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ORIGINAL RESEARCH ARTICLE

Relationships between leaf temperature, stomatal conductance and architecture: potential impact on leaf burning among a range of genotypes in grapevine

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ABSTRACT

In the context of climate change, extreme heatwaves are often observed. The consequences of these events led to leaf and grape burning, as observed in June 2019 in the South of France. Previous observations showed that genotypic variability exists in response to these heatwaves. One of the main hypotheses to explain the differences is that genotypes could differentially regulate their leaf temperature. This temperature is closely associated with stomatal conductance and the amount of energy absorbed by the leaves. This amount of energy is known to be a consequence of plant architecture that determines light interception. This study was performed on a set of 33 genotypes that were selected with different leaf-burning sensitivities to high temperatures. Functional (i.e., stomatal conductance, photosynthesis) and architectural traits (internode length, leaf area and leaf elevation angles) were measured to compute their heritabilities and to determine correlations between these traits. Measurements of stomatal conductance and leaf temperature were performed during 30 measurement periods in 2021 and 2022. Architectural traits were extracted from 3D digitizing. High heritability in architectural traits were observed (around 0.8). Heritability of functional traits, although lower, were not negligible (higher than 0.6) and were partly dependent on the weather conditions during the measurements. A clustering of genotypes based on mean values of their architectural and functional traits revealed that both types of traits could be combined independently. New combinations of traits and their impact on leaf temperature were then examined. Stomatal conductance appeared to be associated with the intensity of the burning symptoms than architectural traits. The genotypes with high stomatal conductance also displayed low leaf temperature in accordance with the evaporative cooling effect. However, these genotypes were also the most sensitive to leaf burn. This likely suggests that leaf burn resulted from a high transpiration rate that could cause embolism under hot and dry weather conditions. For future works, modelling approaches could be of major interest to quantify the relative impact of architectural and functional traits on leaf temperature. Nevertheless, our study shows that leaf temperature is not completely associated with the observed leaf-burning symptoms and that other processes are involved.

KEYWORDS: vegetative vigour, leaf orientation, leaf temperature, stomatal conductance, burning symptoms, genotypic variability

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INTRODUCTION

In the context of global warming, the occurrence of extreme heatwaves is expected to increase in almost all vineyards around the world (Droulia and Charalampopoulos, 2021). These events can cause major risks for the production and the perennity of this crop (Fraga *et al.,* 2020; Lopez-Fornieles *et al.,* 2022). For instance, in the south of France in June 2019, a major heatwave was observed with air temperatures higher than 45 °C (Copernicus, 2020). High temperatures influence plant development and induce a large set of physiological responses at the leaf and plant scales (Feller and Vaseva, 2014) with potential impacts on inter-annual variations in plant growth yield for perennials (Chitwood *et al.,* 2016). High temperature involves an increase in evaporative demand that leads to decreased stomatal conductance (Massonnet *et al.,* 2007 in apple tree; Rogiers *et al.,* 2012 in grapevine). This decreased conductance is commonly considered an adaptive strategy to reduce water loss and embolism in the vascular system (Jones and Sutherland, 1991). However, this response induces a decrease in photosynthesis and an increase in leaf temperature (Tuzet *et al.,* 2003). The increase in leaf temperature is due to a decrease in energy loss by evaporative cooling (Crawford *et al.,* 2012). In extreme cases, leaf-burning symptoms that lead to leaf or entire plant mortality can occur (Webb *et al.,* 2010).

In this context, there is a need to develop new varieties more adapted to high temperatures. Previous analyses made during these heatwaves revealed high genotypic variability in the sensitivity to the leaf burning in a core collection of varieties (Nicolas *et al.,* 2016) that were grown in Montpellier (South of France). There exist two mechanisms that could limit the increase in leaf temperature. Firstly, reducing the amount of light intercepted and secondly maintaining stomatal aperture even under high temperature (Ehleringer, 2000). Previous studies in grapevine showed high genotypic variability in stomatal behaviour under water deficit (Gerzon *et al.,* 2015; Hochberg *et al.,* 2013). Isohydric and anisohydric behaviours were observed in a progeny that originated from a bi-parental population (Syrah × Grenache, Coupel-Ledru *et al.,* 2014). In isohydric plants, stomatal closure occurs even under a moderate water deficit. This behaviour allows for maintaining constant leaf water potential. Conversely, anisohydric plants keep transpiring under a water deficit which leads to decreased leaf water potential (Tardieu and Simonneau, 1998).

The benefit of both types of strategies on the sensitivity to high temperatures requires further investigation. Nevertheless, isohydric behaviour could be detrimental under high temperatures due to the limitation in evaporative cooling. Conversely, the anisohydric behaviour should be beneficial under high temperatures by maintaining leaf transpiration.

The amount of light intercepted by leaves depends on the architectural characteristics of the plants (Fleck *et al.,* 2003; Planchais and Sinoquet, 1998). Among the multitude of architectural traits, leaf shape and size, petiole length, and leaf 3D orientation influence the amount of light intercepted by individual leaves (Falster and Westoby, 2003; Valladares and Brites, 2004). Large genotypic variability in architectural traits has been previously observed in other plants (Costes and Gion, 2015; Perez *et al.,* 2019). The traits that were measured included (i) simple traits such as plant height or trunk diameter that are easy to measure on large populations of individuals (Bartholomé *et al.,* 2016; Liebhard *et al.,* 2003), and (ii) more local traits such as branching density or maximal internode length that are more difficult to measure at high throughput (Segura *et al.,* 2007).

Regarding the genetic origin of the relationship between architectural traits and leaf temperature, Santini *et al.* (2021) and Coupel-Ledru *et al.* (2022) identified putative genes associated with vegetation indices and leaf temperature on a collection of Aleppo Pine and apple trees, respectively. However, in these studies, the architectural traits remained integrative (volume of the canopy, porosity, silhouette to leaf area ratio) and the underlying local characteristics such as internode length, individual leaf area or leaf orientation remained unidentified. In grapevine, ampelography is dedicated to the identification and classification of grapevine cultivars. This discipline is based on 'semi-quantitative' descriptors of cultivar morphology and architecture (OIV, 2018). In comparison, the studies that consider quantitative traits to describe the genotypic variability are rare (only two cultivars in Louarn *et al.,* 2007 for instance). Furthermore, functional traits are rarely considered at the same time as architectural traits. Consequently, the heritability of these traits remains to be explored. In this study, we examined a set of 33 genotypes displaying contrasted architectural traits and different sensitivities to leaf-burning symptoms as observed in June 2019. The study was conducted on potted young plants (one and four-year-old).

We analysed 1) the existing genotypic variability in architectural traits, leaf temperature and stomatal conductance and 2) the relationships between architectural traits, stomatal conductance, leaf temperature and the previously observed leaf burning symptoms. The genotypes were then classified into groups according to their architectural and functional traits (stomatal conductance, leaf water potential, photosynthesis) and their leaf temperature. The objective was to propose new ideotypes that could limit the negative impact of the rise in air temperature.

MATERIALS AND METHODS

1. Plant material and experimental site

Experiments were performed on 33 genotypes that were part of a grapevine core collection (Nicolas *et al.,* 2016) built to represent the genetic diversity of *Vitis vinifera* L. A first subset of 21 genotypes was selected based on the leaf-burning symptoms that resulted from the extreme heatwave of June 2019 in the experimental vineyard at the Institut Agro, Montpellier. The proportion of leaves that were burnt (0–100 %) and the burning intensity on individual leaves (qualitatively noted from 0 to 5) were used to define genotypic classes. Among the 21 genotypes,

9 were defined as 'sensitive' to high temperatures and 12 other ones as resistant. A second subset of 16 genotypes was selected to maximise the variability in architectural traits such as leaf orientation, leaf shape and internode length. These 16 genotypes displayed medium sensitivity to high temperatures in June 2019 (Supplementary Table S1).

The experiments were conducted at the Institut Agro, Montpellier, France (43°.83' N, 38°.53' E) in the summers of 2021 and 2022 on ungrafted, potted plants. Plants were four years old in 2021 and one year old in 2022. The four year old plants were repotted in winter before the experimental period. When the plants were repotted a large part of the root system was cut. This approach greatly reduced the potential impact of the age of the plants. Measurements were performed from the 10th to the 19th of August in 2021 and from the 19th of July to the 8th of August in 2022. The plants were grown in pots of 9L in 2021 and 4L in 2022. Only one annual shoot was kept with all the secondary axes removed on each plant. All the inflorescences were also removed before the anthesis.

The experimental design included all 279 genotypes (with 8 replicates per genotype) of the core collection. The rows had an NW–SE orientation with two lines of pots per row. The distance between each pot along the row was around 0.2 m and the inter-row distance was equal to 1.5 m. The plot was composed of 10 rows with 240 pots per line representing an area of 1036 m². All the individuals of each genotype were gathered together along the rows. In each row, two pots with the same genotype were placed face to face to represent self-shading conditions that could be observed in vineyard conditions. As a consequence, half of the individuals of a given genotype were oriented in the northwestern direction and the other half in the south-eastern direction. The plants that were followed in our studies were randomly located in this experimental plot. The plants were fertirrigated to avoid any water or mineral deficiency and phytosanitary treatments were performed to limit the development of fungal diseases. In 2021, each day, five watering periods of 8 minutes were applied (at 8:00 am, midday, 4:00 pm, 6:00 pm and 11:00 pm) with a water flow rate of 2 L.h-1. This corresponds to 1.33 litres per day. In 2022, the plants were irrigated four times during the day for 9 minutes (at 8:30 am, 11:00 am, 3:00 pm and 7:00 pm) with a water flow of 2 L.h-1, which corresponds to 1.2 litres of added water per day. This amount of water was largely higher than the water transpired by the plants to get an optimum development at this stage (around 0.5 L, data not shown). Regarding the fertilization of the plants, we added the nutritive solution that was added in was composed of 22 % nitrogen. The proportion of nutritive solution in the water added for irrigation was equal to 0.2 %.

2. Measurement of meteorological and physiological variables

Throughout the experiments in 2021 and 2022, air temperature (T) and relative humidity (RH) were measured with a thermo-hygrometer (HMP155 Vaisala; Oy, Helsinki), solar radiation was measured with a pyranometer (LP02 Campbell Scientific Ltd, Shepshed, Leicestershire) and wind speed with an anemometer (A100LK Vector Instruments, Rhyl, UK). Vapour pressure deficit in the air (VPD) was derived from air temperature and relative humidity. All sensors were located in a weather station in close proximity (around 20 m depending on the position of the plants in the experimental plot) to the plants used in the study. Measurements of stomatal conductance (gs) and leaf temperature (Tleaf) were performed with a fluo-porometer (Li-600, LI-COR Biosciences Inc, Lincoln, NE, USA). These measurements were made on four leaves per genotype each year (two leaves on two plants in 2021, and one leaf on four plants in 2022). Measurements were made on sun-exposed leaves during six and eleven days in 2021 and 2022, respectively. The same leaves were tagged and measured throughout the experiments. The measurement days were divided into measurement sessions with one session in the morning and another one in the afternoon (10 sessions in 2021 and 20 sessions in 2022). Each measurement session took around two hours to measure around 60 leaves. The choice of the different measurement sessions was made to maximise the range of climatic conditions in which measurements were performed.

At the end of the experiment in 2022, potential photosynthetic activity was measured with an infrared gas analyzer (LI-6800, LI-COR Biosciences Inc, Lincoln, Nebraska, USA). Four plants per genotype and two leaves per plant were measured. Two conditions were set in the measurement chamber and resulted in two measurements of the photosynthetic activity, Amax at saturation light (photosynthetically active radiation = 1500 µmol m^{-2} s^{-1}) and ambient CO_2 concentration on the one hand and Asat at saturating light and saturating CO_2 concentration (1800 ppm) on the other hand. The other climatic conditions within the measurement chamber were similar for all the measurements (T = 29 °C, VPD between 1.9 kPa and 2.4 kPa); these conditions are known to be non-limiting for photosynthesis in grapevine (Prieto *et al*., 2012). Measurements were performed in the morning between 09:00 and 13:00 h (local time, GMT +2) on fully expanded and sun-exposed leaves located on the 12th node from the shoot extremities. After Amax and Asat measurements, leaf water potential (Ψleaf) was measured on the same leaf with a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Meanwhile, leaf water was also measured on a neighbouring leaf which was placed in a plastic bag for 1 hour before measurement to stop the transpiration (Begg and Turner, 1970). These measurements are known to give an estimate of the stem water potential (Ψstem). All these measurements (Asat, Amax, Ψleaf and Ψstem) were measured on eight leaves per genotype (4 leaves on 4 plants per genotype). Moreover, SPAD values, considered as a proxy of chlorophyll content, were measured using a SPAD-502 Chlorophyll Meter (Konica-Minolta, Tokyo, Japan). These measurements were performed at the end of the experimental periods on leaves located close to the ones measured for photosynthesis activity and on the same plants.

3. Architectural measurements

Two plants per genotype on the western side of the row were digitized both in 2021 and 2022 at the end of the

measurement periods. Digitizing was done with a Polhemus electromagnetic digitizer (3Space Fastrak; Polhemus Inc., Colchester, VT, USA). Seven 3D coordinates on each metamer along the primary axis were recorded. A metamer is the elementary structure of plants composed of one internode and a leaf. In the case of grapevine, a metamer can bear a cluster (at the base of the annual shoots) or one tendril in the opposite position relative to the leaf (Srinivasan and Mullins, 1979). The seven digitised points on this metamer correspond to the following values: the insertion point of the petiole on the stem, the insertion of the blade on the petiole and the five extremities of the five main veins on the leaf blades.

Based on these 3D coordinates, we computed the internode length (IL), the individual leaf area (LA, which was estimated leaf coordinates from previous image analyses of a subset of leaves) and the leaf elevation angles (R) for all the metamers along the main stem. In our study, the elevation angles varied between -90 and 90°. An elevation angle equal to 0° represented horizontal leaves, 90° bending leaves in a downward direction and -90° erected leaves in an upward direction.

3.1. Statistical analysis

All statistical analyses were performed with R software (R Development Core Team, 2013).

A clustering approach was used to characterise the existing variability in the climatic conditions during the different measurement periods (Ward method; Ward Jr, 1963). The variables considered for this clustering were the air temperature (T), relative humidity (RH), wind speed (WS), VPD and incident solar radiation (Rs). For architectural traits (IL, LA and R), a unique value was computed for each plant as the mean values recorded on each phytomer along the stem. Phytomers at the base of the stem (rank < 5) and at its extremity (higher than 80 % of the total phytomer number) were not considered to compute these mean values. Indeed, phytomers at the base were preformed and displayed smaller sizes (Pallas *et al.,* 2009) whereas those at the extremities were not fully expanded resulting in smaller leaves and internodes. Following Barthélémy *et al.* (1997), preformed metamers refer to the metamer that was already present in the latent bud before budburst while neoformed metamers are those that began their development after budburst.

For the architectural and functional traits that were estimated once at the end of the experiments (Asat, Amax, SPAD, Ψleaf, Ψstem), we used a mixed effect model with the genotype as a random effect and the year as a fixed effect to extract the Best Linear Unbiased Predictors (BLUPs). For gs and Tleaf, we computed the BLUPs considering the genotype as a random effect and a fixed effect of the measurement period. The measurement periods were presented in this study as a variable combining the day of measurement and the period of the day (morning or afternoon, e.g., 2021_08_19_am). For gs and Tleaf, the BLUPs were also computed considering separately the data recorded for each type of weather conditions defined from the clustering on climatic data. For all the analyses, genotypic values for each variable were computed as the sum of the BLUPS and the mean of the phenotypic data. Variance estimates of the mixed effect models were used to estimate the broad-sense heritability (H^2) as:

$$H^2 = \frac{{\sigma^2}_G}{{\sigma^2}_G + \frac{{\sigma^2}_R}{n}}$$

where ${\sigma^2}_G$ is the genetic variance, ${\sigma^2}_R$ the residual variance, and n is the number of replicates per genotype. Coefficients of variation of the genotypic values were computed as the ratio of the standard deviations of genotypic values to their mean values.

One-way ANOVAs were used to analyse the impact of the group of sensitivity to burning symptoms on architectural and functional traits. These ANOVA were performed on the genotypic values estimated on all the dates of measurements for gs and Tleaf. The correlations between all the variables were studied. The Pearson coefficients of the correlations were computed and their levels of significance were tested. For the correlations between gs and Tleaf, the residuals between the observed values and the linear relationship were computed, considering the whole dataset or each type of climatic type, independently. Then, the correlations between residuals were analysed for each type of climate.

A clustering (Ward method) on the genotypic values of functional and architectural traits was performed. Principal component analysis (PCA) with the same set of variables was also made. The over or under-representation of each type of genotype ('sensitive', 'resistant') was computed as the ratio of the number of 'sensitive' or 'resistant' genotypes to the total number of both types of genotypes. Since the number of 'sensitive' genotypes was lower than the one of resistant genotypes (9 vs 12), the number of 'sensitive' genotypes in each group was corrected by multiplying this number by 12/9.

RESULTS

1. Climate variability between the measurement periods

Five types of climates covering the 30 experimental periods were detected by the clustering performed on the climatic variables (Figure 1). The first type included six measurement periods and corresponded to the warmest and driest periods (called 'Warmer') with an average temperature (T) of 35.9 °C, incident solar radiation intensity (Rs) of 832 Wm^{-2}, and vapour pressure deficit (VPD) of 4.13 kPa (Table 1). The second type (called 'Warm_dry') corresponded to warm and dry periods but was less stressful than 'Warmer periods' with average T = 31.9 °C and VPD = 3.34 kPa. This group included the largest number of measurement sessions (11) and represented typical weather conditions observed in the Mediterranean areas in the south of France in summer. The third type (called 'Warm_wet') also corresponded to warm periods (T = 32.1 °C). Nevertheless, for this period, higher values of air humidity were observed (RH = 49.5 %).

TABLE 1. Mean values of the climatic variables for the different types of climate in which gs and Tleaf measurements were made.

Type of days	Number of measurement periods	Air temperature (TC_mean, °C)	Air humidity (RH_mean, %)	Solar radiation (SlrW_mean, W.m^{-2})	Wind speed (WS_mean, m.s^{-1})	Air vapor pressure deficit (VPD_mean, KPa)
Warm_dry	11	31.9	29.7	771	1.76	3.34
Cold	7	28.6	48.7	605	1.44	2.02
Colder	3	25.7	57.5	450	0.70	1.44
Warm_wet	3	32.1	49.5	854	2.53	2.41
Warmer	6	35.9	29.8	832	1.87	4.13

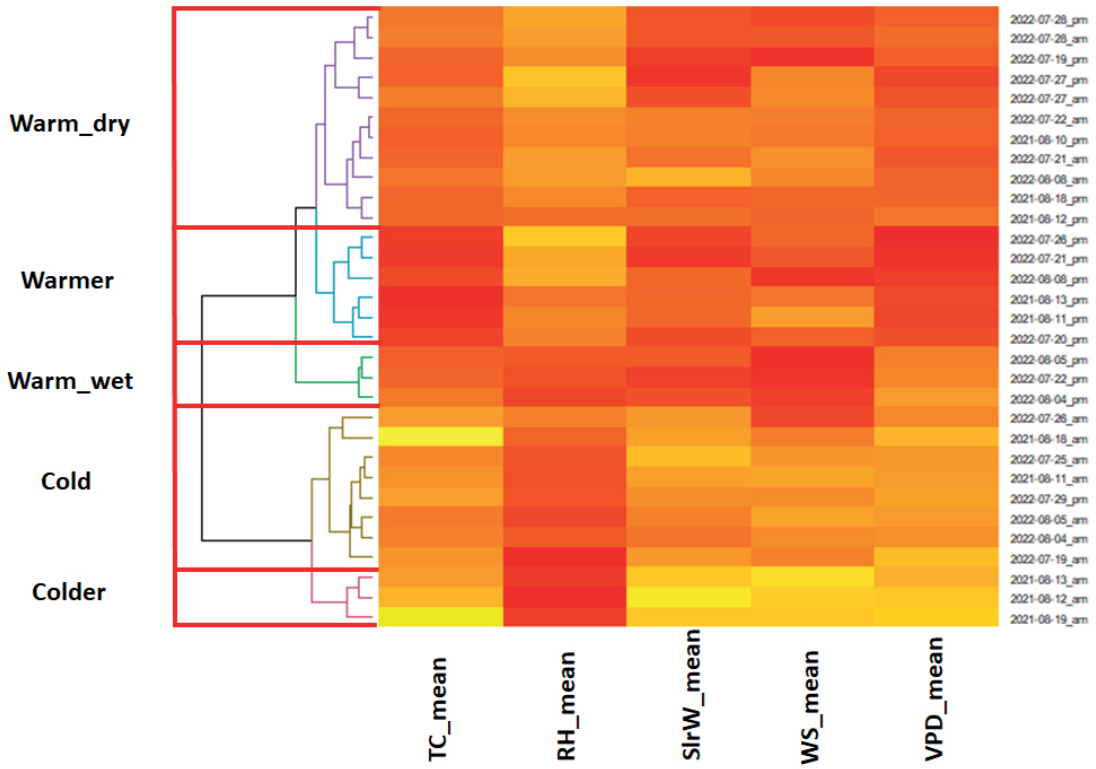


FIGURE 1. Heatmap representation and results of the clustering performed on the climatic variables recorded during the measurement periods in which gs and Tleaf measurements were made.

A colour map (yellow-red) was used to show the normalised values of each climatic variable with yellow and red colours representing low and high values respectively. The rectangles represent the first five groups determined by the clustering. TC_mean: mean temperature during the experimental period, RH_mean: mean relative humidity, SlrW_mean: mean solar radiation intensity, WS_mean: mean wind speed, VPD_mean: mean vapour pressure deficit. The suffix_am, _pm after the date of measurement indicates the period of the day during which the measurements were made (morning and afternoon respectively).

Such kinds of weather were rare and only included three measurement periods observed in 2022, only. The two other groups corresponded to colder periods. For the first group (called 'Cold'), which included seven measurement periods, temperatures still remained quite warm (T = 28.6 °C) and the amount of solar radiation, even lower than for the three other groups, was slightly reduced (Rs = 605 W m^{-2}). The last group corresponded to cloudy periods with incident radiation equal to half of what was observed for the warm and sunny periods (Rs = 450 W m^{-2}). This group also displayed the lowest temperatures (T = 25.7 °C). These weather conditions were observed in 2021, only and are rather unusual in the Mediterranean areas as shown by the low number of periods belonging to this group (3).

2. Variabilities and heritabilities of functional traits measured

The architectural traits (individual leaf area: LA, elevation angle: R and internode length: IL) computed at the end of the experiments were highly heritable when computed in the years 2021 and 2022 separately (Figure 2A). The broad sense heritabilities (H^2) of these traits were lower but remained high (> 0.70) if both years were considered together. R was the most heritable trait (H^2 = 0.88) closely followed by LA (H^2 = 0.73) and IL (H^2 = 0.7). The coefficient of variations of these architectural traits computed on phenotypic values (Figure 2C) was the highest for LA (0.4) and lower for IL and R (0.25).

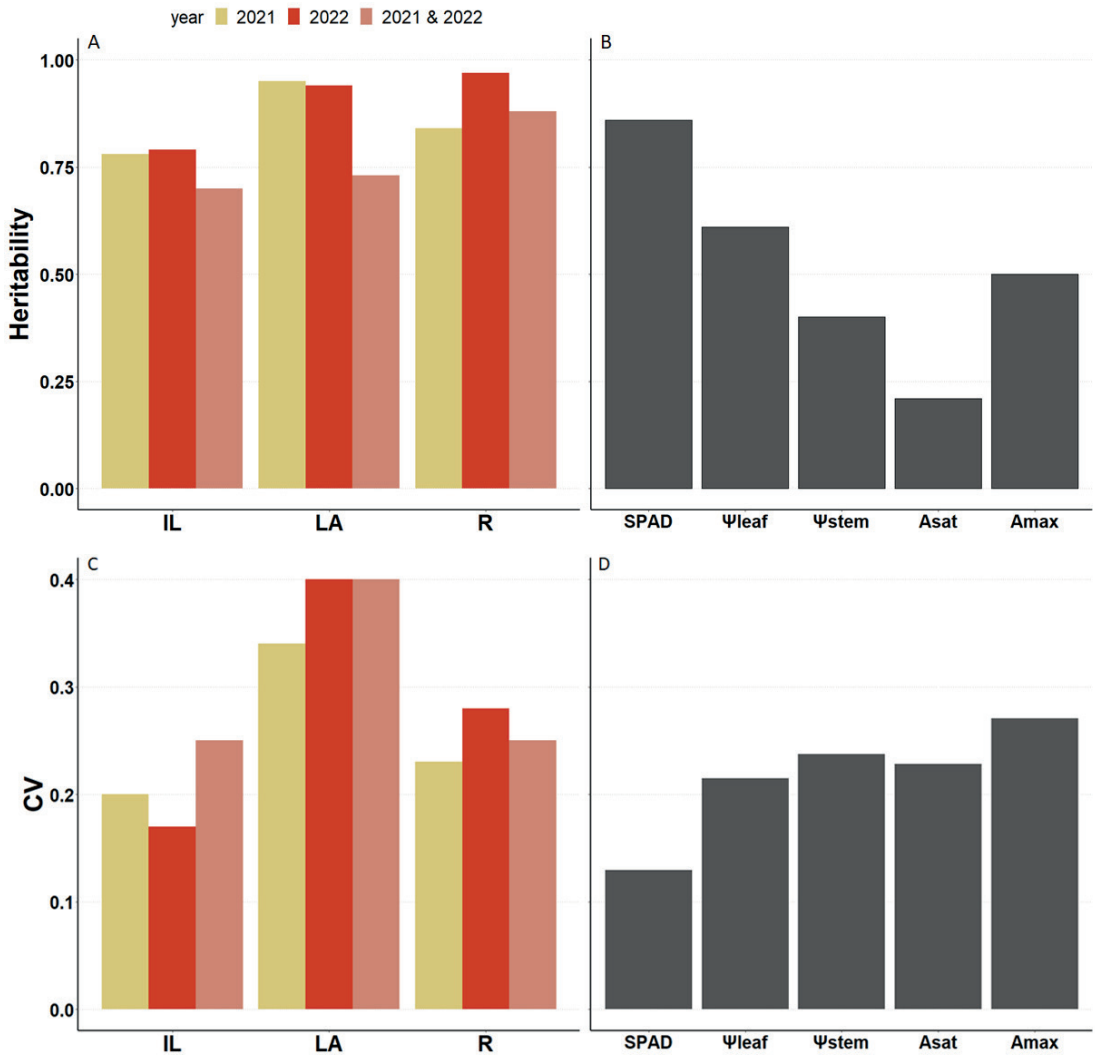


FIGURE 2. (A) Broad sense heritabilities of architectural traits (individual leaf area, LA, leaf elevation angle, R and internode length, IL) computed for the two years of measurement (2021, 2022) or for both years together (B) broad sense heritabilities of functional traits measured at the end of the experiments (SPAD, Ψleaf, Ψstem, Asat and Amax) and (CV) coefficient of variation of genotypic values of the architectural and functional traits.

For the physiological traits measured at the end of the experiment (Figure 2B), H^2 was the highest for SPAD values ($H^2 = 0.86$). It was followed closely by the leaf water potential (Ψleaf) and photosynthesis at saturating light (Amax) for which H^2 were equal to 0.61 and 0.50 respectively. The stem water potential (Ψstem) and the photosynthesis at saturating light and CO_2 concentration (Asat) were the least heritable variables with $H^2 = 0.4$ and 0.21, respectively. The coefficients of variations of these functional traits (Figure 2D) were the lowest for SPAD (0.13) and higher for the four other traits (between 0.21 and 0.27).

3. Variabilities, heritabilities and correlations between stomatal conductance and leaf temperature

Variations in leaf temperatures and stomatal conductance measured during the 30 experimental periods in both 2021 and 2022 were analysed. H^2 of these traits were quite high (higher than 0.6) if both years were considered separately except for Tleaf in 2022 for which $H^2 = 0.33$, only (Figure 3A–C). Finally, when considering both years, the heritability of the functional traits was lower but remained high, above all for leaf temperature ($H^2 = 0.56$). H^2 were also computed by splitting the dataset according to the type of climate (Figure 3B–D). For gs, similar heritabilities were observed for all the types of climate (around 0.5) except for the 'Colder' days for which H^2 was equal to 0.73. It is worth mentioning that only three measurement periods belonged to this group. There was more variability in H^2 values for Tleaf depending on the climatic conditions. H^2 values were the highest for the 'Warmer' ($H^2 = 0.67$), 'Cold' ($H^2 = 0.61$) and 'Colder' ($H^2 = 0.8$) measurement periods. H^2 was lower for 'Warm_Dry' ($H^2 = 0.44$) and 'Warm_Wet' ($H^2 = 0.41$) periods. In that case, no relationships between H^2 and the number of measurement periods were observed. H^2 was similar between the 'Warm_Wet' and 'Warm_Dry' periods whereas three and eleven measurement periods, respectively, belonged to these two groups.

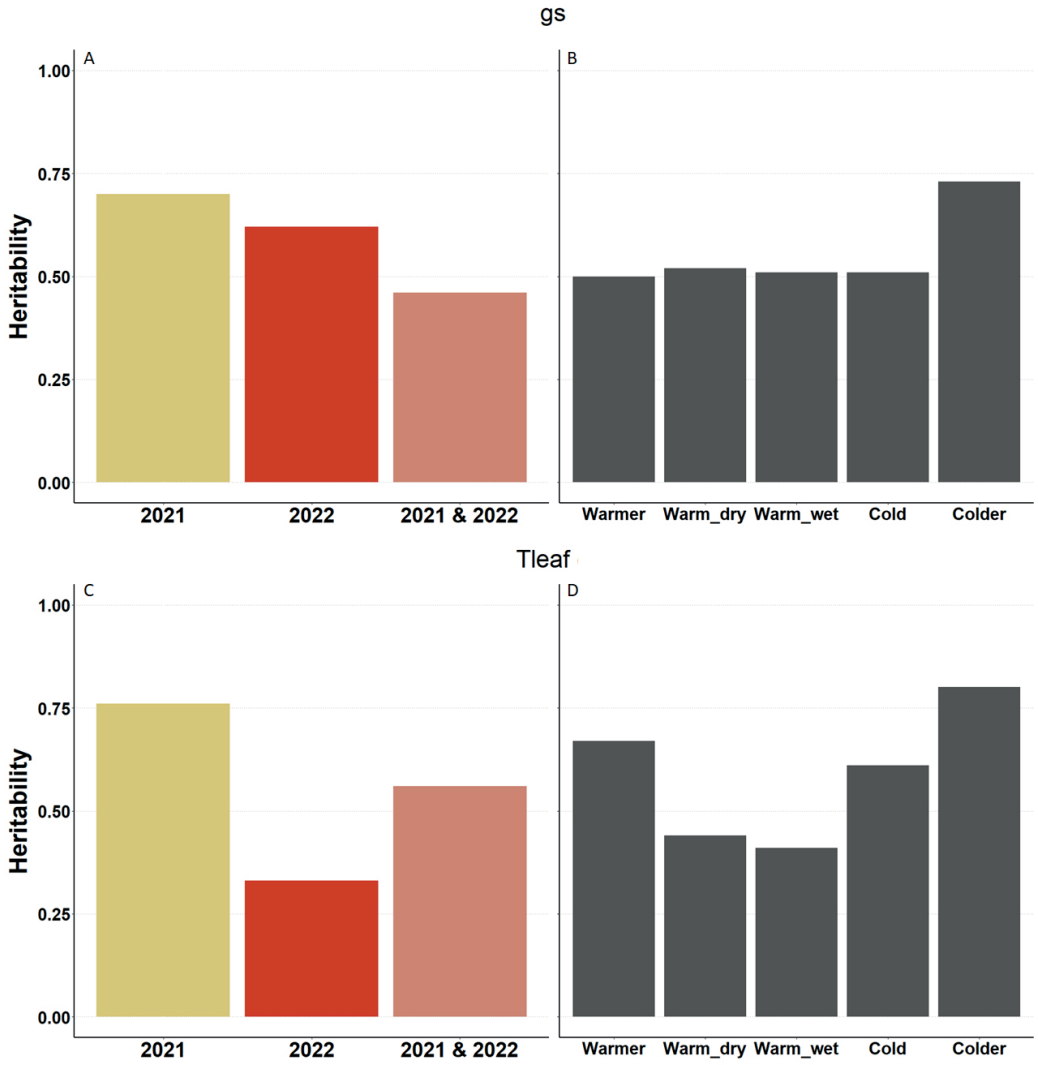


FIGURE 3. Broad sense heritabilities of functional traits (leaf temperature, Tleaf and stomatal conductance, gs) computed all the measurement periods for the two years of measurement (2021, 2022) or for both years together (A, C) and computed considering the data corresponding to each types of measurement periods (B, D) identified with the clustering performed on climatic variables (see Figure 1)

The analysis of correlations between gs and Tleaf revealed a positive correlation (r = 0.22) between both variables which was not expected from the well-known evaporative cooling effect. This was due to lower gs values for colder days compared to warmer ones, likely associated with the cloudiness of the days (Figure 4). In agreement with the evaporative cooling effect, negative correlations appeared if the correlation within each type of climatic condition was considered, except for the colder days. These negative correlations were significant for 'Warmer' (r = -0.54), 'Warm_Dry' (r = -0.58) and 'Cold' (r = -0.33) conditions. Although these correlations were significant, large variability around the general trends was observed with r values always lower than 0.60, revealing contrasted relationships between gs and Tleaf depending on the genotypes. The residuals of the linear relationships between gs and Tleaf were significantly correlated for the 'Cold', 'Warmer' and 'Warm_wet' measurement periods ($r > 0.68$, $p < 0.001$ Supplementary Figure S1).

4. Impact of architectural and functional traits on the sensitivity to extreme temperatures

The differences in the estimated genotypic values of functional and physiological traits for the two classes of genotypes (determined from the burning symptoms observed during the 2019 heatwave) were analysed (Figure 5). First, a significantly higher stomatal conductance was observed for the 'sensitive' genotypes ($p < 0.001$, mean gs = 0.109 mol m^{-2} s^{-1} and 0.113 mol m^{-2} s^{-1} for 'sensitive' and 'resistant' genotypes, respectively). Consistently with the negative correlations observed between gs and Tleaf (Figure 4, considering 'Warmer', 'Warm_dry' and 'Cold' measurement periods), this higher stomatal conductance induced a significantly lower Tleaf for the 'sensitive' genotypes. A lower saturating photosynthesis activity (Asat) was observed for the 'sensitive' genotypes compared to the resistant ones but these differences remained non-significant. For the other functional variables (SPAD, Ψleaf, Ψstem and Amax), no noticeable difference between the class of

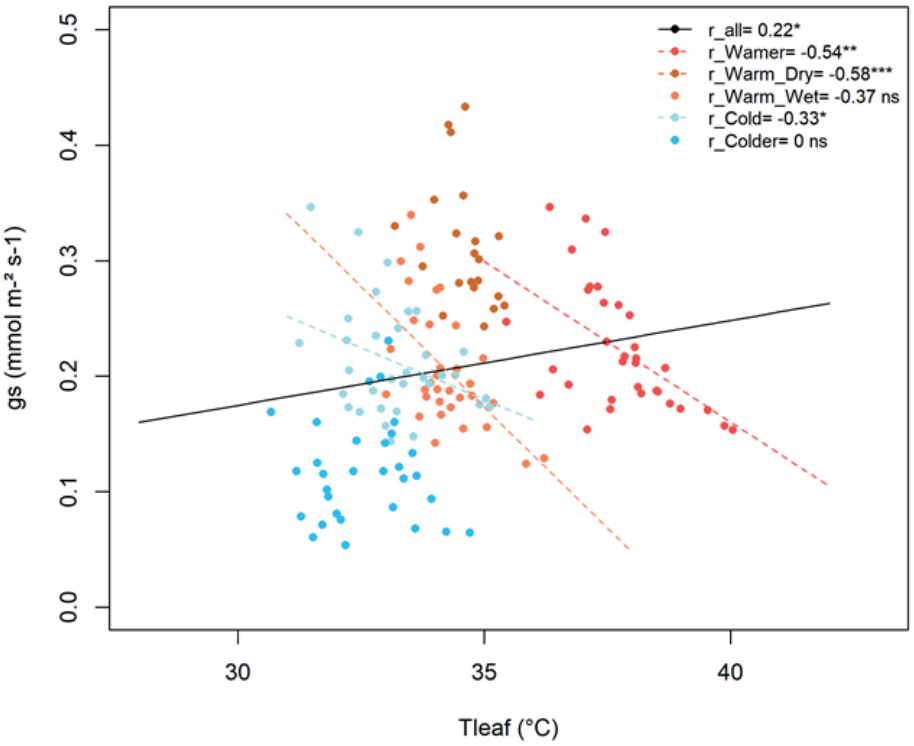


FIGURE 4. Relationships between gs and Tleaf observed in 2021 and 2022 for the different types of climatic conditions.

Points represent the genetic values estimated for each type of climatic condition separately. The continuous black line represents the linear regression for the whole dataset, and dashed lines are the linear regression for each type of climatic conditions. The linear regression is represented when the correlations were significant. The Pearson correlation coefficient and its associated significance is represented in the up right corner of the figure. ***: $p < 0.001$; **: $0.001 < p < 0.01$; *: $0.01 < p < 0.05$; ns: $p > 0.05$.

genotypes ('resistant', 'sensitive') was observed (data not shown). Regarding the architectural traits, the impact of the group of genotypes also remained non-significant at $p < 0.05$, but a tendency to have longer IL ($p = 0.05$) and higher LA ($p = 0.05$) for 'sensitive' genotypes could be observed.

4.1. Identification of genotype classes based on architectural and functional traits—relationships with the sensitivity to leaf-burning symptoms

The results of the principal components analysis (Figure 6) performed on the genotypic values of functional and architectural traits computed on the entire dataset (combining all the experimental periods together) showed that the three first axes explained more than 62 % of the observed variability. The first dimension (explaining 28.0 % of the variability) was positively correlated with IL, LA and negatively with gs and Ψleaf (Supplementary Table S2). These results were consistent with the observed positive correlation between LA and IL and between Ψleaf and gs (Supplementary Figure S2). Moreover, LA and IL were negatively associated with Ψleaf and gs although these correlations were not significant. The second dimension was positively correlated with R and negatively with Ψstem consistently with a negative correlation observed between both traits. The third dimension was mainly associated with the variation in Tleaf which appeared to be uncorrelated with all the other variables, except with gs.

The hierarchical clustering performed on the genotypic values revealed the existence of four main groups of genotypes differing in both architectural and functional traits. Groups 2 and 3 (5 and 8 genotypes, respectively) mainly differed in LA, IL, gs and Ψleaf values (Table 2), and were, thus, well discriminated by the first dimension of the PCA. The mean coordinates on the first dimension were equal to -2.39 and 1.66 for groups 2 and 3, respectively. Group 2 gathered the genotypes with the largest vegetative development and low gs, while the opposite was observed for Group 3 (small genotypes with high gs). Group 4 (8 genotypes) included the genotypes with high gs and medium vegetative development. It differed from the other groups mainly due to their low R and low values on the second dimension of the PCA. Finally, Group 1 (12 genotypes) had a medium vegetative vigour, similar gs values to those of Group 2 and were different from the three other groups due to their high Tleaf values (Dim. 3 of the PCA).

'Resistant' and 'sensitive' genotypes were not equally distributed among the groups defined by the clustering. A higher representation of 'resistant' genotypes was observed in Group 1 (medium-size plants, with low gs and high Tleaf), and a higher representation of 'sensitive' genotypes in Group 4 (medium-size plants with high gs). A higher representation of 'sensitive' genotypes was also detected in Group 2 (largest plants with low gs) which was the group including the lowest number of genotypes.

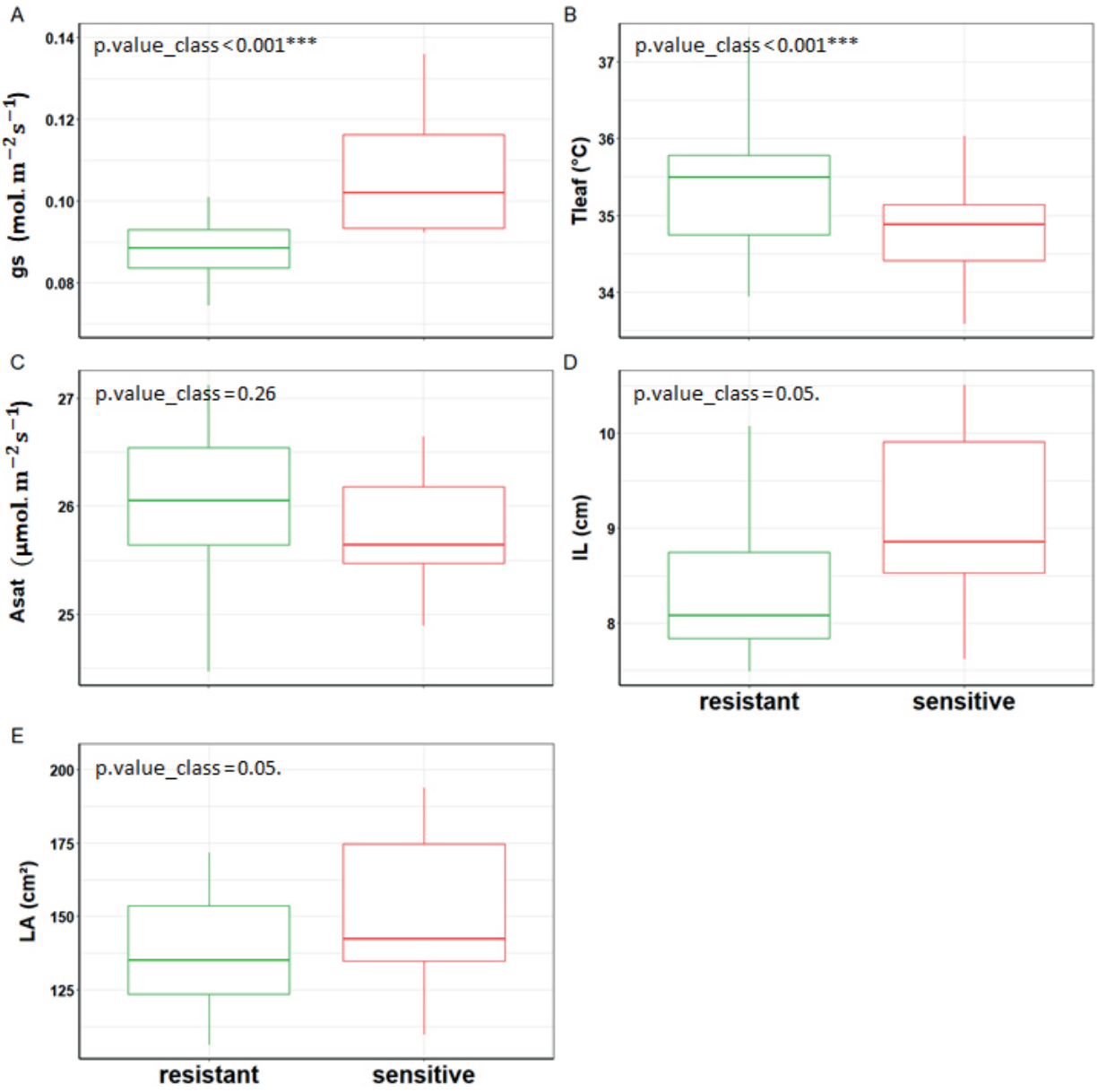


FIGURE 5. Box plot representation of the physiological (gs, Tleaf, Asat) and architectural traits (IL, LA) depending on the class of genotypes identified from the burning symptoms observed in June 2019.

The values represented on each boxplot are the genotypic values computed on the whole dataset (21 measurement dates for gs and Tleaf). A one-way ANOVA with the genotype class effect was performed. The significance of genotype class effect is represented on the top leaf corner of each sub-figure. (***: $p < 0.001$; $0.10 < p < 0.05$, ns: $p > 0.05$)

TABLE 2. Mean values of architectural and functional traits for the different groups identified from the clustering approach, number of genotypes per group and repartition of genotypes within each group depending on their sensitivity to leaf burning symptoms ('ratio of resistant to sensitive genotypes').

Goups	Number of genotypes	IL (cm)	LA (cm^2)	R (°)	gs ($mol.m^{-2}\ s^{-1}$)	Tleaf (°C)	SPAD (SPAD unit)	Ψleaf (bar)	Ψstem (bar)	Amax ($\mu mol.m^{-2}\ s^{-1}$)	Ratio of 'resistant' to 'sensitive' genotypes
1	12	8.3	144.1	49.0	0.17	35.1	35.9	8.4	5.0	13.4	3.8
2	5	9.8	187.2	53.0	0.16	33.9	37.0	7.6	4.7	13.6	0.5
3	8	8.2	119.4	56.9	0.23	33.7	40.3	8.6	4.8	14.3	1
4	8	8.6	150.5	38.3	0.23	33.8	37.9	8.5	5.1	13.7	0.4

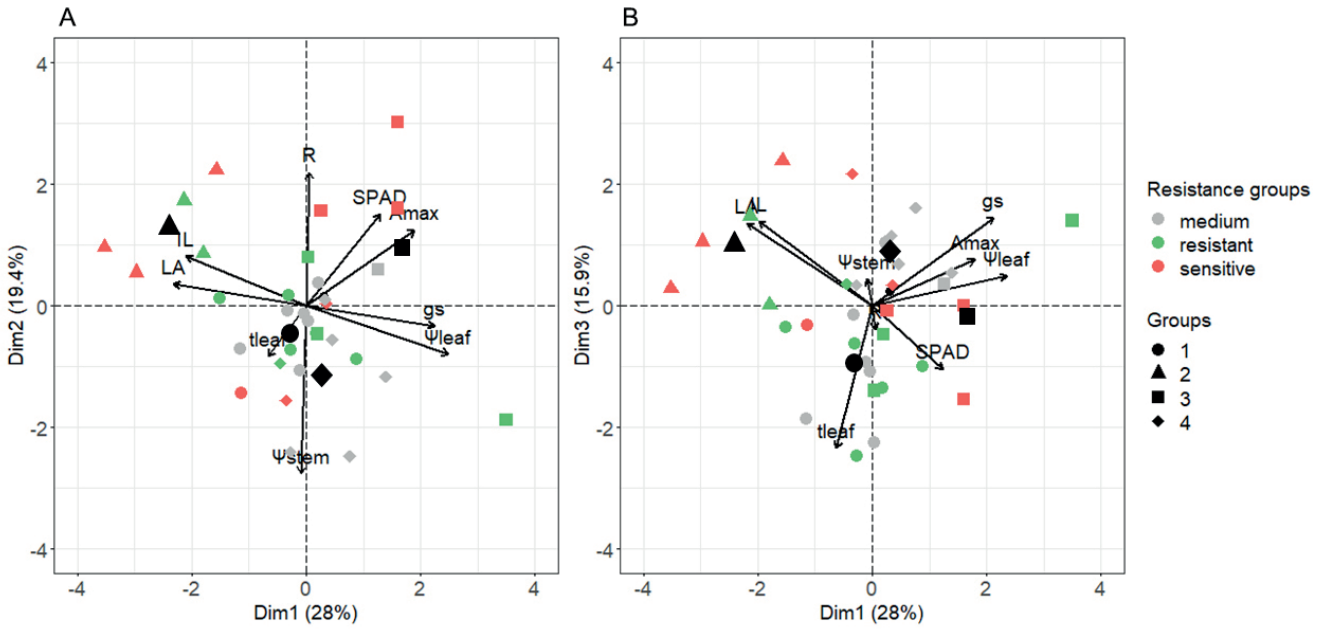


FIGURE 6. Principal component analysis performed on the genotypic values of both architectural and functional traits.

Projection of individuals and variables in the two first dimensions of the PCA (A) and in the first and third dimension (B). The percentage of variability explained by each dimension is represented in the axis labels. Groups represented by different symbols were detected using a clustering approach (Ward method). The biggest symbols in black represent the barycenter of each group in the two projections (Dim 1 and 2; Dim 1 and 3). Different colours refer to the sensitivity to leaf burning symptoms observed in 2019.

Moreover, some variability in the distribution of the group of genotypes based on the burning symptom was observed in the PCA, even if the differences were low. Indeed, the mean coordinates on the first three axes of the PCA were equal to 0.26, 0.07 and -0.31, respectively on Dim.1, 2 & 3 for the resistant genotypes while the mean coordinates were equal to -0.63, 0.77 and 0.47 for the sensitive ones.

DISCUSSION

Phenotyping the functional and architectural traits of a diverse range of grapevine genotypes should help to identify combinations of traits favourable to plant functioning under climate change. In particular, our study was designed to propose ideotypes with adapted architecture that could limit the increase in leaf temperature through the regulation of their stomatal conductance. The results presented in this study are based on a unique set of data with more than 2700 measurements of leaf temperature and stomatal conductance performed on 33 genotypes during 30 measurement periods. This dataset was complemented with digitizing data to get an exhaustive description of 3D plant architecture. Indeed, extrapolating data from potted vine to field conditions is challenging. Vineyards are often prone to water stress which could modify the conclusion of our study. Nevertheless, in our study, we took special attention to growing plants under well-watered conditions. We could hypothesize that our results could be more easily extrapolated to irrigated vineyards. Another point that could deserve the extrapolation of the results to vineyard conditions is that plants in vineyards are older and are subject to different training systems which are not similar to the one used in this study (only one shoot growing per plant). Although, previous results in apple trees showed that the genotypic variability in architectural traits (in apple trees, for example) is conserved during tree ontogeny.

1. Analyses of architectural traits revealed their high heritability levels

The results show that architectural traits (IL, LA, R) were highly heritable (Figure 2). A higher heritability in LA compared to IL has been observed which is consistent with previous observations (Sreelathakumary and Rajamony, 2004; Tena *et al.,* 2016). Moreover, this heritability remained high if both years 2021 and 2022 were considered together, although plants did not have the same age in both years (one and two-year-old). The maintenance over the years in the architectural traits has been observed in previous studies with trees (Segura *et al.,* 2007). Nevertheless, in trees, ontogenetic gradients characterised by an overall reduction in the length of the growth units and their ramifications have been observed over the years (Renton, 2006). In our case, the system we studied did not follow the natural plant ontogenetic gradient as grapevines are strongly pruned every year to leave only a few growing buds (one main axis in our case). In grapevine, this ontogenetic gradient could be observed only for minimal pruning systems (Torregrosa *et al.,* 2021). One of the most noticeable results of this study is the high heritability of the leaf elevation angle (R). High heritability in leaf angle has been previously observed among a population of *Olea europaea* (García-Verdugo *et al.,* 2010) and on a panel of maize hybrids grown in a greenhouse (Perez *et al*., 2019), but the studies on the architectural traits in perennials remain rare.

Compared to previous studies, a significantly lower heritability in leaf angle (R) could have been expected in the present study on potted grapevines grown at rather high density under fluctuating climates. In fact, R depends on many factors other than the genotype such as phototropism and the turgor of leaves and petioles (Nieves-Cordones *et al.,* 2019). Leaf inclination could also be modified under shading conditions, or in response to high temperatures that induce hyponastic growth (Hunter *et al.,* 2020; Mullen *et al.,* 2006; van Zanten *et al.,* 2010). It could be argued that in our study, climatic conditions in both years were similar enough not to induce specific variation in leaf angle associated with stressful environments.

In this study, we consider a mean value at the plant scale for each architectural trait taking care not to include preformed metamers and those located at the top of the canopy that displayed lower sizes. This approach was consistent because of the high stability in internode length and leaf area observed on the "middle" part of the stem (Pallas *et al.,* 2009). Conversely, intra-plant variability in leaf orientation was previously observed when comparing different training systems (Mabrouk *et al.,* 1997). The leaf azimuth angle was shown to be affected by the training systems as well as by the relative orientation between the leaf and the inter-row (Hunter *et al.,* 2020). The azimuth angle was not considered in our study. Finally, it is important to note that the vines were not of the same age during the study and the experiment was conducted in different-sized pots. Nevertheless, the plants that were four years old were reported at the beginning of the experiments and a large part of the roots was removed. These practices strongly reduced the potential impact of plant age.

2. Functional traits are rather less heritable than architectural traits and independent of each other

Functional traits (stomatal conductance, leaf water potentials, photosynthesis) and the resulting leaf temperature showed heritability values lower than the ones of architectural traits (Figure 3). The only exception was the very high heritability value observed for SPAD despite a quite low range of variation in this measurement. Previous studies in other crops suggested that SPAD could be a relevant indicator to discriminate genotypes (Kamphorst *et al.,* 2020), but as far as we know this study is the first one showing the relevance of this trait to discriminate genotypes in grapevine.

Studies reporting high heritabilities of functional traits or leaf temperature were rare on perennials with sometimes opposite conclusions. Ludovisi *et al.* (2017) did not find any impact of genotypic variability on canopy temperature on poplar whereas Coupel-Ledru *et al.* (2019) observed medium heritability in canopy temperature. In contrast with these studies that evaluate the genotypic variability in functional traits through general proxies computed from airborne imaging, we directly measured these variables on specific leaves. Obviously, our approach gives direct access to the variables but also has some drawbacks since we extrapolate the plant behaviour from a measurement performed on single leaves. Functional traits strongly varied within a canopy due to leaf age, position, morphology or nitrogen content (Bruschi *et al.,* 2003; Buckley *et al.,* 2013; Le Roux *et al.,* 1999). This high level of within-plant variability could explain the lower heritability values than observed from architectural traits although we took care of measuring leaves with similar age and position along the stem.

Heritability of stomatal conductance and temperature also varied depending on weather conditions (Figure 3B–D). Interestingly, the heritability of stomatal conductance was the highest on cold days when VPD values did not strongly impact stomatal conductance (Soar *et al.,* 2006). The lower heritability in stomatal conductance under warmer conditions is likely associated with the reduced range of variability under stressful environments. This hypothesis is in accordance with previous results showing lower variability in the genetic values under water deficit conditions (Lopez *et al.,* 2017).

Similar to previous studies (Sadras *et al.,* 2012), a negative relationship between leaf temperature and stomatal conductance was observed (Figure 4). This negative relationship was observed in almost all the weather conditions, except under the coldest ones likely because in these conditions, the stomatal aperture is low due to the low light conditions on cloudy days (Massonnet *et al.,* 2007). Moreover, high consistency in the behaviour of the genotypes for their response of gs to Tleaf under contrasted weather conditions was observed in our study. Such a result could be of major interest to extract genotypic parameters that could be used in modelling approaches simulating stomatal conductance depending on climatic variables in grapevine (Prieto *et al.,* 2012).

No strong correlation between functional and architectural traits was observed. This is in accordance with previous studies showing that architectural and functional traits are under independent genetic controls (Coupel-Ledru *et al.,* 2022). The only correlation observed was the negative correlation between Ψleaf and leaf area. This relationship likely results from the intertwined relationships between these two kinds of variables as larger leaves had a higher potential evaporative demand (Pereira & Kozlowski, 1977).

3. Variations in leaf temperature are mainly associated with stomatal regulation but are independent of the observed burning symptoms

The genotypes with different sensitivities to burning symptoms observed in 2019 significantly differ in their stomatal behaviour and also, to a lower extent in their architectural traits (Figure 5). Basically, the genotypes that were the least sensitive to burning symptoms displayed higher stomatal conductance and higher vegetative vigour. Low vegetative vigour (shorter internode and smaller leaf) could be an advantage under high temperatures to reduce the amount of light intercepted and leaf temperature by increasing self-shading within the canopy (Da Silva *et al.,* 2014; Pearcy *et al.,* 2005). However, leaf temperature is also influenced by other aspects such as stomatal behaviour and it

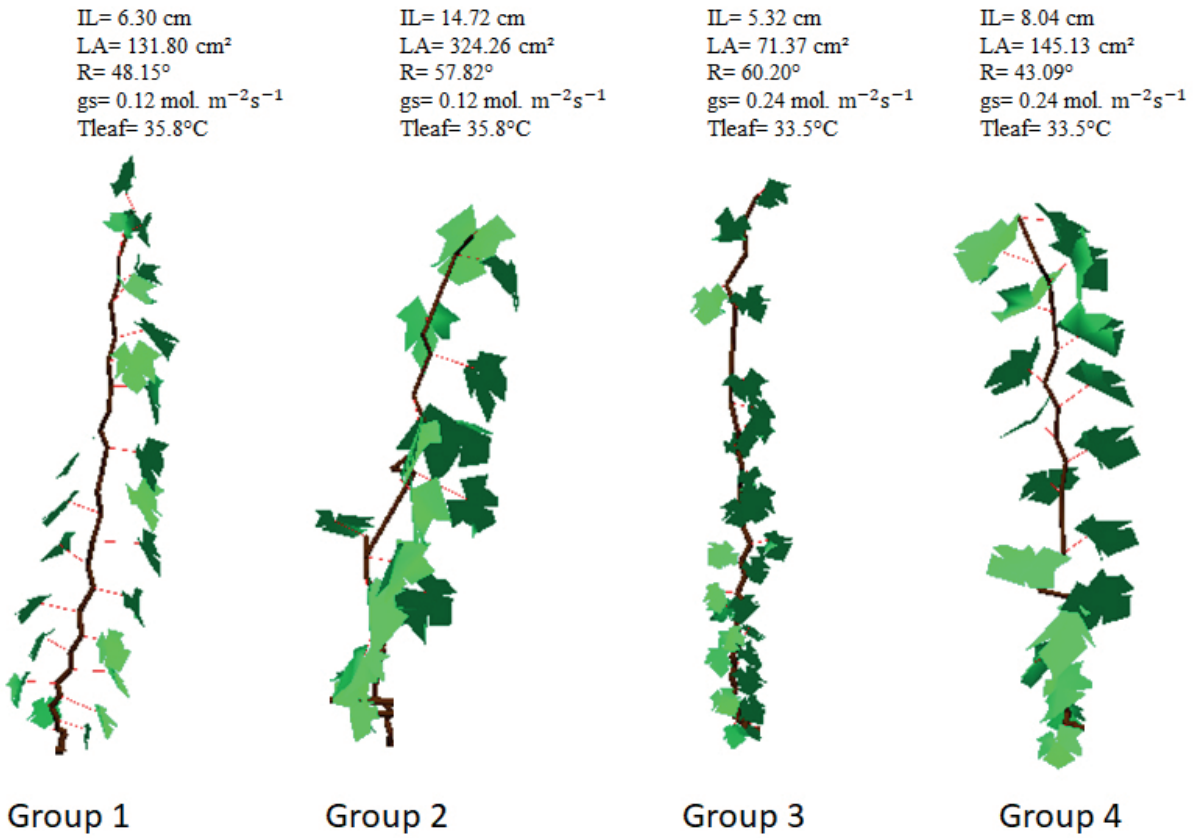


Figure 7. 3D mockups built from digitizing of four individuals belonging to the four different groups of genotypes identified with the clustering performed on architectural and functional traits.

For each individual, the corresponding mean internode length (IL), leaf area (LA), elevation angles (R), stomatal conductance (gs) and leaf temperature (Tleaf) is represented on the top of the mockups

remains difficult to conclude the relative contribution of the different variables on leaf temperature. Running sensitivity analyses on models that integrate 3D plant representation (e.g., Perez *et al.,* 2018) and equations to compute the leaf energy balance could be of major interest to solve this question (Albasha *et al.,* 2019; Bailey *et al.,* 2016) (Figure 7).

In our experimental conditions, the 'resistant' genotypes did not show higher stomatal conductance and lower leaf temperature than the sensitive genotypes as could have been expected from the evaporative cooling effect. By contrast, the resistant genotypes displayed a lower stomatal conductance with limited leaf cooling. On the opposite, the genotypes that were observed as sensitive in 2019 displayed lower temperatures due to higher stomatal conductance. This result could be considered counterintuitive, but it should be noted that the maximal temperature we reached in our experiment (37.08 °C) was far below the maximal temperature observed in 2019 (46 °C), making it difficult to fully extrapolate our results. Moreover, it is important to keep in mind that leaf temperature is possibly not completely associated with the observed leaf-burning symptoms. Other physiological adjustments such as the accumulation of heat shock proteins could explain the observed genotypic differences (Carvalho *et al.,* 2014; Sabehat *et al.,* 1998). Another hypothesis that we propose is that the strategy to keep the stomata open under very high air evaporative demand could be unfavourable for the hydraulic integrity of the plants. This behaviour would eventually cause some hydraulic failure in the vascular system under high evaporative demand conditions (Charrier *et al.,* 2018; Hochberg *et al.,* 2013).

CONCLUSION

This study evaluated architectural and functional traits and the resulting leaf temperature on a set of grapevine cultivars. It reveals high heritability in architectural traits and showed that leaf temperature was associated with changes in stomatal behaviour more than in architecture. It also suggests that the sensitivity to leaf burning is likely associated with high stomatal conductance that could cause embolism under major heatwaves. This study was performed on 33 genotypes. Therefore, further studies are required with larger populations if the objective is to detect associated genetic polymorphisms. Moreover, further studies need to be performed to analyse the genericity of the results of this study in vineyard conditions. To reach this objective, in-field high throughput measurement techniques should be deployed. We suggest making use of the T-Lidar methodology for architectural traits (Boudon *et al.,* 2014), and near-infra-red (NIRS) measurements/imaging for assessing functional traits (Ryckewaert *et al.,* 2022).

These approaches could be coupled with new statistical methods including artificial intelligence to compute functional traits of interest from NIRS measurement and target specific organs within the canopy from the T-Lidar point clouds (Harfouche *et al*., 2023).

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Author's contribution

MM, BP, TS and AC designed the experiments; ACL performed the phenotypic analyses of burning symptoms and contributed to the definition of the panel of genotypes; MM, RB did the experimental measurements, MM and BP performed the statistical analyses and wrote the manuscript including the revisions of TS and AC.

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