive tree literature (e.g., Alfieri et al., 2019; IOC, 2022), and provides a more quantitative assessment of these based on traits.

#### 4.3. Wood anatomy plasticity, sap conduction potential, and drought

For the 8 varieties sampled in the Porquerolles orchard and in their main cultivation area, the variations in slope and intercept of the lumen area of vessels - branch diameter relationship reveal the plasticity of the sap conduction system, i.e. the adaptation of conduction potential to different environmental conditions, among which aridity conditions seem to predominate (Fig. 5, Fig. 6).

Sap conduction potential may be considered as robust (little plasticity) in 'Arbequina' (Spain), 'Chemlali' (Tunisia), 'Meski' (Tunisia), 'Menara' ('Picholine Marocaine') (Morocco), and 'Blanc de Payzac' (France) varieties, which display a moderate or low variation in y-intercept and slope from Porquerolles to MCA (Figure S3). As the result, between their main growing area and Porquerolles, the increase in aridity conditions for 'Blanc de Payzac' and the decrease for the other varieties, particularly for 'Menara' - 'Picholine Marocaine' known for its great ecological plasticity (Terral and Ater, 2016; Barbara et al., 2020), do not seem to affect conductivity.

Conversely, other varieties do not seem to follow the same trend, such as those composing group 3, indicating a lack of adaptation in sap conduction potential (Figure 5; Figure 6; Figure S4). 'Négrette des Vans' and 'Tanche' whose main cultivation area is situated in France at the northernmost edge of the olive tree range (subhumid - humid conditions), do not appear to acclimate to the more arid conditions of Porquerolles. This is evidenced by a strong decrease in the slope of the LAV variation model between their main cultivation area and the Porquerolles orchard. Indeed, these varieties seem to struggle in the Porquerolles orchard, as indicated by a low or even total absence of fruit production and a recurring infestation of Sooty mold, a cryptogamic disease associated with fungi development on trees due to mealy bug exudate. In the case of the 'Grossane' variety, distributed over a very limited area with aridity conditions similar to those on the island of Porquerolles, the differences in slope could be attributed to variations in edaphic parameters, which were not considered in this study.

Finally, as explained in the previous section, the 'Ecijano' ('Lechín de Sevilla', Spain) and 'Amigdalolia' (Greece) varieties (Group 2) appear to exhibit significant differences from the varieties in Group 1A and 1B, particularly those adapted to semi-arid or dry conditions. Indeed, they surpass the upper limits of the prediction confidence interval of the linear regression (Fig. 4). While comparative references for these varieties in their main cultivation area are lacking, we can notice that these varieties achieve similar conduction potential as other varieties but with considerably lower water resources. This seems the case of 'Menara - Picholine Marocaine' in the sub-humid region of the Rif (Northern Morocco) or 'Blanc de Payzac' at the northern limit of the olive tree distribution area in France. Therefore, we can hypothesize that these varieties may exhibit exceptional adaptability and resilience to challenging aridity conditions.

## 5. Conclusions

These findings raise critical questions about the sensitivity and resilience of olive varieties to climate change, particularly in the face of increasing aridity (Fraga et al., 2020). The Mediterranean basin stands out as one of the regions most profoundly affected by climate change, experiencing warming surpassing the global average increase by 20% and a decline in rainfall (IPCC, 2022). This shift could necessitate increased irrigation, especially in the Eastern and Southern regions of the Mediterranean, potentially posing severe resource challenges for local populations (Kaniewski et al., 2023).

Against this background, the results of this study offer an initial insight, using eco-anatomical data to quantify traits related to sap conduction, into the cultivated olive tree's adaptation to climatic conditions and the underlying ecophysiological mechanisms. They raise questions about the potential risks of sap conduction failure faced by various olive tree varieties in the context of increasing aridity, particularly the

vascular cambium's inability to establish efficient vessels for transporting sap.

The future objective for the olive cultivation sector is thus to devise strategies to mitigate the impacts of climate change. One such strategy is to select varieties that are tolerant to low water resources, meaning those for which limited water availability does not adversely affect tree growth or fruit production. Future varietal breeding programs should prioritize characteristics indicative of water-stress resistance, as revealed in this study – the capacity of varieties to adjust their sap conduction potential while ensuring valuable production. Consequently, the planting of drought-tolerant or drought-resistant varieties, such as those identified in this study, as well as newly developed water-stress resistant genotypes from breeding programs, emerges as a coherent alternative. It is plausible that the distribution area of the olive tree will expand northward and in altitude, aligning with the broader expansion of the Mediterranean region and, more significantly, its restriction in Eastern and Southern Mediterranean areas. Varieties originating from semi-arid areas, particularly those from the Southern shore of the Mediterranean (e.g., 'Meski' or 'Chemlali'), appear to be promising candidates, showing predisposition to replace varieties from the northern shore of the Mediterranean. Varieties cultivated toward the northern limit of the olive tree's distribution area, like 'Negrette' and 'Tanche' (France), seem highly sensitive to increased aridity.

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### CRediT authorship contribution statement

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### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Supplementary materials

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### Data availability

Data will be made available on request.

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