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# Drought survival and recovery in grasses: Stress intensity and plant–plant interactions impact plant dehydration tolerance

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## Abstract

Plant dehydration tolerance confers drought survival in grasses, but the mortality thresholds according to soil water content (SWC), vapour pressure deficit (VPD) and plant–plant interactions are little explored. We compared the dehydration dynamics of leaf meristems, which are the key surviving organs, plant mortality, and recovery of Mediterranean and temperate populations of two perennial grass species, *Dactylis glomerata* and *Festuca arundinacea*, grown in monocultures and mixtures under a low-VPD (1.5 kPa) versus a high-VPD drought (2.2 kPa). The lethal drought index (LD<sub>50</sub>), that is, SWC associated with 50% plant mortality, ranged from 2.87% ( $\psi_s = -1.68$  MPa) to 2.19% ( $\psi_s = -4.47$  MPa) and reached the lowest values under the low-VPD drought. Populations of *D. glomerata* were more dehydration-tolerant (lower LD<sub>50</sub>), survived and recovered better than *F. arundinacea* populations. Plant–plant interactions modified dehydration tolerance and improved post-drought recovery in mixtures compared with monocultures. Water content as low as 20.7%–36.1% in leaf meristems allowed 50% of plants to survive. We conclude that meristem dehydration causes plant mortality and that drought acclimation can increase dehydration tolerance. Genetic diversity, acclimation and plant–plant interactions are essential sources of dehydration tolerance variability to consider when predicting drought-induced mortality.

## KEYWORDS

*Dactylis glomerata*, drought acclimation, drought recovery, *Festuca arundinacea*, intraspecific variability, leaf meristem, lethal drought, relative yield, senescence

## 1 | INTRODUCTION

Rising temperatures are expected to increase the frequency and intensity of drought in southern Europe, with plenty of evidence that this is already occurring (Ault, 2020; IPCC, 2019). More frequent

extreme events threaten the survival of perennial species, and large-scale drought-induced mortality has been reported in forests (Peñuelas et al., 2018; Schuldt et al., 2020) and grasslands (Hovenden et al., 2017; Winkler et al., 2019). Understanding and predicting drought-induced mortality has become crucial to anticipate the

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response of ecosystems to climate change and evaluate their long-term resilience to extreme events (Mitchell et al., 2016; Norton et al., 2016). Drought-induced mortality depends primarily on plant dehydration tolerance, a strategy allowing plants to survive at a low level of tissue dehydration (Volaire, 2018). However, the methodologies to assess dehydration survival remains a challenging issue since drought survival of perennial species varies according to combined factors, that is, plant traits and physiological properties, environmental conditions and plant–plant interactions (Trugman et al., 2021).

First, plant drought survival varies between species and populations, but the underlying traits and their significance remain debated. Stress physiology applied to comparative ecology identified key traits accounting for phenotypic variations and functioning within and across species (Reich, 2014). These trait-based approaches showed significant relationships between drought adaptation and hydraulic traits across species and environments (Choat et al., 2018; Li et al., 2018), suggesting a strong contribution of hydraulic failure to plant dry-down in trees (Blackman et al., 2019). Similar approaches showed that embolism resistance significantly varies in herbaceous species depending on the aridity level of their geographical origin (Lens et al., 2016; Volaire et al., 2018). In grasses, leaf vulnerability to hydraulic failure was associated with leaf osmotic potential at full turgor (Griffin-Nolan et al., 2019) and reflected drought adaptation (Wilcox et al., 2021). Leaf traits are generally assumed to inform the ability of plants to survive drought, and, in this context, leaf wilting (also called 'leaf desiccation' or 'leaf death') is a usual proxy of whole plant death (Brodribb et al., 2016; Johnson et al., 2018). However, leaf blades differ from leaf bases, that is, the enclosed bottom parts of the leaves, including the meristematic tissues, since they have distinct water potential regulations and respond differently to drought stress (Matsuda & Riaz, 1981; Munns et al., 1979). Meristematic tissues in grasses were shown to survive water stress better than most plant tissues (Barlow et al., 1980) since apices are a strong sink for carbohydrates within the plant throughout severe stress (Schnyder & Nelson, 1989; Spollen & Nelson, 1988, 1994) conferring efficient osmotic adjustment in those tissues (West et al., 1990). Hence, the usual focus on leaves underscores the importance of surviving organs which are usually not the lamina blade but the meristematic tissues in grasses (Volaire et al., 1998) and, equivalently, the vascular cambium in trees (Hammond et al., 2021; Mantova et al., 2021). In perennial grasses, the ability of plants to 'stay green' and remain photosynthetically active under moderate drought (i.e., dehydration avoidance) trades off with the ability to survive under severe drought (i.e., dehydration tolerance, Bristiel et al., 2017; Keep et al., 2021). Hence, dehydration avoidance in leaves is often inversely correlated with dehydration tolerance in meristems that enhance survival under severe drought when most leaves have senesced (Volaire, 2018). Therefore, focusing on the surviving organ is necessary to assess dehydration tolerance and unravel the mechanisms and processes triggering drought mortality in trees (Mantova et al., 2021) and herbaceous species (Zwicke et al., 2015).

Second, plant dehydration tolerance can differ between environments, as the nature and the intensity of drought trigger different

stress responses in plants. While most traits are usually measured in standardized and optimum conditions to assess and compare plant ecological strategies, for example, hydraulic safety versus hydraulic efficiency (Gleason et al., 2016; Holloway-Phillips & Brodribb, 2011; Liu et al., 2021), they hardly predict when plants reach critical dehydration thresholds causing their mortality (Blackman et al., 2019). Instead, the response functions of physiological, phenotypic or even demographic traits to water deficit should better identify such critical thresholds, providing a complementary insight into drought adaptation (Volaire et al., 2020). Like the 'lethal temperature' index ( $LT_{50}$ ), which estimates plant frost tolerance as the critical temperature associated with 50% plant mortality under freezing (Paquin & Mehuys, 1980), the 'lethal drought' index ( $LD_{50}$ ), that is, the critical soil water content (SWC) (or potential) associated with 50% plant mortality could be a promising way to assess plant dehydration tolerance. Similarly, assessing the dynamics of leaf senescence (LS) and leaf meristem water content (LMWC) could help identify the physiological basis of tissue dehydration tolerance and provide a mechanistic link to mortality (Martinez-Vilalta et al., 2019). Additionally, assessing drought severity requires standardized metrics (Bradford et al., 2020) of the 'edaphic drought' (e.g., soil water availability, SWC) and the 'atmospheric drought' (e.g., vapour pressure deficit [VPD]). Most studies used the desiccation time during drought, at a constant standardized evaporative demand, to assess the response of hydraulic traits (e.g., Blackman et al., 2019). However, the duration of stress is difficult to interpret for comparing different environments with contrasting stress intensity, drought events with contrasting timing or species/populations with contrasting growth dynamics (Poorter et al., 2012). Instead, the cumulated soil water deficit over time should better reflect drought intensity dynamics.

Finally, plant–plant interactions may also affect plant dehydration tolerance. The coexistence influence trait expression and phenotypes of associated plants (terHorst et al., 2018; Wang & Callaway, 2021), impacting their adaptation to drought (Zenes et al., 2020). Furthermore, biodiversity is increasingly recognized to buffer plant communities against the negative impacts of climate extremes (Isbell et al., 2017; Loreau et al., 2021) like drought (Wagg et al., 2017; Wright et al., 2021) due to positive plant–plant interactions (e.g., facilitation) and complementarity effects among plants (e.g., niche difference), which together have a potentially positive effect (i) on plant survival during drought and (ii) on plant recovery after the drought (Haberstroh et al., 2021). However, few studies have assessed how positive or negative interactions between neighbouring plants directly affect plant dehydration tolerance, drought survival and drought recovery (Griffin-Nolan et al., 2021). To date, field evidence shows either positive (Hisano et al., 2019), negative (Young et al., 2017) or mixed (Grossiord et al., 2014) effects due to biodiversity, revealing the complexity of predicting the outcome of plant–plant interactions under drought. The balance between the positive and negative effects of interactions depends on several factors, among which the species/populations and drought intensity appear essential (Ploughe et al., 2019; Sthultz et al., 2007).

Plant–plant interactions improve drought survival and recovery under increased aridity, but mainly when a nurse species ‘protects’ the others against the impacts of drought (He et al., 2013; Soliveres et al., 2015). More specifically, plant–plant interactions were found to positively affect plant dehydration tolerance, allowing plants to survive more intense and recurrent drought in species mixtures only in some combinations of woody and herbaceous species (Shihan et al., 2020). On the other hand, drought can asymmetrically affect species with a low dehydration tolerance, giving a competitive advantage to the species with the highest dehydration tolerance (Craine & Dybzinski, 2013). As a result, drought-induced mortality can be exacerbated for some species in a community, resulting in potentially permanent changes in ecosystem functioning after the recovery. Plant–plant interactions are a crucial issue in understanding the resilience of grasslands since diverse grass communities may become more resilient through the local expansion of drought-tolerant species in the face of climate change (Craine et al., 2013). Moreover, migrations of grass species are expected, for example, the predicted biogeographical areas of Mediterranean populations of perennial grasses will extend towards the current temperate areas under a future climate scenario in Europe (Keep et al., 2021; Shihan et al., 2022). Grasslands may then increasingly contain populations of various origins and levels of adaptation to drought in the future, and for instance, the association of Mediterranean and temperate populations of grass species is advocated to enhance forage crop resilience (Norton et al., 2016). Studying the effects of biotic interactions on drought survival of contrasting model grass communities can provide general response patterns for associated species/populations with different drought strategies (Craine et al., 2013).

This study explores the sources of variation of plant dehydration tolerance in different populations (Mediterranean vs. temperate origin) of two perennial grass species *Dactylis glomerata* L. and *Festuca arundinacea* Schreb., under intense droughts of contrasting VPD levels. We addressed the following questions: (1) Do dehydration tolerance and post-drought recovery consistently vary with species strategy, population origin, and VPD levels? We expected that *D. glomerata* would be more dehydration-tolerant than *F. arundinacea*, which exhibits a strong dehydration avoidance strategy due to its deep rooting system (Volaire & Lelievre, 2001), and that a high-VPD drought would be more stressful and favour the Mediterranean versus the temperate populations of each species. (2) Do plant–plant interactions influence dehydration tolerance and recovery? We hypothesized that mixing species and/or populations with contrasting survival strategies would facilitate the survival of the most dehydration-tolerant populations. (3) Do soil water deficit and leaf tissue dehydration correlate to each other and determine plant mortality under different abiotic (VPD levels) and biotic (plant mixtures) environments? We hypothesized that dehydration of leaf tissue, especially meristematic tissue, would dynamically reflect soil water deficit and trigger plant mortality below a population-specific threshold. Addressing these questions will help identify reference traits and indices to assess plant dehydration tolerance for different types of drought stress.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant material

*D. glomerata* (Dg) and *F. arundinacea* (Fa) are two cool-season perennial grass species (Poaceae). We tested two populations with different biogeographical origins for each species, one from the Mediterranean (Med) and the other from temperate regions (Tem). These populations are forage crop cultivars (cv), described in (Poirier et al., 2012), selected either from Mediterranean germplasm (Dg, cv Medly; Fa cv Centurion) or temperate germplasm (Dg cv Ludac; Fa cv Sony). Previous work showed that the Mediterranean populations (MedDg, MedFa, hereafter) survived more than the temperate populations (TemDg, TemFa, hereafter) under a range of climatic scenarios, suggesting that intraspecific variability in drought adaptation can be significant (Poirier et al., 2012).

### 2.2 | Experimental design

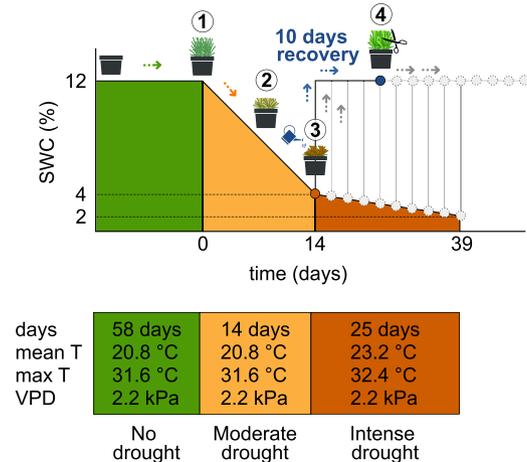
We conducted two successive pot experiments with two contrasting VPD levels in a heated glasshouse at the INRAE Centre in Montpellier (France). For both experiments, we tested the populations of each species in monocultures, in 2-component mixtures (i.e., pairs of species made from either the Mediterranean or temperate populations), and in a 4-component mixture (i.e., all the four populations mixed). We used a substitutive design to evaluate the changes in plant–plant interactions (interspecific vs. intraspecific interactions) across the different plant mixtures. The plant density was 20 plants per pot and was maintained constant across the different mixtures, that is, 10 or 5 individuals of each population were grown in the 2- or 4-component mixtures, respectively.

We used short PVC pots (20 cm wide, 23 cm deep) to ensure that plants had access to exactly the same quantity of available water in each pot at the beginning of the experiment. To this end, we filled the pots with the same quantity of dry substrate (80% sand, 10% loam, 10% clay). The 140 pots (20 pots of each mixture type) were fully randomized and moved around weekly within the glasshouse. The local climatic variables were recorded every 10 mn in the glasshouse using a Campbell Datalogger to monitor the differences in VPD. SWC was monitored by gravimetry by weighing all pots daily. The relationship between SWC and soil water potential ( $\psi_s$ , MPa) had been defined previously (Volaire & Lelievre, 2001) as  $\psi_s = -104.66 \times \exp(-1.44 \times \text{SWC}) - 0.003$ .

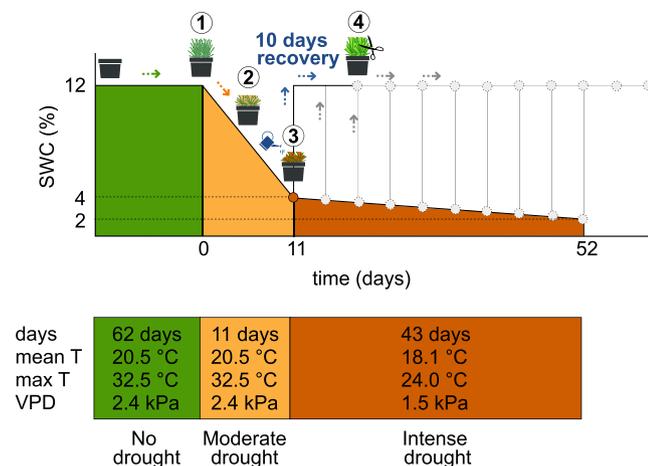
After sowing on 11 October (first experiment) and on 21 November (second experiment), both experiments followed the same four successive phases (Figure 1):

- (1) ‘Installation phase’ (before the drought): We transplanted the plants (at the three tiller-initial stages) into pots on 20 November (first experiment) and 9 January (second experiment). The pots were fully irrigated, alternatively with water and a Hoagland complete nutrient solution (Hoagland no. 2, Merck), for 58 and

## (a) High-VPD drought



## (b) Low-VPD drought



**FIGURE 1** Experimental design of the pot experiments: (a) a high-VPD drought experiment (39 days) with high temperatures (mean = 23.2°C, max = 32.4°C) and VPD (2.2 kPa), and (b) a low-VPD drought experiment (52 days) with moderate temperatures (mean = 18.1°C, max = 24.0°C) and VPD (1.5 kPa). We measured the dehydration tolerance and the post-drought recovery of Mediterranean and temperate populations of two grass species, *Dactylis glomerata* and *Festuca arundinacea*, grown in monocultures, 2-component mixtures, and 4-component mixtures. Four stages are highlighted: (1) a 'no-drought' establishment stage (in green) at field capacity (12% SWC) maintained by irrigation; (2) a 'moderate drought' stress stage (in yellow) during which plants faced moderate soil water deficit (from 12% to 4% SWC) until complete growth cessation; (3) an 'intense drought' survival stage (in brown) during which plants faced a severe water deficit (from 4% to 2% SWC) with increasing drought-induced mortality; and (4) a 'post-drought recovery' stage after rehydration at field capacity (12%) allowing non-limiting regrowth. Differences in VPD between the experiments were significant during the 'intense drought' stage, during which we monitored the response of leaf tissues (senescence, water content) and assessed plant mortality to progressively decreasing SWC. We then assessed plant post-drought biomass production after 10 days of recovery. SWC, soil water content; VPD, vapour pressure deficit.

62 days for the first and second experiments, respectively, until the plants were well developed. The environmental conditions were similar for both experiments, with a mean temperature of 20.5°C and a mean daily VPD of 2.3 kPa.

- (2) 'Stress phase' (moderate drought): We stopped the irrigation on 21 January (first experiment) and 28 February (second experiment). Before starting the measurements, we ensured that the SWC of all pots was stabilized at field capacity (12%) so that all plants had the same initial amount of available water. Without irrigation, the SWC decreased daily during 14 and 11 days for the first and second experiments, respectively, until reaching 4% (−0.33 MPa), a threshold corresponding to a cessation of elongation for the studied species (Volaire & Lelièvre, 2001). The environmental conditions were kept similar to before.
- (3) 'Survival phase' (intense drought): Below the 4% SWC threshold, we differentiated the climatic conditions of both experiments. The first experiment had a high mean temperature (23.2°C) and VPD (2.21 kPa) conditions (hereafter called 'high-VPD drought'), while the second experiment had a lower mean temperature (18.1°C) and VPD (1.46 kPa) conditions (hereafter called 'low-VPD drought'). Depending on the treatments, the 'plant survival phase' lasted a maximum duration of 21–29 days under the high-VPD drought and 38–43 days under the low-VPD drought (Figure 1). The most dehydration-tolerant population could not survive in our experimental conditions when SWC reached 2% (−5.88 MPa). For each treatment, we successively sampled the pots (with decreasing SWC along time) as explained in the Section 2.3. It means that plants of each pot experienced a unique drought duration since we sampled pots with the largest possible range of SWC (between 4% and 2%) to cover the largest range of plant survival (from 100%, that is, all plants alive or regrowing after 10 days, to 0%, that is, all plants dead, with no visible leaf regrowth).
- (4) 'Recovery phase' (rehydration): Each pot sampled (according to its level of decreasing SWC) was first processed to measure the final water status of three tillers, then immediately rehydrated to field capacity (12%) for 10 days to ultimately measure plant survival rate (see below) and growth resumption (see below). The differentiated climatic conditions were maintained.

We conducted both experiments in spring to avoid the expression of summer dormancy, that is, the seasonal reduction of growth induced in summer by temperatures and day length, that differs between the origin of populations (Norton, Lelièvre, et al., 2006; Norton, Volaire, et al., 2006).

## 2.3 | Measurements

We performed all measurements during the plant survival phase (SWC, final water status and senescence of plants) and the recovery phase (plant survival and recovery). Beginning at 4% SWC, we sampled 1–3 pots of each species/population and mixture as SWC

decreased by 0.2% increments (thus at 10 successive dates, with different pots at each date) during the entire plant survival phase until the complete plant death was reached (around 2% SWC for MedDg). Sampling dates were closer to each other in the high-VPD drought experiment than in the low-VPD drought experiment, reflecting the duration difference in the plant survival stage between the two experiments (Figure 1). For each pot sampled, we randomly selected and uprooted three tillers of each species/population and separated the leaf samples into three fractions: (1) the first 20 mm of enclosed leaf bases which constituted the surviving meristematic aerial organs; (2) the remaining green aerial tissues and (3) senescent aerial tissues. We determined the LMWC by measuring the ratio between the fresh and oven-dried (at 60°C for 48 h) mass of leaf meristems. We determined LS by measuring the ratio between the dry mass of the senescent and the green fractions of leaf laminae.

Once sampled, each pot was fully rehydrated back to field capacity (12% SWC) for 10 days during the plant recovery phase. After the 10 days, we measured the number of surviving plants (with at least one regrowing leaf) in each species/population and calculated the plant survival rate as the ratio between the number of surviving plants and the initial number of plants (minus the sampled tillers for the measurement of plant water status before rehydration) in the pots ( $n = 20$ ). We assessed the recovery of each population by harvesting and weighing their oven-dried aboveground biomass. No measurement on belowground organs was performed since all root systems entirely and densely colonized the pot volumes (4 L) and did not reflect belowground strategies reliably.

## 2.4 | LD<sub>50</sub> indices

Following a similar method to that used to calculate the LT index (Paquin & Mehuys, 1980), we calculated the LD index to determine and compare the dehydration tolerance of species and populations in the different mixtures and drought experiments (Bolte et al., 2016). The LD<sub>50</sub> describes the drought intensity causing 50% mortality in plant populations, respectively, allowing for standardized dehydration tolerance measurements. In our case, the LD indices were calculated using residual SWC as a drought intensity indicator. Therefore, plants with lower LD<sub>50</sub> were the most dehydration tolerant and survived longer at lower SWC. Following Bolte et al. (2016), we derived the LD indices using the response curves of plant survival ( $S$ ) as a function of SWC. The survival rate was fitted by a logistic function, which best reflects the mortality dynamics caused by a decrease in SWC over time. The logistic function was in the form:

$$S = \frac{1}{1 + e^{-(\beta_0 - \beta_1 \text{SWC})}}, \quad (1)$$

where  $\beta_0$  and  $\beta_1$  are two parameters describing the inflection point and the growth rate of the response curve. Similarly, we used the response curve of plant survival ( $S$ ) as a function of LS and LMWC instead of SWC to determine the values of LS (LS<sub>50</sub>) and LMWC (LMWC<sub>50</sub>), that is, the value of LS and LMWC associated with 50% plant mortality, respectively.

## 2.5 | Post-drought relative yield (RY) indices

We used the RY index (de Wit et al., 1965) to compare the effects of plant–plant interactions between mixtures and monocultures. We calculated the RY using the plant biomass production of each population as follows:

$$RY_i = 2 \times \frac{Y_{i,x}}{Y_{i,m}}, \quad (2)$$

where  $Y_{i,x}$  is the final biomass of the population  $i$  observed in mixtures, and  $Y_{i,m}$  is the corresponding biomass observed in monoculture.  $RY = 1$  indicates that plant–plant interactions have similar effects in the mixture than in monoculture.  $RY > 1$  indicates that plant–plant interactions have more positive effects (i.e., more facilitation) on the population  $i$  in the mixture than in monoculture.  $RY < 1$  indicates that plant–plant interactions have more negative effects (i.e., more competition) on the population  $i$  in the mixture than in monoculture. Additionally, we calculated the Relative Yield Total (RYT) to compare the total post-drought plant biomass production of mixtures relative to monocultures. RYT is the sum of the RYs of all component populations in a mixture:

$$RYT = \frac{1}{2} \times \sum_{i=1}^n RY_i, \quad (3)$$

where  $n$  is the total number of populations in the mixture.  $RYT = 1$  indicates that there is no significant mixture effect.  $RYT > 1$  indicates that the mixture has higher biomass than the average of the monocultures (i.e., a positive mixture effect). Similarly,  $RYT < 1$  indicates that the mixture has lower plant biomass than the average of the monocultures (i.e., a negative mixture effect).

## 2.6 | Statistical analyses

All analyses were conducted in R version 4.0 (RCore-Team, 2020). We tested the differences in LD<sub>50</sub>, LS<sub>50</sub> and LMWC<sub>50</sub> using generalized linear models (GLM) with a binomial error distribution as is consistent with the logistic function defined in Equation 1. We also included the population identity (MedDg, MedFa, TemDg, TemFa), plant mixture type (1-, 2-, 4-components) and VPD levels (high-VPD, low-VPD) as independent variables in the GLMs. To ensure the relevance of the full models, based on the three variables and their interactions, we tested reduced models with fewer variables (one or two) and compared the models using the Akaike Information Criteria corrected for small samples (AICc). The full models were considered the best in all the cases ( $\Delta AICc > 2$ ). The significance of the independent variables within the GLMs was tested using a likelihood-ratio test. The relationships between LD<sub>50</sub>, LS<sub>50</sub>, LMWC<sub>50</sub>, and between RY, SWC, LD<sub>50</sub> were analysed using bivariate linear regressions. Student's  $t$  tests were performed to test whether RY and RYT indices significantly differed from 1. The differences in RY between populations, mixtures, and experiments were analysed with an analysis of variance followed by a post hoc Tukey test. The same method was used to test the differences in RYT between mixtures and experiments.

### 3 | RESULTS

#### 3.1 | Variations in plant survival, LD<sub>50</sub>

Plant survival was significantly affected by SWC and the VPD level and varied according to plant species/population identity and mixture (Table 1). Plant mortality started when SWC fell below 4% (Figure 2a–d). It then considerably increased from 3% to 2% SWC, that is, after 10–40 days of drought, depending on VPD (high-VPD vs. low-VPD drought), and was almost total below 2% SWC. The total mortality of all plants was reached earlier (21 days), at a higher SWC (2.65%), under the high-VPD drought than under the low-VPD drought (41 days), for which very low values of SWC (1.96%) were recorded on average. The mean LD<sub>50</sub> was 2.87% ( $\psi_s = -1.68$  MPa) under the high-VPD drought and 2.19% ( $\psi_s = -4.47$  MPa) under the low-VPD drought, indicating a higher mortality rate under the high-VPD drought.

Overall, *D. glomerata* had significantly lower LD<sub>50</sub> (−0.21%,  $F = 63.58$ ;  $p < 0.0001$ ) than *F. arundinacea*. The Mediterranean *D. glomerata* (MedDg) population survived at the lowest SWC and was the most dehydration-tolerant, especially under high-VPD drought conditions (Table 2). In contrast, the Mediterranean *F. arundinacea* (MedFa) population was the least dehydration-tolerant and died at the highest SWC. The temperate populations of both species (TemDg, TemFa) were intermediate. Furthermore, LD<sub>50</sub> marginally differed between monocultures and mixtures (Figure 2a–d, Table 2). In most cases, the LD<sub>50</sub> was significantly lower when plants grew in mixtures ( $F = 2.89$ ,  $p = 0.0826$ ), especially in the 2-component mixtures (−0.06%), indicating that plants had a higher dehydration tolerance in mixtures than in monocultures. Only the temperate *D. glomerata* population had the inverse trend, with a higher LD<sub>50</sub> in mixtures. The differences in LD<sub>50</sub> among plant mixtures were the highest under the low-VPD drought.

#### 3.2 | Relationship between plant survival and leaf tissue dehydration

LS exponentially increased from 13% to 100% with decreasing SWC (Figure 2e–h) while in parallel, the LMWC strongly decreased from 77.89% to 10.69% on average (Figure 2i–l), both with significant differences between VPD levels and plant populations (Table 1). LS and LMWC were also significant determinants of plant survival (Figure 3a,b). The mean LS<sub>50</sub> and LMWC<sub>50</sub>, corresponding to 50% plant mortality, were respectively 92% and 35% under the high-VPD drought and 88% and 28% under the low-VPD drought (Table 2), indicating a higher leaf tissue (lamina and meristem) dehydration under the high-VPD drought. *D. glomerata* had significantly higher LS<sub>50</sub> (+7.38%,  $F = 30.01$ ;  $p < 0.0001$ ) and lower LMWC<sub>50</sub> (−15.93%,  $F = 65.60$ ;  $p < 0.0001$ ) than *F. arundinacea*, showing that its mortality occurred at higher LS and a lower meristem water content. However, no significant difference was found between the temperate and Mediterranean populations of each species, whether for LS<sub>50</sub> ( $F = 2.60$ ,  $p = 0.1070$ ) or LMWC<sub>50</sub> ( $F = 0.26$ ,  $p = 0.7727$ ). Similarly, no significant difference was between mixtures for LS<sub>50</sub> ( $F = 0.11$ ,  $p = 0.8960$ ) or LMWC<sub>50</sub> ( $F = 0.04$ ,  $p = 0.9634$ ).

LD<sub>50</sub> was positively related to LS<sub>50</sub> and negatively to LMWC<sub>50</sub> (Figure 4a,b), indicating that higher leaf tissue dehydration rates confer higher drought survival in response to soil water shortage. The relationships were tighter under the low-VPD drought than the high-VPD drought.

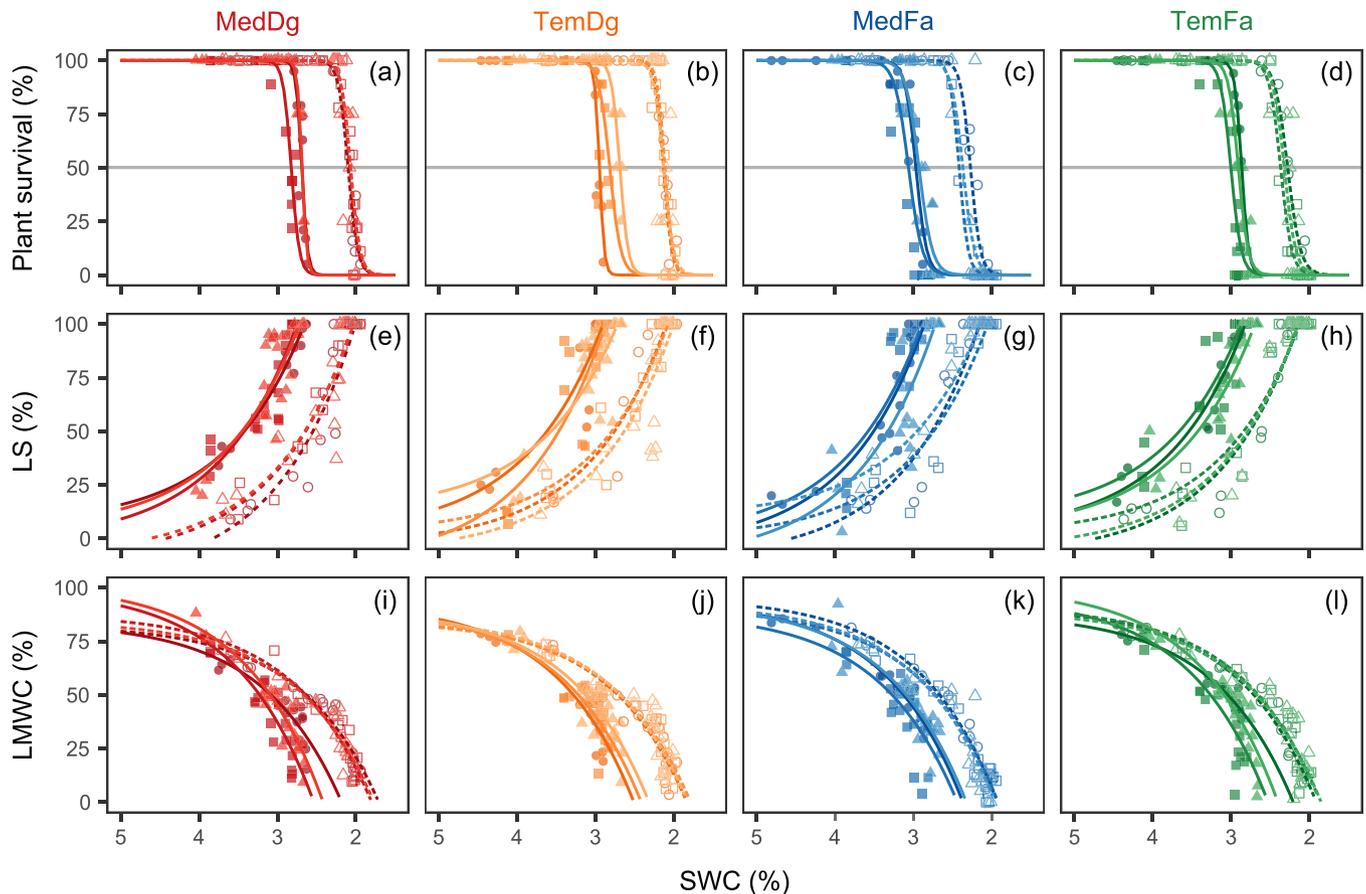
#### 3.3 | Differences in post-drought recovery

The mean post-drought biomass was 1.41 gm<sup>−2</sup> and ranged from 0 to 3.66 gm<sup>−2</sup> across monocultures and mixtures. The mean RYT<sub>Biomass</sub> was 1.65, meaning that mixtures produced 65% more biomass after drought than the average of monocultures. However, we found high variations in RYT ( $SD = 1.02$ ), which was explained by significant

**TABLE 1** Likelihood ratio  $\chi^2$  and significance ( $p < 0.05$  in bold) of GLM parameters explaining the variability in plant survival, leaf senescence (LS) and leaf meristem water content (LMWC) during the severe drought phase (SWC < 4%).

Variables	Plant survival		LS		LMWC	
	$\chi^2$	$p$	$\chi^2$	$p$	$\chi^2$	$p$
SWC	288.2	<0.0001	672.3	<0.0001	1522.4	<0.0001
VPD level	120.7	<0.0001	110.0	<0.0001	147.7	<0.0001
Population	97.67	<0.0001	11.80	0.0081	6.63	0.0849
Mixture	8.87	0.0118	3.48	0.1752	8.15	0.0170
VPD level × Population	1.19	0.7547	3.68	0.2981	7.71	0.0526
VPD level × Mixture	5.23	0.0733	8.85	0.0120	7.70	0.0213
Population × Mixture	9.07	0.1698	4.85	0.5632	8.95	0.1766
VPD level × Population × Mixture	5.81	0.4453	7.34	0.2907	6.43	0.3770

Abbreviations: GLM, generalized linear model; SWC, soil water content; VPD, vapour pressure deficit.

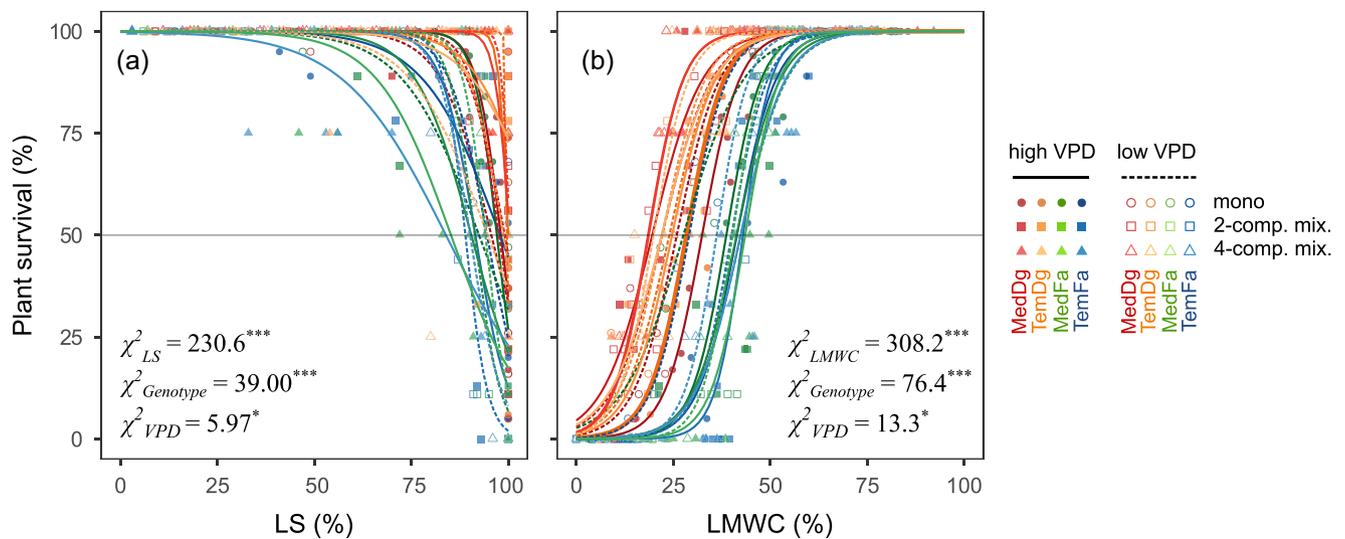


**FIGURE 2** Response of (a–d) plant survival, (e–h) leaf senescence (LS) and (i–l) leaf meristem water content (LMWC) to drought intensity as defined by residual soil water content (SWC). Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations) grown in monocultures (circles), 2-component mixtures (rectangles), and 4-component mixtures (triangles). Data points filling and line type refer to the VPD levels (solid points and lines: high-VPD drought; open points and dashed lines: low-VPD drought). The 50% survival lines show the inflection points used to derive the lethal drought indices ( $LD_{50}$ ). VPD, vapour pressure deficit.

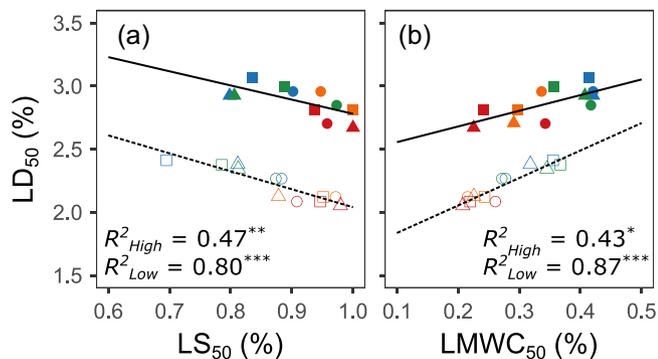
**TABLE 2** Lethal drought indices calculated as the soil water content associated with 50% plant mortality ( $LD_{50}$ , %), and the corresponding rates of leaf senescence ( $LS_{50}$ , %) and leaf meristem water content ( $LMWC_{50}$ , %) for each of the Mediterranean and temperate populations of *Dactylis glomerata* and *Festuca arundinacea* grown in 1-, 2- or 4-component mixtures under either high-VPD or low-VPD drought conditions.

Species	Population	Mixture	$LD_{50}$		$LS_{50}$		$LMWC_{50}$	
			High-VPD	Low-VPD	High-VPD	Low-VPD	High-VPD	Low-VPD
<i>Dactylis glomerata</i>	Mediterranean ('Medly')	1-comp.	2.70	2.09	95.8	90.8	34.3	26.1
		2-comp.	2.81	2.09	93.8	94.6	24.2	22.0
		4-comp.	2.67	2.05	100	97.9	22.5	20.7
	Temperate ('Ludac')	1-comp.	2.96	2.12	94.7	97.2	33.6	21.5
		2-comp.	2.81	2.12	100	95.1	29.7	24.3
		4-comp.	2.70	2.12	100	87.8	29.1	22.6
<i>Festuca arundinacea</i>	Mediterranean ('Centurion')	1-comp.	2.96	2.27	90.1	88.3	42.1	27.8
		2-comp.	3.07	2.41	83.5	69.5	41.3	35.5
		4-comp.	2.92	2.38	79.8	81.2	42.1	31.8
	Temperate ('Soni')	1-comp.	2.85	2.27	97.3	87.4	41.7	27.1
		2-comp.	2.99	2.38	88.9	78.5	35.7	36.1
		4-comp.	2.92	2.34	80.6	81.2	40.7	34.5

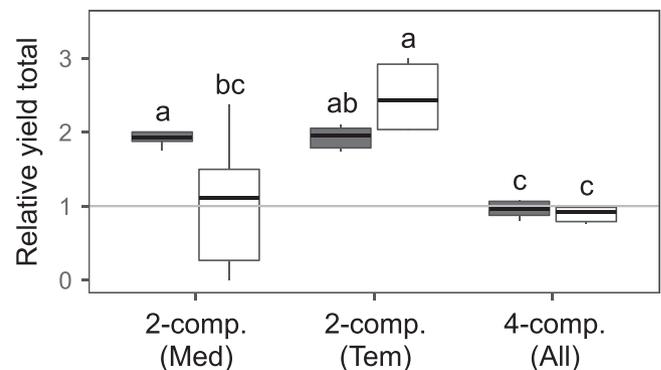
Abbreviation: VPD, vapour pressure deficit.



**FIGURE 3** Relationship between plant survival and (a) leaf senescence (LS) and (b) leaf meristem water content (LMWC). Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations) grown in monocultures (circles), 2-component mixtures (rectangles), and 4-component mixtures (triangles). Data points filling and line type refer to the VPD levels (solid points and lines: high-VPD drought; open points and dashed lines: low-VPD drought). The 50% survival lines are shown. VPD, vapour pressure deficit.



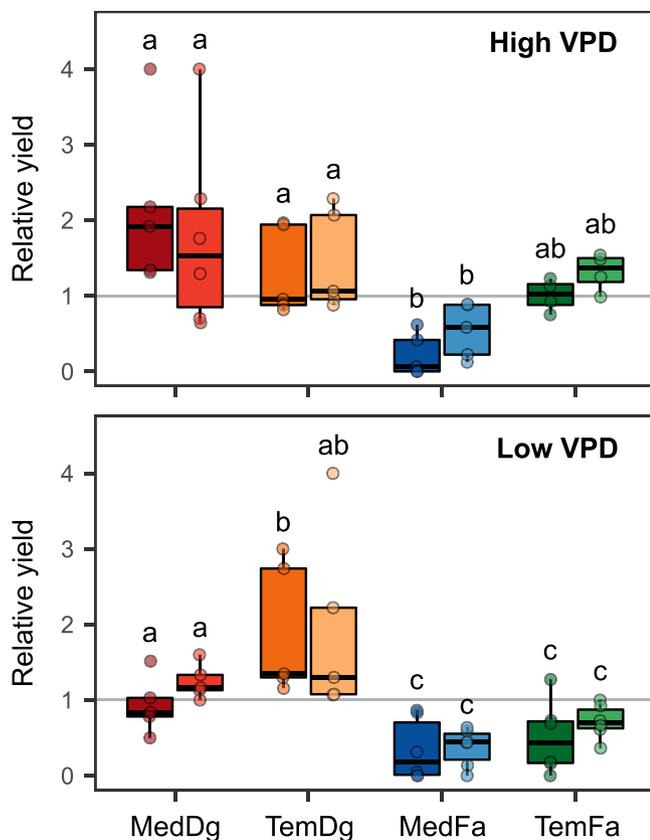
**FIGURE 4** Relationship between lethal drought (LD<sub>50</sub>) and the corresponding (a) leaf senescence (LS<sub>50</sub>) and (b) leaf meristem water content (LMWC<sub>50</sub>). Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations) grown in monocultures (circles), 2-component mixtures (rectangles), and 4-component mixtures (triangles). Data points filling and line type refer to the VPD levels (solid points and lines: high-VPD drought; open points and dashed lines: low-VPD drought). VPD, vapour pressure deficit.



**FIGURE 5** Distribution of post-drought relative yield total (RYT) indices calculated with plant biomass production across all plant mixtures. Boxplot filling indicates the VPD level (dark grey: high-VPD drought; white: low-VPD drought). The horizontal lines ( $y = 1$ ) represent the neutral value for which RYT indices do not differ from monocultures. The mixing effect was positive (or negative) for values above (or below) the line. Letters indicate significant differences between mixtures and VPD levels (Tukey HSD). VPD, vapour pressure deficit.

differences between mixtures ( $F = 10.6$ ,  $p < 0.001$ ) in interaction with VPD levels ( $F = 8.44$ ,  $p = 0.002$ ). For instance, the temperate mixtures always had  $RYT > 1$  ( $p < 0.001$ , Student's  $t$  test), while the Mediterranean mixtures had  $RYT > 1$  only under the high-VPD drought (Figure 5). Additionally, the temperate mixtures had, in general, higher RYT than the Mediterranean mixtures. The RYT did not differ from 1 for the 4-component mixtures with all the populations ( $p > 0.05$ , Student's  $t$  test), indicating no difference with the average monocultures (Figure 5).

Within mixtures, *D. glomerata* had significantly higher RY ( $F = 3.98$ ,  $p < 0.001$ ) than *F. arundinacea*, showing that *D. glomerata* recovered better after a drought than *F. arundinacea* when grown together in mixtures (Figure 6). However, no difference was found between the temperate and Mediterranean populations of each species. Drought intensity (residual SWC) affected RY in opposite ways for the two species: RY significantly increased above one with increasing drought intensity for *D. glomerata*, and decreased below one for *F. arundinacea* (Figure 7). The effect of drought intensity on

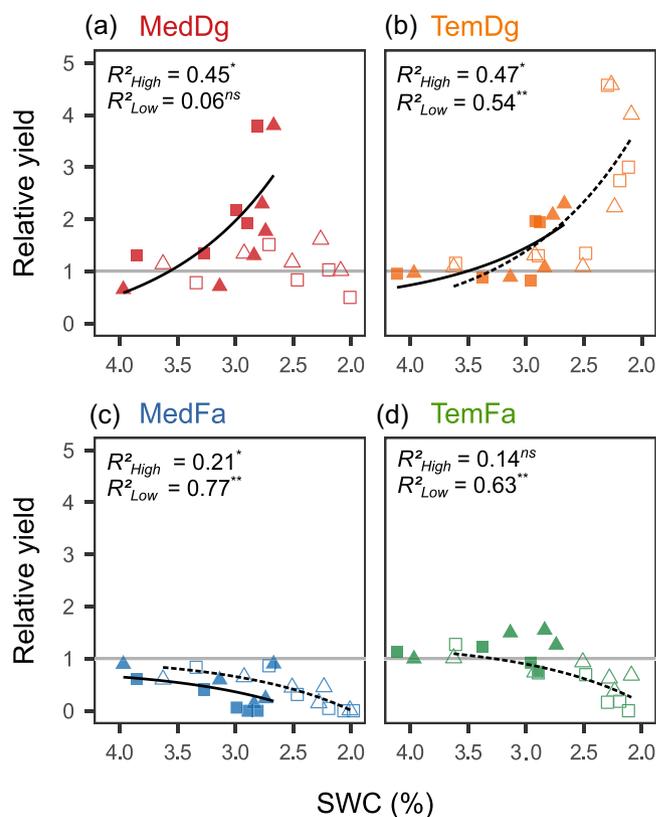


**FIGURE 6** Differences in post-drought relative yield (RY) calculated plant biomass production between species and populations. Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations), while colour intensity indicates the type of plant mixture (dark colours: 2-component mixtures; light colours: 4-component mixtures). The shape of data points and boxes refers to VPD levels (solid circles and boxes: high-VPD drought; open circles and boxes: low-VPD drought). The light grey horizontal lines ( $y = 1$ ) represent the neutral value for which RY indices do not differ from monocultures. Letters indicate significant differences between populations and mixtures (Tukey HSD). VPD, vapour pressure deficit.

RY was the strongest under the low-VPD drought in all types of mixtures. Finally, RY was negatively related to  $LD_{50}$  (Figure 8).

## 4 | DISCUSSION

Our results highlight that dehydration tolerance can be identified by considering processes at the whole plant level (e.g., mortality/survival rate) and at the vital organ level (e.g., water status of surviving meristems) as a function of drought intensity (e.g., SWC). This methodology addresses the main limitations of current approaches focused on leaf or xylem traits that rarely measure whole-plant survival or the dehydration sensitivity of meristematic zones in the plants (Brodrribb et al., 2021). The LD indices (e.g.,  $LD_{50}$ ), reflecting plant dehydration tolerance, varied with all the tested factors,

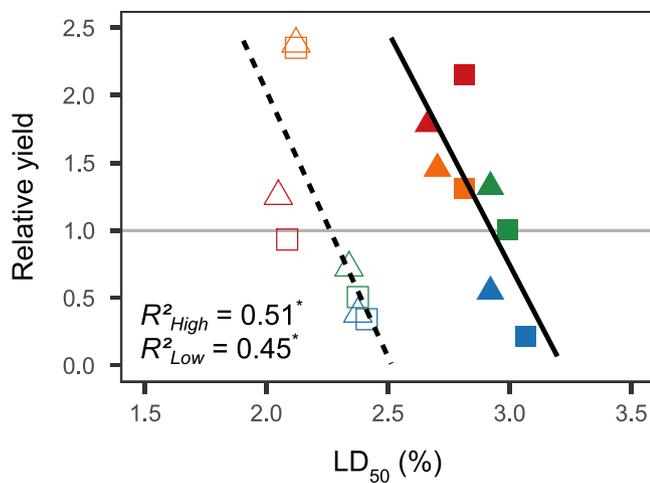


**FIGURE 7** Response of population relative yield (RY) calculated plant biomass production to drought intensity as indicated by residual SWC. Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations) grown in 2-component mixtures (rectangles), and 4-component mixtures (triangles). Data points filling and line type refer to the VPD level (solid points and lines: high-VPD drought; open points and dashed lines: low-VPD drought). The dashed horizontal lines ( $y = 1$ ) represent the neutral value for which RY indices do not differ from monocultures. SWC, soil water content; VPD, vapour pressure deficit.

revealing that plant survival and post-drought recovery depend on VPD levels and plant–plant interactions for a given plant species and population.

### 4.1 | Dehydration tolerance varies with the type of drought, species and populations

Plants had a greater dehydration tolerance under a low-VPD prolonged drought than under a short, high-VPD drought, regardless of the species or population considered ( $\chi^2 = 120.7$ ,  $p < 0.0001$ , Table 1). The general increase in dehydration tolerance suggests the possibility of plant acclimation, provided drought stress remained progressive enough, with moderate temperatures and VPD. Enhanced plant acclimation under a low-VPD drought can be ascribed to the prolonged maintenance of photosynthetic activity (+6.88 days with senescence lower than 50% in the low-VPD vs.



**FIGURE 8** Relationship between lethal drought ( $LD_{50}$ ) and the relative yield (RY) calculated plant biomass production. Colours indicate the species and populations (red and orange: the Mediterranean and temperate *Dactylis glomerata* populations; blue and green: the Mediterranean and temperate *Festuca arundinacea* populations) grown in 2-component mixtures (rectangles) and 4-component mixtures (triangles). Data points filling and line type refer to the VPD level (solid points and lines: high-VPD drought; open points and dashed lines: low-VPD drought). VPD, vapour pressure deficit.

high-VPD drought). As leaves stayed green for longer, allowing the maintenance of carbon assimilation with reduced growth, probably resulted in the accumulation of more soluble carbohydrates, especially in leaf meristems (strong sink), conferring them higher membrane stability to survival under low VPD (Rui & Dinney, 2020; Volaire, 1995; West et al., 1990; Zwicke et al., 2015). Conversely, a high-VPD drought can prevent acclimation with a rapid reduction of SWC (i.e., 'source-driven stress') combined with an intense evaporative demand (i.e., 'demand-driven stress'). Drought dynamics, and more generally, the type of drought (Mayr, 2021), need to be better assessed and accounted for to predict drought-induced mortality.

Comparing two species, we also show that species-specific strategies strongly determine plant dehydration ( $\chi^2 = 99.67$ ,  $p < 0.0001$ , Table 1). As expected, we found that *D. glomerata* was more dehydration-tolerant and survived better than *F. arundinacea*, especially under low-VPD drought conditions (Figure 2, Table 2). Indeed, drought survival of *F. arundinacea* primarily relies on a dehydration avoidance strategy permitted notably by a deep root system and water uptake in deep soil layers (Missaoui et al., 2017). In our experiments, root foraging was restricted by the small soil volume of pots, preventing dehydration avoidance. This strategy is relevant under moderate drought or when some soil water is still accessible (Volaire, 2018). It can be analysed by growing plants in long columns to express potential rooting depth (Bristiel et al., 2019). Conversely, dehydration tolerance is the main strategy ensuring plant survival under severe droughts when the soil water reserve is not accessible or depleted. These strategies are combined in plants growing in field conditions but their respective contribution to survival cannot be

easily assessed since their expression depends on local abiotic factors (e.g., soil depth, soil water reserve, drought intensity). We, therefore, need and propose a standardized methodology to assess and measure these major strategies independently, such as dehydration tolerance in this study. Our methodology, in standard conditions, allows disentangling dehydration tolerance from dehydration avoidance.

The Mediterranean population of *D. glomerata* significantly differed from others, especially under the high-VPD drought conditions that are more likely to occur in warmer and drier areas. It was the most dehydration-tolerant, probably due to its superior ability to accumulate carbohydrates under higher temperatures and drought (Volaire et al., 1998).

## 4.2 | Dehydration tolerance and post-drought recovery vary with plant-plant interactions

We show that plant-plant interactions create an additional source of variation in plant dehydration tolerance ( $\chi^2 = 8.87$ ,  $p = 0.0118$ , Table 1) that has been rarely tested previously (Griffin-Nolan et al., 2021). As expected, we found opposite responses between the two species, suggesting a positive relationship between plant dehydration tolerance and benefits from biodiversity effects in mixtures. Therefore, we confirm that species identity and how neighbours use water are essential to consider in the outcome of plant-plant interactions during drought (Shihan et al., 2020). For instance, *D. glomerata*, the most dehydration-tolerant species, had an equivalent, and in some cases even better, dehydration tolerance ( $LD_{50}$ ) and survival rates in mixtures than monocultures (Figure 2, Table 2). In contrast, *F. arundinacea*, the dehydration-sensitive species, always had a lower dehydration tolerance and survival rates in mixtures. Indeed, drought-induced mortality reduced plant density in mixtures but affected *F. arundinacea* more than *D. glomerata*. As a result, the remaining plants of *D. glomerata* benefited from additional *per capita* amount of water and mineral resources, explaining their improved plant survival in mixtures (Gessler et al., 2017; Hofer et al., 2017) and probably their strong competitive effects on *F. arundinacea* plants (Craine & Dybzinski, 2013). Reduced water evaporation through litter accumulation and water release from dead biomass potentially also explained how dead neighbours, especially *F. arundinacea*, could indirectly affect *D. glomerata* in mixtures during drought (Wilson, 2014). Here, LS and LMWC of *D. glomerata*, both associated with dehydration tolerance, were higher and lower in mixtures than in monocultures. This ultimately led to higher dehydration tolerance. Although they were not tested here, carbohydrate and nutrient concentration changes depending on the relative rates of leaf growth versus LS of each population in monocultures, 2- and 4-component mixtures can also be explicative (Keep et al., 2021). Plastic adjustments in response to changes in plant-plant interactions are potentially important mechanisms underlying the variation of plant dehydration tolerance in plant communities, impacting drought survival.

Similarly, we show that post-drought recovery, a critical component of drought survival and resilience, varies with plant–plant interactions across plant mixtures. As for dehydration tolerance, the recovery of dehydration-tolerant populations benefited more from interspecific interactions than dehydration-sensitive populations. The Mediterranean and temperate populations of *D. glomerata* had either better or at least equal recovery in mixtures than in monocultures, while the *F. arundinacea* populations showed the opposite response (Figure 6). The increasing effects of interspecific interactions on recovery, whether positive (for *D. glomerata*) or negative (for *F. arundinacea*) with increasing drought intensity (Figure 7), reveals the importance of local environmental context (Ploughe et al., 2019; Stultz et al., 2007). In the end, plant mixtures had better post-drought recoveries than monocultures (Figure 5), resulting from the different effects of plant–plant interactions on (1) plant survival during drought and (2) plant growth after drought (Haberstroh et al., 2021). Whatever the type of drought, the positive effects of interspecific interactions on *D. glomerata* populations, especially during the recovery phase, compensated for, and in some cases even exceeded, the negative effects on *F. arundinacea* populations, as a result of a better use of water and mineral resources (Gessler et al., 2017; Hofer et al., 2017). Despite changes in plant density, we support that plant diversity improves the resilience capacity to drought in grass mixtures (Tilman & Downing, 1994), as found in forests (Grossiord et al., 2014; Hisano et al., 2019). This effect could be even higher when complementary drought strategies are associated together and allow recovering productivity after drought (Wright et al., 2021), for example, in natura where *F. arundinacea* can efficiently better ‘avoid’ dehydration by capturing water from deep soil layers, reducing interspecific competition and maximizing ecosystem functioning (Godoy et al., 2020).

### 4.3 | Tolerance to soil dehydration mirrors tolerance to leaf meristem dehydration

We demonstrate that plant dehydration tolerance, measured as a function of SWC, was positively related to plant tissue dehydration tolerance, especially of leaf meristems, the surviving organs in grasses ( $\chi^2 = 230.6$ ,  $p < 0.0001$ , Figure 3). Therefore, the term ‘dehydration tolerance’ can irrespectively apply to plant responses to soil water deficit or its key-organ tissue dehydration. Plants were found to survive at tissue hydration as low as 20% (Table 2), below the threshold defined at the molecular level for differentiating dehydration and desiccation, that is, 30% water content (Zhang & Bartels, 2018). This threshold of leaf meristem dehydration was associated with the capacity of plants to recover after a severe water deficit. Likewise, recent results on trees showed that the differences in stem relative water content were directly related to the capacity to recover from drought (Mantova et al., 2021), confirming that measures of plant water content capture critical thresholds during drought and the associated dehydration processes (Martinez-Vilalta et al., 2019; Sapes & Sala, 2021).

Plant dehydration tolerance was also positively related to LS ( $\chi^2 = 308.2$ ,  $p < 0.0001$ , Figure 3). The soil water potential associated with 50% plant mortality ranged from  $-1.68$  to  $-4.47$  MPa, below what is usually regarded as the permanent wilting point ( $-1.5$  MPa), confirming that the wilting point is not suitable to define the impending mortality of perennial grasses since they are more dehydration tolerant than most annuals (Volaire, 2003). We found that the most dehydration-tolerant plants were also the most rapidly senescent, notably in *D. glomerata*. In this case, senescence is an active process that reduces water loss and allows grasses to dry without dying (Munné-Bosch & Alegre, 2004). The sacrifice of leaf blades can be interpreted as a way to protect enclosed leaf base meristems by reallocating carbohydrates to these sink tissues (West et al., 1990). The senescence or dehydration dynamics support the trade-off between dehydration avoidance in leaf laminae and dehydration tolerance in leaf meristems following the growth-stress survival trade-off (Bristiel et al., 2017). Trees have not shown this trade-off since their permanent death usually correlates with the amount of dead aboveground biomass (Chakraborty et al., 2017). As co-existing young trees and shrubs were less dehydration-tolerant than perennial grasses (Shihan et al., 2020), the relative dehydration tolerance of a range of woody and herbaceous species should be compared in the future. Finally, LS is not an unequivocal sign of impending death in perennial grasses and should be interpreted in light of plant responses under rehydration after drought. This result questions how far leaf traits can be the best proxy of whole plant dehydration tolerance, which is increasingly recognized to be based on the survival of meristematic tissues.

### 4.4 | Measuring dehydration tolerance to assess drought survival

This study successfully shows that plant dehydration tolerance ( $LD_{50}$ ) can be measured using a method previously used to measure cold tolerance ( $LT_{50}$ ). The analogy is intuitive since both drought and frost induce cellular dehydration (Pearce, 2001; Verslues et al., 2006). Hence, solute accumulations, osmotic adjustment and modification of the properties of cell walls help to tolerate the dehydration induced by low water potential under both frost and drought (Close, 1997; Hare et al., 1998; Krasensky & Jonak, 2012). The accumulation of solutes (carbohydrates, proteins) contributes to dehydration tolerance, particularly in meristematic tissues under harsh abiotic conditions in winter and summer (Kong & Henry, 2018). We demonstrate that meristem dehydration is likely to cause plant mortality and that drought acclimation can increase dehydration tolerance, as shown with cold hardiness (Armstrong et al., 2020). These results regarding the prediction of drought survival have a few important implications that we discuss below.

First, our method is integrative as it tests whole plants with their rooting systems, although we controlled rooting depth to the same access to water to compare tolerance levels to similar soil dehydration. In natura, drought survival combines dehydration

tolerance associated with cavitation tolerance (Volaire, 2018). Although to a very low rate, the aptitude to maintain water uptake is crucial for the survival of perennial grasses that otherwise die when roots are severed (McWilliam & Kramer, 1968). However, roots are rarely considered when measuring plant traits to predict drought survival. It is assumed that tree roots become hydraulically isolated from the soil at stomatal closure and that subsequent dehydration is independent of soil dry-down (Blackman et al., 2019). Moreover, the classical measurement of loss of conductivity of xylem tissues ( $P_{50}$ ) has mainly been carried out on detached branches or grass stems (Lens et al., 2013; Urli et al., 2013) and more recently on grass leaves (Jacob et al., 2022; Ocheltree et al., 2016), as a marker of xylem embolism resistance. However, as plant dry-down time was found to be unrelated to embolism resistance, it is now advocated to consider rooting depth that determines plant water availability and survival times (Blackman et al., 2019). Hydraulically vulnerable trees were shown to survive better than hydraulically resistant species due to their rooting system and access to deep water (Chitra-Tarak et al., 2021). Therefore, traits measuring hydraulic vulnerability may better underlie dehydration tolerance than drought survival ability. Both dehydration tolerance and rooting traits associated with efficient water uptake should be necessary and complementary to analyse and predict drought survival according to the variability of soil and climate conditions.

Second, our method is dynamic as it measures dehydration tolerance on plants subjected to a progressive drought (soil water deficit) over time (6–9 weeks without irrigation) which can be regarded as realistic compared with field-drought conditions (Poirier et al., 2012). Our results showed that acclimation significantly impacted dehydration tolerance. Conversely, the measurements of hydraulic traits, such as the loss of conductivity ( $P_{50}$ ), are usually performed at a very short time scale (minutes to hours) or a few days for the optical measurement of embolism (Brodribb et al., 2016; Mayr, 2021). As they are measured in standardized conditions, they give trait values that predict an overall plant vulnerability but cannot account for the acclimation effect revealed in this study. Moreover, the timing of extreme drought events can affect plant functioning to a larger extent than drought intensity (Forner et al., 2018; Hovenden et al., 2017), suggesting the importance of phenological adaptations particularly. Perennial grasses have seasonal patterns of potential growth, from a low growth potential to full dormancy, conferring a high survival to abiotic factors in the harsh seasons (Keep et al., 2021). The timing of dehydration tolerance measurement should therefore account for the phenological adaptations of species/populations.

Finally, our method allows measuring dehydration tolerance under restricted access to soil water in standardized soil and growth conditions experiments. We suggest that measuring the dehydration tolerance of a large range of plant species, including plants of contrasting growth forms, along with measuring their leaf and root traits, could significantly improve our understanding of drought survival strategies.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.21834459>

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