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SHORT COMMUNICATIONS

Potential of ethanol to reduce grapevine transpiration

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ABSTRACT

This study investigates whether ethanol (EtOH) modulates response to drought in grapevine, as demonstrated previously in *Arabidopsis*, rice and wheat. We ran a potted-cutting experiment with a progressive soil water deficit. Plants pre-treated with 250 mM EtOH solutions exhibited slower depletion of the fraction of transpirable soil water (FTSW), compared to controls. While 250 mM EtOH decreased transpiration in the early days, these EtOH pre-treated plants maintained higher leaf transpiration than controls after 10 days of soil water depletion. The FTSW threshold for the transpiration process was significantly higher in plants treated with 250 mM EtOH than in controls. These results suggest that EtOH may alter grapevine response to drought, leading to potential water savings in wine-growing regions prone to high water shortages, linked to climate change. This should encourage further testing under various vineyard conditions.

KEYWORDS: drought, ethanol, Gamay cuttings, *Vitis vinifera*, water savings

INTRODUCTION

Many recent studies show that ethanol at physiological concentrations can promote plant development or their adaption to various stresses (Diot *et al*., 2024). These authors define 'physiological concentrations' as those typically found in various plant organs, ranging from 0.1 to 1 mM, with several examples provided in this viewpoint article. In particular, the work of Bashir *et al*. (2022) demonstrated that ethanol could induce a better tolerance to drought in several plant species, including Arabidopsis, rice and wheat. This induced acclimation is particularly interesting in the context of climate change, which is expected to increase water stress in certain geographical areas, such as the Mediterranean region (Cramer *et al*., 2018; IPCC, 2021). Given that viticulture is particularly developed in this region (OIV, 2022), we sought to test the effect of ethanol on grapevine under controlled conditions of water stress, to verify if the observations of Bashir *et al*. (2022) apply to this species.

Experiments were conducted on potted grapevine cuttings, monitoring the weight of the pots to estimate plant transpiration (Lanari *et al*., 2015). This gravimetric method also enabled the estimation of the fraction of transpirable soil water (FTSW), a variable widely used to quantify soil water deficit and its impact on the plant's main functions (Sinclair, 2005). Yet, leaf expansion exhibits the highest sensitivity to FTSW (higher FTSW threshold), followed by plant transpiration and leaf senescence (Kang *et al*., 2024). Based on the original results in grapevine, presented here, we hope to quickly stimulate further research in several teams to find the appropriate conditions of EtOH application for the various varieties and geographical situations encountered in vineyards affected by water stress episodes.

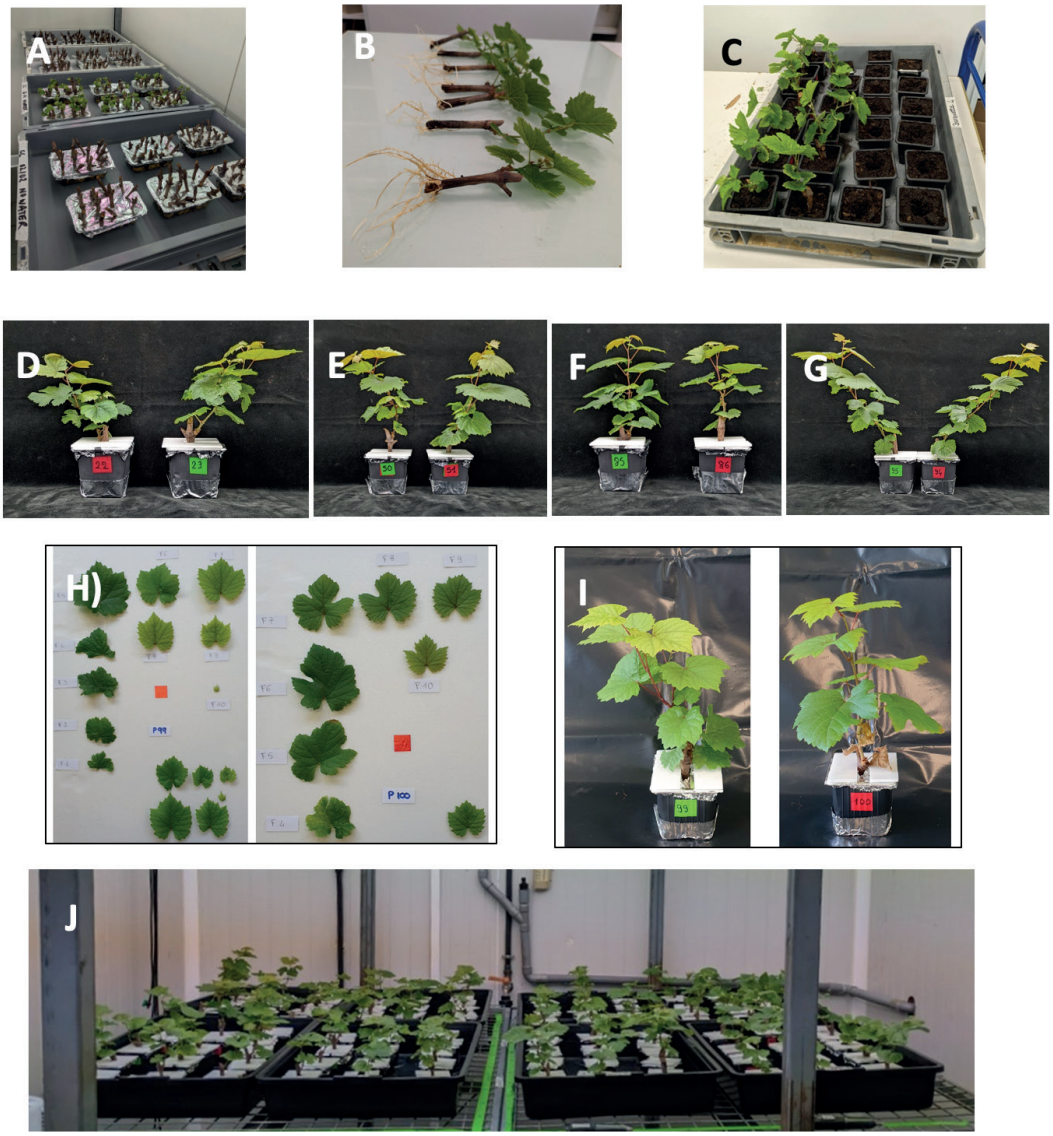


FIGURE 1. Various stages of the culture of Gamay cuttings: A) bare root cuttings in water; B-C) repotting after one month; D-G) variability of cuttings; H) measurement of leaf surface with Easy Leaf Area; I) example of dry leaves on the bottom at the end of the experiment; J) set-up in the growth chamber.

MATERIALS AND METHODS

1. Plant material

Grapevine cuttings were made from one-year-old dormant Gamay shoots (*Vitis vinifera*), clone 787, from a collection of genetic material whose plant material is tested to be safe for the main vine viruses (IFV Sud-ouest, Peyrole, France). The cuttings were prepared as described by Mullins (1966), with the following modifications. Single-node cuttings, 5 cm long with two cutter scars at the bottom to facilitate rooting, were disinfected with active chlorine (1.5% v/v) for one minute and rinsed three times with running water. Then, 12 cuttings were placed in 250 ml plastic crates filled with 150 ml water and covered with aluminium foil to hold the cuttings up, the lower end was immersed in water, the bud facing upwards (Figure 1A). The cuttings were left for one month in a growing chamber at 25 °C/20 °C 16 h/8 h (day/night) with the light set to 250 $\mu mol.m^{-2}.s^{-1}$. The water level was maintained at the initial filling mark.

2. Ethanol treatments applied to potted cuttings

One-month cuttings (Figure 1B and 1C) were transferred into 105 ml nursery plastic pots, filled with P.A.M.2 Proveen substrate (Proveen, Netherlands) and saturated with water. Plants were left to settle down and develop roots for one week in a growing chamber 25 °C/20 °C (day/night) with a 16 h photoperiod providing 250 $\mu mol.m^{-2}.s^{-1}$ photosynthetically active radiation at the top of the plants. Over the week, the plants were maintained at full soil water capacity, corresponding to 100 % of available water or FTSW equal to 1. The pots were covered with aluminium foil on the top and an additional 3 mm polystyrene sheet (Depron, Germany) was added onto the top to limit soil evaporation (Figure 1D to 1J). Evaporation did not exceed 10 % of the total available soil water after 30 days (Figure S1). Then, the day prior to the beginning of the water deficit, 52.5 ml of ethanol solutions at various concentrations were poured onto the pots, after removing temporarily the bottom aluminium foil to allow run-off of the solution into a saucer.

The ethanol concentrations tested in this study were 0, 0.4, 2, 10, 50 and 250 mM. These concentrations correspond to ethanol/water ratios of 0, 0.002, 0.012, 0.06, 0.29 and 1.46 % (v/v), respectively. The range was chosen with 5-fold increments to minimise errors from soil variability. Pairs of plants one well-watered (WW) and one water-stressed (WS) were established for all EtOH doses. A total of eight biological replicates were set up; in each one, we added one pot without any plant, to measure the evaporation of the pot. Thus, the experiment was performed with 12 treatments = two watering levels × 6 EtOH levels, applied to eight biological replicates, thus, a total of 96 potted cuttings + eight pots with no cutting, reaching a set-up of 104 pots (Figure 1J).

3. Soil water status measurements

The day following the ethanol treatment, the watering of Water Stress "WS" pots was stopped, while the Well-Watered "WW" pots were maintained at FTSW = 1. FTSW was calculated from pot weights, as described previously (Lebon *et al*., 2006). The daily FTSW (FTSWd) was calculated from pot weight on d day (pot weight d), the pot weight at full soil water capacity (pot weight fc), and the pot weight when the daily transpiration rate decreased to less than 10 % of WW controls of the same EtOH treatment (pot weight 10 %), which is considered as the minimum threshold of transpirable soil water (Sinclair & Ludlow, 1986). Prior to water deficit treatment, pots were irrigated to saturation and after the excess water had drained, the pots were weighed to estimate the pot mass at full soil water capacity. Each pot was weighed daily, twice for the WW, before and after re-watering. FTSWd was then determined as follows (eq. 1):

$$FTSWd = (\text{pot weight d} - \text{pot weight 10 \%}) / (\text{pot weight fc} - \text{pot weight 10 \%}) \quad \text{(eq. 1)}$$

4. Grapevine transpiration and leaf area measurements

Water loss for individual plants over the last 24 h was calculated from the pot weight difference: we used the pot weight after irrigation at d-1 day (pot weight d-1) and the pot weight before irrigation at d day (pot weight d) for WW (see eq. 2). Then, transpiration rate per leaf area (E) was determined by dividing the daily pot weights difference by the total leaf area values measured as close as possible to the transpiration date (eq. 2).

$$E\ (g\ .\ cm^{-2}.\ d^{-1}) = [\text{pot weight d} - (\text{pot weight d-1})] / \text{total leaf area} \quad \text{(eq. 2)}$$

The leaf area of all plants was estimated using a regression between the longest leaf vein and the leaf area of 233 leaves. The leaf area was determined with the "easy leaf area" application (https://www.quantitative-plant.org/software/easy-leaf-area). The obtained regression was Leaf Area (cm^2) = 1.4956 * Length of the longest vein (cm)^ 1.8339, with $R^2 = 0.9114$.

For this purpose, leaf main vein lengths were measured twice, once around day 3 and once around day 8. The calculation of plant transpiration on days 2, 3, 4 and 5 was performed using the first set of leaf area estimates, and the transpiration of days 6, 7, 8, 9 and 10 was calculated using the second set of leaf estimates.

5. Normalised transpiration rate (NTR) and NTR response to soil water status

Daily plant transpiration values (T in $g\ .\ pot^{-1}.\ d^{-1}$) from day 1 to around day 13 (except for 250 mM up to day 24) were normalised as described by King and Purcell (2017), according to equation 3. Briefly, a correction factor (CF) was calculated to adjust for differences in transpiration among plants within an EtOH treatment under WW conditions. The correction factor was calculated while all plants were WW (before Day 0) by dividing the water loss of individual plants by the average water loss of the WW plants at the same EtOH dose. A second correction was made to account for differences in transpiration that occurred among days after the initiation of water deficit treatment. Water loss for individual plants

was divided by the average water loss for WW plants of the same EtOH treatment (T_WW average). NTR for each plant for a given weighing interval was:

$$NTR = [T/(T_WW\ average)]/CF \quad \text{(eq. 3)}$$

Then the response of NTR at the whole plant level to FTSW was fitted according to equation 4 (Muchow & Sinclair, 1991), in which "a" is the model parameter describing the response of NTR to FTSW, "a" characterises the curvature of the fit. As the "a" parameter increases, the sensitivity of the NTR strengthens at a given same FTSW value. The FTSW threshold (FTSWt) represents the FTSW at which NTR (modelled by equation 4) starts to decrease (5 % reduction compared to maximum NTR, as proposed for nonlinear models by Sadras and Milroy, 1996). A higher FTSWt indicates a higher sensitivity to water deficit (Andrianasolo *et al*., 2016).

$$NTR = 1/[1 + 9 \times \exp(a \times FTSW)] \quad \text{(eq. 4)}$$

6. Re-watering of WS plants and experiment ending

After preliminary tests, the re-watering time for the WS plants was when at least two top leaves in the canopy began to wilt. The plants were re-watered with 30 ml the first day, and then the amount of water was calculated daily to reach FTSW = 0.95. The plants were harvested one week after re-watering. The WW plants and their corresponding WS plants (being part of the same pair, as defined above) were harvested on the same day. The harvest period was spread over a week from day 28 to day 34 after the beginning of the experiment. On the harvest day, all leaves and roots were collected and the leaf area was estimated directly with the Easy Leaf Area application. The percentage of dried leaves was calculated over the seven oldest leaves, as at day 0 there was a minimum of seven leaves per plant (example of dry leaves in Figure 1I). Finally, the roots were dried at 60 °C for at least 72 h and then weighed.

7. Statistical treatments

All fitting and statistical analyses were performed with RStudio version 4.2.1, using the packages 'car' and 'rstatix'. Data normality and homoscedasticity hypotheses were first assessed using Shapiro-Wilk tests and Brown-Forsythe tests, respectively. According to the cases, pairwise comparisons were performed with Student's, Welch's or Wilcoxon's tests. Fits of NTR to FTSW were performed using the non-linear least squares (NLS) regression model. The goodness of fit was assessed by calculating the Rsquare (R^2), root mean square error (RMSE) and mean squared error (MSE).

RESULTS

1. Ethanol maintained higher Fractions of Transpirable Soil Water than controls both for Well-Watered and Water-Stress pots

The changes in the Fraction of Transpirable Soil Water (FTSW) over a three-week period in potted one-node cuttings were plotted for WW pots (Figure 2A) and WS pots (Figure 2B). FTSW of WW pots were brought up daily to 0.95 (*i.e.*, 95 % of available soil water). The results show the FTSW just before re-watering the WW pots. Most WW pots remained above 0.7, regardless of the EtOH concentration used for priming. Occasionally, 250 mM plants showed significantly higher values than controls (Figure 2A and Table S1). On the other hand, the FTSW of WS pots gradually decreased after their last irrigation on day 0. In plants primed with 250 mM EtOH, the FTSW displayed a lower decrease than in control conditions (Figure 2B and Table S1). Finally, given that there was a negligible decrease in FTSW in pots without plants due to soil evaporation (Figure S1), we assumed that changes in FTSW were primarily due to whole plant transpiration.

2. Ethanol slowed down the grapevine transpiration

Figure 3 shows the changes in transpiration per unit of leaf area from day 3 to day 10, a period with the biggest FTSW

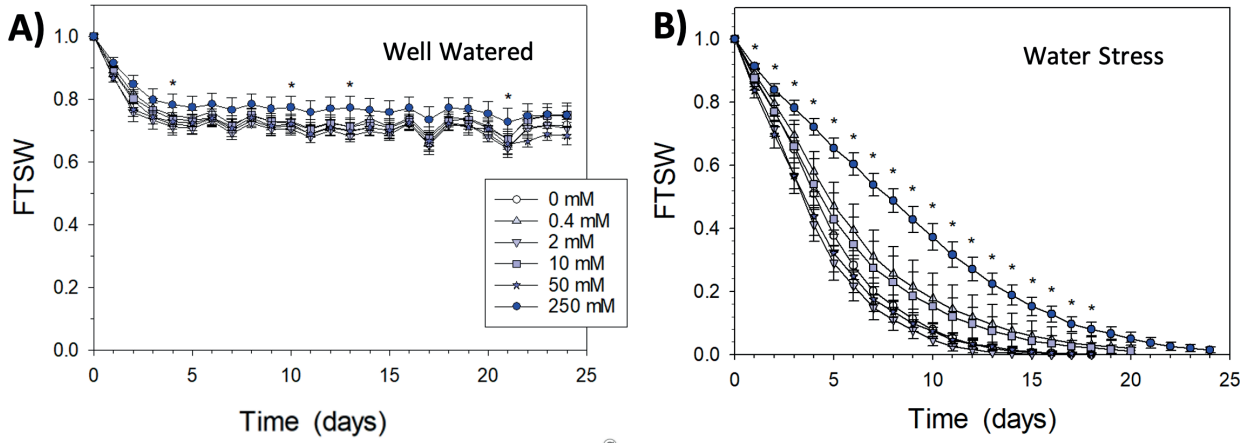


FIGURE 2. Effects of ethanol (EtOH) priming on the Fraction of Transpirable Soil Water (FTSW) as a function of time after « soil water deficit » initiation in potted Gamay one-node cuttings. When FTSW equals to 1, it represents 100 % of the soil available water. A) FTSW just before daily rewatering the well-watered plants, WW, B) water stress plants, WS, irrigation stopped at day 1. n = 8, error bars show S.E. * stands for significant differences at 0.05 between 0 and 250 mM (details in Table S1).

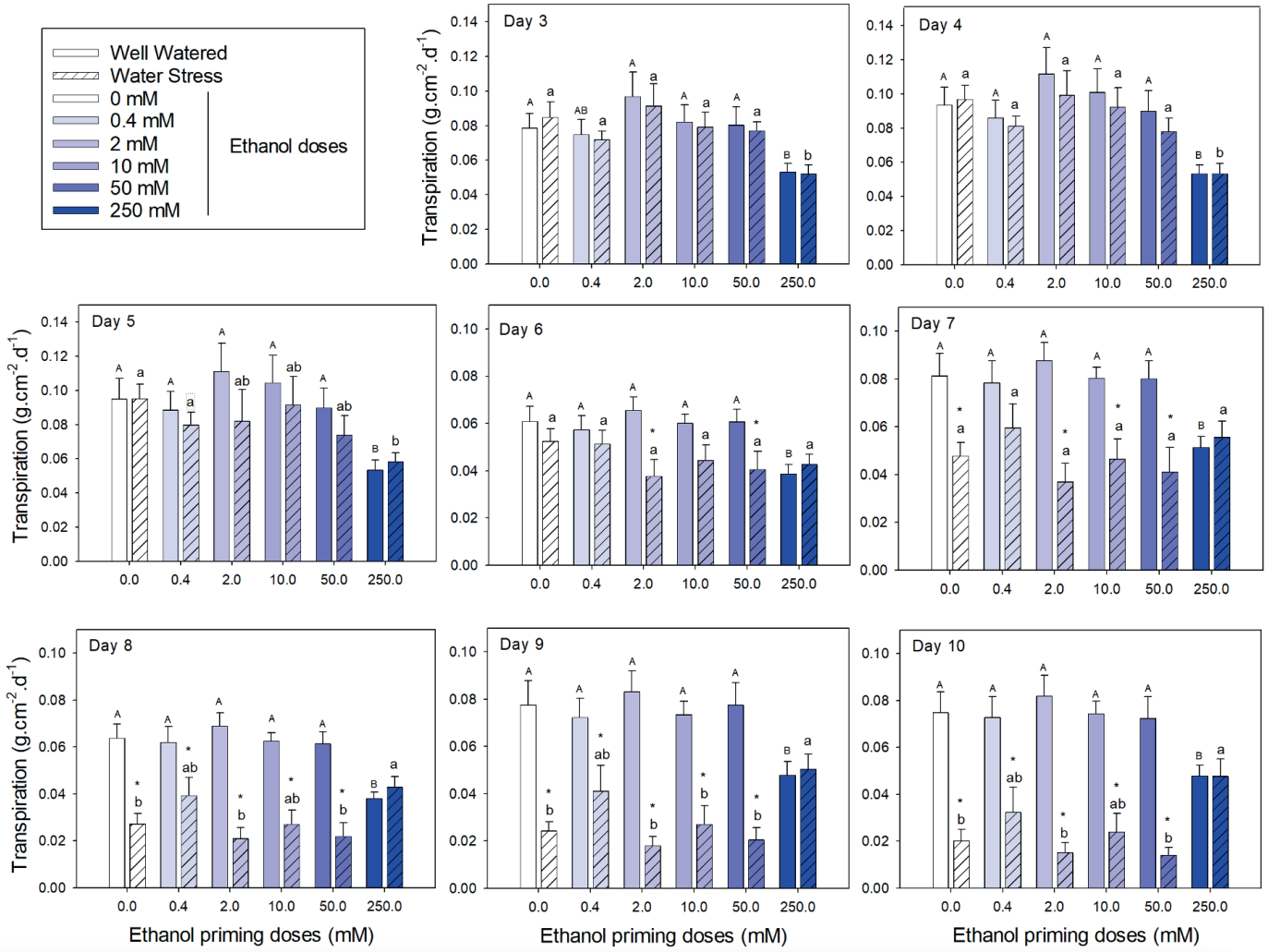


FIGURE 3. Effects of ethanol (EtOH) priming on transpiration rate per leaf area (E) of Gamay one-node cuttings in pots, from day 3 to day 10 after the initiation of soil water deficit n = 8, error bars show S.E.; all statistical details in Tables S2 and S3; multiple comparisons: capital letters to compare within WW; small caps to compare within WS; * stands for significant differences at 0.05 between WW and WS within the same EtOH dose.

differences between the various treatments (as highlighted in Figure 2). The transpiration of WS plants started to be significantly lower than WW plants from day 6 (Figure 3; Tables S2 and S3). It is noticeable that 250 mM EtOH reduced significantly plant transpiration, in comparison to controls with no EtOH treatment, from day 3 to day 5 in WS plants, and from day 3 to day 10 in WW plants. We also observed that, compared to the controls, the transpiration of WS plants treated with EtOH showed opposite trends at the beginning and the end of the experiment. For example, WS cuttings treated with 250 mM of EtOH had a lower rate of transpiration than WS controls with no EtOH at days 3, 4 and 5, but displayed higher transpiration than WS controls at days 8, 9 and 10 (Figure 3 and Table S2).

3. Ethanol altered the plant transpiration response to FTSW

The normalised transpiration rate (NTR) response to FTSW is shown in Figure 4. NTR started at 1 (to the right of the graph) when the plants transpired at the same rate as the WW plants within the same EtOH treatment, then dropped to lower values (to the left of the graph) when FTSW became a limiting factor for transpiration. According to the values of R2, RMSE and MSE (Table S4), the performance of non-linear fitting was satisfactory. The FTSW threshold (FTSWt) from which NTR dropped below 0.95 was determined. We observed that priming plants with 250 mM led the plants to switch the FTSWt to higher values (FTSWt =0.67) than plants primed with lower doses (FTSWt < 0.50) (Figure 4 with p-values detailed in Table S4). Regarding the "α" parameter, the curvature coefficient, pairwise comparisons showed significant differences between 0, 0.4 mM and 50 mM, compared to 250 mM (Table S4 and S5). Thus, priming plants with 250 mM EtOH showed an earlier regulation of transpiration in response to progressive soil drying.

4. Soil water deficit and ethanol differentially impacted the leaf development and senescence

As shown in Figure S2, the soil water deficit limited the leaf expansion over the 4-week trial. At the end of the experiment, the average leaf area of the WW control plants was just above 200 cm² (Figure S2), while one of the WS control plants

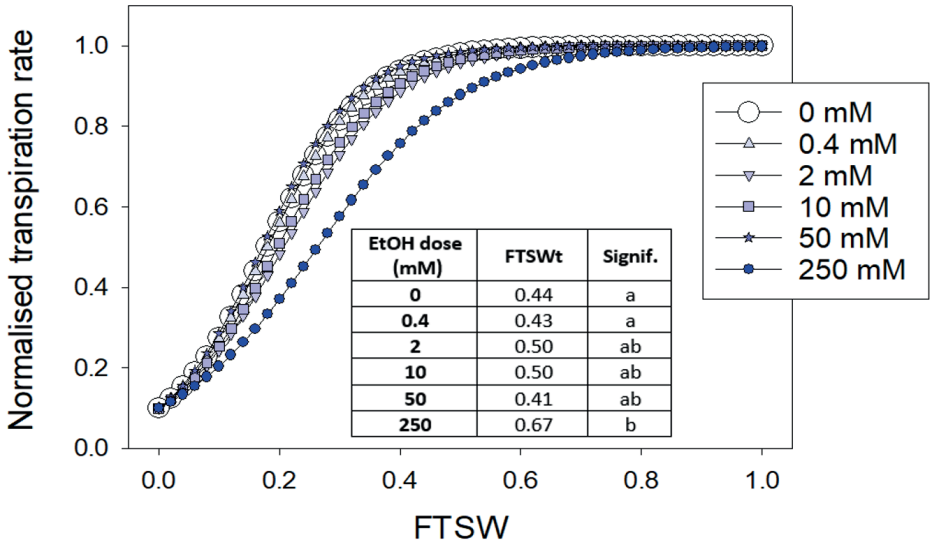


FIGURE 4. Fitted response of normalised transpiration rate (NTR) at the whole plant level to the fraction of transpirable soil water (FTSW) for six ethanol priming doses 0, 0.4, 2, 10, 50 and 250 mM. The curve fitting and calculations have been performed with the R software as described in Material and methods (see fitting quality parameters in Table S4). In the included table, FTSWt stands for FTSW threshold at which NTR maximum was reduced by 5 %. Significant differences are highlighted by differences letters determined at $p < 0.05$ using pairwise comparison methods (see Material and Methods and detailed p-values in Tables S4 and S5).

was just above 100 cm². The EOH priming also reduced the leaf expansion, this was particularly noticeable in the plants primed with 250 mM EtOH which were harbouring an average leaf area twice smaller than the controls (0 mM EtOH) in WW plants and WS plants (Figure S2). All statistical details are given in Table S6.

The results of Figure S3 showed that, at harvest, WW plants harboured around 10 % of dried leaves, while WS plants harboured around 80 % of dried leaves (Figure S3). In none of these two series, WW and WS, the ethanol changed significantly the % of dried leaves. Additional results showed that ethanol treatments did not change significantly root weight, measured at the end of the experiment (Figure S4). All statistical details are given in Table S7 and Table S8.

DISCUSSION

1. Ethanol reduces water use by potted cuttings

Water is becoming a scarce resource and the risk of excessive drought linked to climate change is a serious concern for vineyard management (van Leeuwen *et al.*, 2024). The FTSW dropped from 1 to less than 0.1 after 15 days, on average, in most water-deprived plants (Figure 2B), which is consistent with the dynamics reported in other studies on grapevine with different pot sizes and various climatic conditions (Lebon *et al.*, 2006). The most obvious effect of ethanol priming was the slower drop of FTSW after priming with 250 mM for WS plants, which corresponds to a dilution of 1.4 % EtOH/water (v/v) (Figure 2B). Interestingly, a limitation of FTSW drop between two irrigation events was also observable at some times in WW plants pre-treated with 250 mM EtOH (Figure 2A), which may present interest to limit water use in irrigated grapevines.

2. Ethanol reduces cutting transpiration

As demonstrated by Bashir *et al.* (2022) in three other plant species, the EtOH priming reduced plant transpiration in grapevine (Figure 3). The strongest effect was obtained with 250 mM EtOH. This EtOH concentration reduced transpiration in both WW and WS plants, already three days after the EtOH treatment. Interestingly, the WS plants treated with this 250 mM concentration maintained a higher transpiration rate than WS controls (pre-treated with water alone) after 8 days of the experiment. This effect could be beneficial in cases of combined water deficit and heat stress, as transpiration is critical to cooling down leaf temperature (Costa *et al.*, 2012). Ultimately, EtOH supply could save water at the vineyard scale, while also protecting the canopy from heat stress. These preliminary results clearly prompt us to test EtOH treatments on a larger scale.

3. Ethanol modulates the FTSWt at which transpiration decreases

The progressive soil drying led to lower effects of plant transpiration from FTSWt equal to 0.44 on plants not subjected to ethanol priming (Figure 4). This value is very close to 0.4, the value reported for grapevines in previous studies using the two-segment plateau regression procedure (Lebon *et al.*, 2003, Hofmann *et al.*, 2014). FTSWt values were calculated using the two-segment plateau regression procedure resulting in lower values than those obtained in our study with the inverse exponential model (Kang *et al.*, 2024). The response of transpiration to FTSW is employed in various dynamic crop models to monitor vineyards' water status (Lebon *et al.*, 2003; Valdés-Gomez *et al.*, 2009;

Ramos *et al*., 2014; Er-Raki *et al*., 2021), and it is worth noting that ethanol is modulating this response. Notably, priming with 250 mM EtOH resulted in an earlier regulation of transpiration with FTSWt equal to 0.67 (instead of 0.44 for 0 mM EtOH, Table S4). Ultimately, priming with 250 mM EtOH reduced transpiration and leaf growth both for WW and WS plants at first, but favoured transpiration recovery for WS plants after 8 days.

4. Ethanol effects on leaf development

The EtOH effect was also observed when looking at the green leaf area at harvest in WW plants, around four weeks after trial beginning (Figure S2) with a slight stimulation of leaf area at 2 mM, regardless of the water-deficit conditions. These results also showed that high doses of ethanol (250 mM) limited the leaf development whatever the water treatment. This response to exogenous ethanol has already been observed in oilseed rape by Wu *et al*. (2019). However, the water deficit induced a stronger effect than ethanol in reducing leaf growth, clearly limiting leaf development in all WS cases compared to WW cases.

The observation of high percentages of dry leaves, mainly in WS plants (Figure S3), was as expected a classical plant response to water deficit (Fischer & Turner, 1978). According to Hochberg *et al*. (2017), older basal leaves are characterised by greater connectivity in the xylem and higher vulnerability to embolism propagation, leading to the functional protection of apical younger leaves. In our case, the choice of the harvest date, based on the wilting of top leaves, which did not occur for 250 mM treatment, was probably not relevant and too late. The experiments with potted cuttings, reported here, were initiated following a preliminary series of trials with bare root cuttings (Figure S5) which showed that a sudden removal of water resulted in less leaf mortality when the cuttings were pre-treated with EtOH.

Nevertheless, the absence of ethanol effect on the percentage of dry leaves in WW plants (Figure S3), always below 10 %, proved that those EtOH concentrations were not toxic. In further experiments, ethanol should be tested in grafted plants as most grapevines are grafted nowadays.

CONCLUSION

We showed that ethanol priming induces a slowdown of the grapevine transpiration, which was obvious with the 250 mM dose. This concentration corresponds to an ethanol dilution of 1.4 % in water, which could be easy to implement. However, in the vineyards, the effective EtOH doses might be different and would need adapted experimental plans to be determined. Future studies should also consider additional variables, including gas exchange to assess the impact of EtOH on photosynthesis, leaf water potential, as well as its effects on leaf temperature, along with the risk of sunburn. Clearly, the impact of EtOH on yield is another critical parameter to monitor. A previous study (Chervin *et al*., 2005) demonstrated that spraying ethanol increased berry weight by 10 %; however, these experiments did not focus on the water relations within the vines.

This clearly requires more studies to better understand this type of biochemical response being linked to chemical priming, which is now attracting more attention from the scientific community (Sako *et al*., 2020; Salinitro *et al*., 2021).

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AUTHOR CONTRIBUTIONS

NAK, AP, AD, PM and CC conceptualised the project and designed the research. OY provided the Gamay cuttings. NAK, BQ, PM and CC performed the cuttings experimentations. NAK, PM and CC ran statistical tests. All co-authors contributed to writing and editing the manuscript.

DATA AVAILABILITY

The data underlying this article will be shared upon request to the corresponding authors.

DECLARATION OF COMPETING INTEREST

The authors declare they have no conflict of interest.

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