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RESEARCH ARTICLE

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Drought survival is positively associated with high turgor loss points in temperate perennial grassland species

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Abstract

1. Turgor loss point (π_{tlp}) has been suggested to be a key trait for drought resistance in woody species. In herbaceous grassland species, the role of π_{tlp} for species drought survival has not yet been tested, although grasslands are projected to experience more frequent and intense droughts with climate change.
2. To gain insights into the role of π_{tlp} for drought resistance of temperate perennial grassland species, we assessed π_{tlp} of 41 species common in Germany (20 forbs, 21 grasses). We directly related them to the species' comparative whole-plant drought survival and midday leaf water potentials under drought (Ψ_{MD}) assessed in a common garden drought experiment, and to species moisture association.
3. Species drought survival increased with increasing π_{tlp} across all species as well as within forbs or grasses separately. Ψ_{MD} was positively related to π_{tlp} and drought survival. Our results imply that high π_{tlp} promotes drought survival of common perennial European temperate mesic grassland species by enabling them to maintain high leaf water potentials under drought, that is, a desiccation avoidance strategy. However, π_{tlp} was not related to species moisture association.
4. The positive relationship between π_{tlp} and drought survival in herbaceous grassland species was opposite to the negative relationship previously established in woody plants, implying that mechanisms of drought resistance differ between woody and herbaceous species. Our results highlight the necessity of directly testing the relationship of functional traits to whole-plant drought survival in different plant life forms, before using trait assessments for predicting plant responses to drought.

KEYWORDS

desiccation avoidance, drought strategy, Ellenberg indicator values for soil moisture, functional traits, habitat association, midday leaf water potential, osmotic potential at full hydration

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1 | INTRODUCTION

Grasslands worldwide are influenced by drought (Gibson, 2009). Drought resistance—the capacity to survive periods of low water availability—varies widely among species within and across plant communities, including in grasslands (e.g. Buckland, Grime, Hodgson, & Thompson, 1997). Species differential drought resistance may lead to changes in community composition and species abundance across time and space (Harrison, Gornish, & Copeland, 2015; Tilman & El Haddi, 1992; Weaver, 1968). In Europe, the frequency and severity of drought events are expected to increase even during the growing season (Spinoni, Vogt, Naumann, Barbosa, & Dosio, 2018). A thorough understanding of the drought resistance of grassland species and the underlying mechanisms is necessary to predict the responses of grassland communities to changing drought regimes.

Plants exhibit a wide range of morphological, anatomical and physiological mechanisms that allow them to withstand drought. Mechanisms of drought resistance in perennial plants can be categorized into (a) mechanisms of desiccation tolerance, which allow plants to sustain physiological activity despite low water potentials and (b) mechanisms of desiccation avoidance, which enable plants to maintain high water potentials during drought through maximizing water uptake and water storage, and minimizing water loss (Comita & Engelbrecht, 2014; Levitt, 1972). Efficient avoidance of desiccation leads to the maintenance of high midday leaf water potentials under drought (Ψ_{MD}), which thus provide a comparative measure of desiccation avoidance across species (Comita & Engelbrecht, 2014).

The question of which mechanisms are important for species differential drought resistance has been a focus of a large body of research (e.g. Chaves, Maroco, & Pereira, 2003; McDowell et al., 2008; O'Brien et al., 2017; Skelton, West, & Dawson, 2015). Various morphological or physiological traits are broadly related to habitat moisture gradients in perennial herbaceous species (Belluau & Shipley, 2018; Craine et al., 2013; Griffin-Nolan et al., 2019; Shipley et al., 2017; Tucker, Craine, & Nippert, 2011). However, relations are generally weak and not consistently observed (Májeková, Martínková, & Hájek, 2019), and insights into the functional role of traits for species drought resistance remain limited. Recent studies have tested relations between physiological traits and leaf mortality under drought (Belluau & Shipley, 2017; Ocheltree, Nippert, & Prasad, 2016). However, aboveground drought mortality does not necessarily reflect whole-plant drought resistance since many grassland species can resprout from belowground organs after drought, and leaf abscission may even promote plant survival under drought by minimizing water loss (Volaire, Thomas, & Lelievre, 1998). To rigorously test the role of mechanisms underlying species' differential drought resistance, traits need to be directly related to species' comparatively assessed whole-plant drought survival. Surprisingly, experimental studies of comparative whole-plant drought survival remain scarce and restricted to woody species (Engelbrecht et al., 2007; O'Brien et al., 2017). To our knowledge, no study has directly related potentially important mechanisms of drought resistance to whole-plant drought survival across multiple herbaceous species, severely limiting our ability to predict consequences of drought for grassland systems.

Turgor loss point (π_{tlp}), the leaf water potential at which the turgor pressure of leaf cells equals zero, has long been considered a crucial parameter in plant water relations (Cheung, Tyree, & Dainty, 1975). It varies widely among plant species and has more recently been suggested to be a useful proxy of species drought resistance (Bartlett, Scoffoni, & Sack, 2012; Griffin-Nolan et al., 2019). A *low* (more negative) π_{tlp} can allow the leaf to remain turgid despite decreasing leaf water potential (Ψ_{leaf}) and thereby maintain photosynthesis, water transport, transpiration and growth, conferring high drought resistance as a mechanism of desiccation tolerance. On the other hand, a *high* (less negative) π_{tlp} may also promote drought resistance by leading to early stomatal closure, and thus enabling plants to maintain high water potentials and hydration even under declining soil water status, reflecting a mechanism of desiccation avoidance.

In woody species, a *low* π_{tlp} has been shown to be related to high survival under natural drought (Zhu, He, et al., 2018), and to increasing species associations with habitat dryness at global (Bartlett, Scoffoni, & Sack, 2012), regional (Mitchell, Veneklaas, Lambers, & Burgess, 2008; Zhu, Chen, et al., 2018) and local scales (Lenz, Wright, & Westoby, 2006; Maréchaux et al., 2015). Together, these studies provide strong evidence that in woody species a low π_{tlp} promotes drought resistance as a mechanism of desiccation tolerance.

In herbaceous species, in contrast, the knowledge about the association between π_{tlp} and drought resistance is indirect and inconsistent. For example, in C_4 perennial grasses, species with high leaf resistance to hydraulic failure exhibited low π_{tlp}, consistent with woody species (Ocheltree et al., 2016), but species from drier habitats had higher π_{tlp} than those from wetter habitats, which is opposite to the trend in woody species (re-analysed from Liu & Osborne, 2014). In most studies focusing on herbaceous species, π_{tlp} was unrelated to their distributional association with the dryness of habitats (Farrell, Szota, & Arndt, 2017; Griffin-Nolan et al., 2019; Májeková et al., 2019; Ocheltree et al., 2016) or biomes (re-analysed only for herbaceous species from Bartlett, Scoffoni, & Sack, 2012). In a recent study, π_{tlp} was instead positively correlated with the wet extremes of species distributions (Griffin-Nolan et al., 2019), which was attributed to competition from more acquisitive (high-π_{tlp}) species limiting the distribution of low-π_{tlp} species into wetter habitats. Overall, in herbaceous species, the role of π_{tlp} for whole-plant drought resistance and distribution remains elusive, and its potential as a predictor of species drought resistance is still unclear.

In our study, we tested two alternative hypotheses for the relationship of π_{tlp} with drought resistance in grassland species: (a) a *low* π_{tlp} is related to high whole-plant drought survival, implying a strategy of desiccation tolerance that allows maintenance of stomatal conductance and physiological activity, consistent with woody species; or (b) a *high* π_{tlp} is associated with high whole-plant drought survival and high Ψ_{MD}, suggesting a strategy of desiccation avoidance that minimizes water loss, for example, through stomatal closure, contrasting to woody species. We also assessed if π_{tlp} is accordingly related to species association with habitat moisture. To test these hypotheses, we assessed π_{tlp} for 41 temperate perennial grassland species and related them to comparative species whole-plant drought survival and Ψ_{MD} assessed in a common garden drought experiment, and to their moisture association.

2 | MATERIALS AND METHODS

2.1 | Study species

We initially chose 43 temperate grassland species (Table S1), 22 forbs and 21 grasses, common in Germany. Species were selected based on the following criteria: (a) perennial, the dominant life history strategy in European temperate grasslands (Ellenberg et al., 1991), (b) high abundance and frequency in 150 long-term grassland plots located in three areas across Germany (Socher et al., 2012), (c) to include different life forms, that is, forbs and grasses and (d) to represent a wide range of moisture associations based on Ellenberg's moisture index (*F* value from 3 to 7; Ellenberg et al., 1991). The selected species were from 34 genera and nine families, and all have C_3 photosynthesis. Seeds were bought from commercial suppliers (Rieger-Hofmann and Saaten Zeller, Germany) and germinated in a greenhouse in mid-March 2015. Plants were transplanted to larger pots for the measurement of π_{tlp} in the greenhouse in mid-June 2015, and to plots in the common garden drought experiment for the assessments of comparative whole-plant drought survival and Ψ_{MD} in the first week of June 2015.

Two of the 43 species established poorly and had low survival even in well-watered plots (<70%; Sun, Jung, Gaviria, & Engelbrecht, 2019). We therefore excluded them from the analyses presented in the main text. Analyses including or excluding these two species yielded qualitatively the same results (see Tables S2 and S3).

2.2 | Assessments of turgor loss point

Plants were grown in the greenhouse in pots (7 cm diameter × 36 cm depth), filled with sandy soil, under well-watered and regularly fertilized conditions until assessment of π_{tlp} from November 2015 to February 2016. The temperature in the greenhouse was kept around 22°C during the day and 18°C at night, and humidity was about 50%.

To validate the 'osmometer method' (Bartlett, Scoffoni, Ardy, et al., 2012) that assesses π_{tlp} from measurements of osmotic potential at full turgor with an osmometer for our species set, we measured π_{tlp} with the long-established pressure–volume curve (*P–V* curve) method (Tyree & Hammel, 1972; for details see Method S11), and osmotic potentials at full turgor with an osmometer (Bartlett, Scoffoni, Ardy, et al., 2012; for details see Method S1) on a subset of our focal species (7 forbs, 7 grasses; see Table S1). Tight and significant positive regressions emerged between π_{tlp} assessed with *P–V* curves and osmotic potential at full turgor assessed with the osmometer (Figure 1), and the relations remained significant within our focal forb or grass species separately. The relations also were significant within other plant life forms and photosynthetic pathways, when including previously published data, and slopes did not differ between groups (Figure 1).

Leaf osmotic potential at full turgor was consequently determined for all species with an osmometer ($\pi_{\text{o-osmo}}$; VAPRO 5500, Wescor). Six individuals per species were rehydrated overnight in the dark and measurements were taken on one leaf disc per plant following Bartlett, Scoffoni, Ardy, et al. (2012). π_{tlp} was modelled based on the regression equation between $\pi_{\text{tlp-}P\text{–}V}$ and $\pi_{\text{o-osmo}}$ from our 14 species as:

$$\pi_{\mathrm{tlp}} = 0.645 \times \pi_{\mathrm{o-osmo}} - 0.942 \tag{1}$$

2.3 | Whole-plant drought survival and midday leaf water potential

To directly assess comparative whole-plant drought survival and Ψ_{MD} across multiple species, we exposed all species to uniform experimental drought conditions in a common garden in the Ecological Botanical Garden of the University of Bayreuth, Germany. The area has mean annual temperature and precipitation of 8.7°C and 745 mm, respectively (1998–2007, data: Ecological Botanical Garden). Plants were transplanted to 72 plots (1 m × 2 m) in a 20 cm grid with one individual per species being randomly assigned to each plot. All plots were covered with transparent rain-out shelters. After an initial acclimation period under well-watered conditions, irrigation was discontinued on 3 August 2015 for half of the plots for 10 weeks, considered to exceed a 1000-year extreme event in the area (based on recurrence time, Jentsch et al., 2011). In the drought treatment, the permanent wilting point (−1.5 MPa) was reached 26 ± 9 days (*M* ± *SD*) after ceasing irrigation (assessed at 15 cm soil depth with gypsum blocks, GB-1 and KS-D1, Delmhorst, NJ). Drought survival was assessed weekly throughout the experiment based on living above-ground tissues, and the whole-plant drought survival was additionally determined in the next growing season (June 2016) to account for resprouting from surviving belowground organs. Species survival ranking remained consistent throughout the experiment, indicating that it was independent of drought duration and intensity. For further analyses, we focused on the whole-plant drought survival assessed in June 2016. For details on the common garden experiment, see Jung, Gaviria, Sun, & Engelbrecht (2020).

Ψ_{MD} was measured in eight randomly selected plots in the drought treatment (i.e. generally eight individuals per species) when most plants had started wilting (8–15 August 2015). To ensure comparability across species and to avoid any bias introduced by

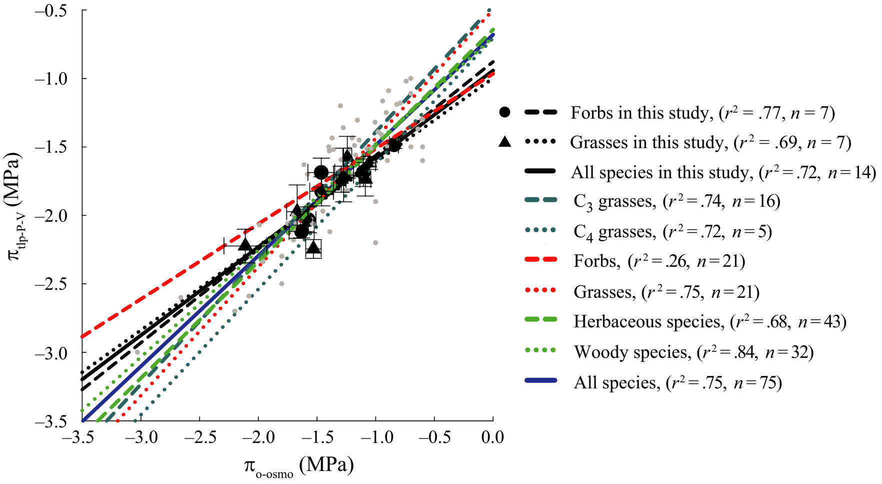

FIGURE 1 Turgor loss point measured with traditional *P–V* curve methods ($\pi_{tlp\text{-}P\text{-}V}$) was significantly related to osmotic water potential at full turgor assessed with an osmometer ($\pi_{o\text{-}osmo}$) across all 14 grassland species, and separately within the forbs and grasses measured in our study. Additionally, relations are shown for C_3 and C_4 grasses, grasses and forbs, and herbaceous and woody species combined from this and previous studies (Bartlett, Scoffoni, Ardy, et al., 2012; Bartlett, Scoffoni, & Sack, 2012; Griffin-Nolan et al., 2019; Gotsch et al., 2015; Ocheltree et al., 2016; Farrell et al., 2017; Májeková et al., 2019). Relations were significant within each of the species groups (all $p < .05$, see legend for r^2 values) and slopes did not differ between grasses versus forbs (this study nor combined), C_3 versus C_4, nor herbaceous versus woody species (all $p > .1$). Data points are species *M* ± *SE* for three individuals per species for 14 grassland species in our study (large symbols), and species means for the data from published literature (small grey dots; not differentiated between groups for clarity). The joint regression equation is: $\pi_{tlp} = 0.807 \times \pi_{o\text{-}osmo} - 0.680$, n = 75 species

sampling date, we sampled plants plot by plot, that is, one individual of each species per day. Measurements were taken with leaf cutter psychrometers (Merrill Specialty Equipment) to minimize destructive sampling that may influence drought responses. One leaf disk per individual (diameter 0.6 cm) was sampled from a healthy, mature leaf, avoiding major leaf veins from 11:30 a.m. to 12:30 p.m. Samples were equilibrated in a water bath at 25°C for 5 hr and measurements were taken with a PSYPRO™ water potential system (Wescor, Inc.). Ψ_{MD} were analysed based on previously established calibration curves with five standard NaCl solutions for each sensor.

2.4 | Species association with moisture

We characterized species association with moisture at the local scale using Ellenberg indicator values for moisture (*F* value, Ellenberg et al., 1991; see Table S1) and at the large scale using species annual rainfall niches. Species annual rainfall niches were assessed at a spatial resolution of 1 km^2 based on overlying occurrence information of each focal species from the Bien database (Enquist, Condit, Peet, Schildhauer, & Thiers, 2016) on rainfall data (CHELSA version 1.2; Karger et al., 2017). We assessed the median, 5th percentile, and 95th percentile of the annual rainfall niche for each species.

2.5 | Statistical analyses

We tested differences of Ψ_{MD} and π_{tlp} among species using one-way ANOVAs and between life forms (forbs and grasses) using *t* tests. The difference of whole-plant drought survival between forbs and grasses was tested using a generalized linear model (GLM) with a binomial distribution (see below).

To assess the association of π_{tlp} with desiccation avoidance, we analysed the relationship between Ψ_{MD} and π_{tlp} with a Pearson's correlation, and we tested for a difference of this relationship between forbs and grasses with a SMA test. We analysed the effects of Ψ_{MD} and π_{tlp} on whole-plant drought resistance based on three different parameters: (a) whole-plant drought survival as alive or dead (binary data), (b) per cent survival in the drought treatment relative to the number of individuals at the start of the drought (% survival) and (c) the ratio of % survival in the drought plots relative to % survival in the well-watered plots (survival ratio).

We focused the analyses on the binary whole-plant drought survival data (alive/dead) because they represent the primary and untransformed dataset. We analysed the effects of Ψ_{MD} or π_{tlp} on survival using a GLM with a binomial distribution with whole-plant drought survival as response variable and Ψ_{MD} or π_{tlp} as independent variable and tested it with a likelihood ratio test (Chi-square test). We included the effect of life form and its interactions with Ψ_{MD} or π_{tlp} to test whether the effects of Ψ_{MD} and π_{tlp} on survival differed between forbs and grasses. We also tested the effects of Ψ_{MD} and π_{tlp} on % survival and survival ratio with Pearson's correlations. All models yielded qualitatively similar results (Table S3).

We further used a mediation test to evaluate if the effects of π_{tlp} on whole-plant drought survival were indirectly mediated through Ψ_{MD}, that is, high π_{tlp} allowing plants to maintain high Ψ_{MD}, leading to high drought survival (hypothesis 2), or if there was a direct effect of π_{tlp} on whole-plant drought survival. The direct and indirect effects of π_{tlp} on whole-plant drought survival and their significances were assessed with Mplus Version 7.4 using the maximum likelihood method with bootstrap = 10,000 (Muthén, Muthén, & Asparouhov, 2016).

We tested the relationships between π_{tlp} and species moisture association based on *F* value (excluding generalist species with *F* value *x*) and annual rainfall niches (median, 5th and 95th percentile) using Pearson correlation. We additionally tested differences in π_{tlp} between species categorized as associated with dry habitats (*F* value 3, 4) and with wet habitats (*F* value 6, 7), excluding intermediate species with *F* value 5 or generalists (compare Májeková et al., 2019).

SMA tests were done using the R-package SMATR3 (Warton, Duursma, Falster, & Taskinen, 2012), and the remaining analyses were with the R base package in R (R Core Team, 2017).

3 | RESULTS

Midday leaf water potentials under drought (Ψ_{MD}) and turgor loss points (π_{tlp}) varied significantly across the 41 focal species (Table S2). π_{tlp} ranged from −2.30 ± 0.12 MPa to −1.49 ± 0.02 MPa (*M* ± *SE*) in our study and were well within published data for herbaceous species under irrigated conditions, that is, −3.2 MPa to −0.43 MPa (Figure 1; Bartlett, Scoffoni, & Sack, 2012; Griffin-Nolan et al., 2019). Forbs had significantly higher Ψ_{MD} and π_{tlp} than grasses (Figure 2a,b; Table S2). Between 42% and 100% of the individuals survived the experimental drought in the focal species, with whole-plant drought survival (alive/dead) being higher in forbs than in grasses (Figure 2c).

π_{tlp} was significantly positively related to Ψ_{MD} across all 41 species ($p < .001$; GLM; Figure 3a; also see Table S3). Thus, species that lost turgor at high water potentials maintained high leaf water potentials under drought (i.e. effectively avoided desiccation). π_{tlp} was strongly related to whole-plant drought survival with species with higher π_{tlp} exhibiting higher survival across all 41 species ($p < .001$; GLM; Figure 3b; Table S3). Ψ_{MD} also had a strong positive effect on whole-plant drought survival across all 41 species ($p < .001$; GLM; Figure 3c; Table S3). π_{tlp} and Ψ_{MD} were both consistently significantly positively related to above-ground survival after various durations of drought (week 2–week 9; GLMs; all $p < .01$ for π_{tlp} and all $p < .001$ for Ψ_{MD}, data not shown), indicating that the relation was independent of drought duration and intensity. The effects of π_{tlp} and Ψ_{MD} on whole-plant drought survival remained significant when forbs and grasses were analysed separately (Table S3) and did not significantly differ between the two life forms (Table S4). A mediation test showed that effects of π_{tlp} on whole-plant drought survival were predominantly indirect, that is, through maintenance of high Ψ_{MD} (Figure 4), while the direct effect was not significant. π_{tlp} was unrelated to Ellenberg's moisture index ($p \gg .1$) and did not differ between the species associated with dry habitats and with wet habitats (*t* test, $p \gg .1$). π_{tlp} was also unrelated to the species rainfall niches.

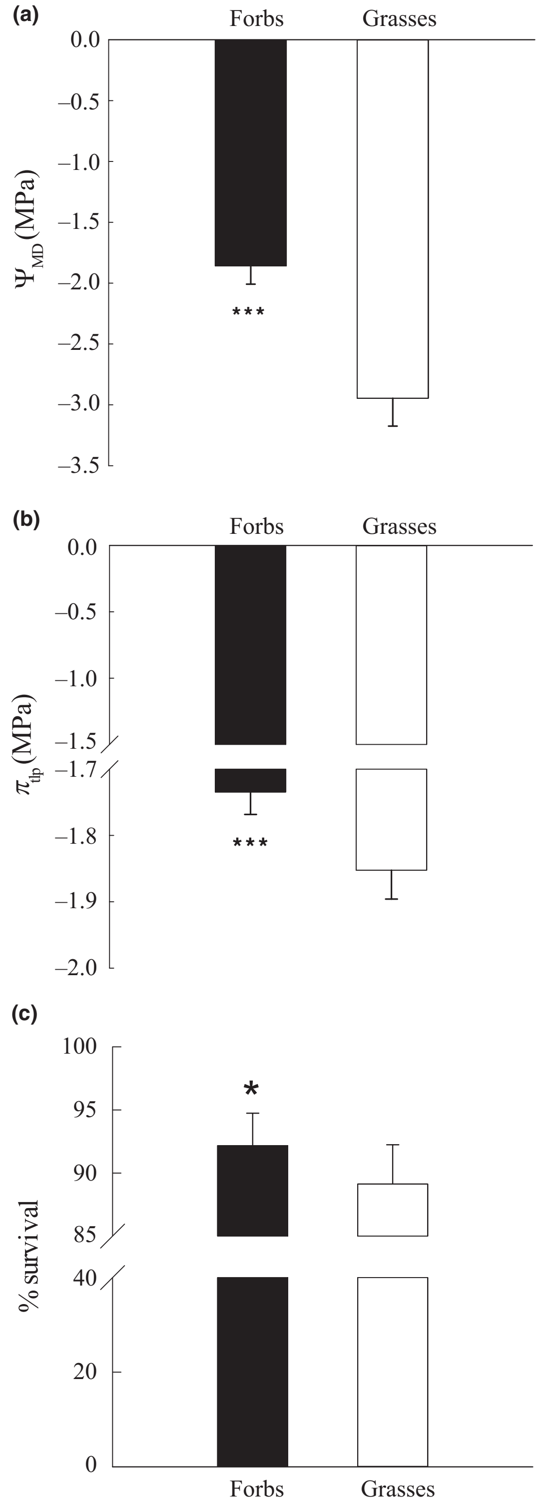

FIGURE 2 Comparisons between forbs and grasses of (a) midday leaf water potentials under drought (Ψ_{MD}), (b) turgor loss points (π_{tlp}) and (c) species whole-plant drought survival. Significance of differences between forbs (*n* = 20) and grasses (*n* = 21) is given as ***$p < .001$, *$p < .05$ [*t* tests in (a) and (b), GLM with a binomial distribution in (c)]; the figure (c) shows % survival for visual understandability

4 | DISCUSSION

4.1 | Turgor loss point, desiccation avoidance and drought survival in temperate grassland species

The positive relations between π_{tlp} and whole-plant drought survival across all 41 species as well as within forbs and grasses clearly showed that in common perennial European temperate mesic grassland species a *high* π_{tlp} is associated with high whole-plant drought survival. We also showed that the positive relation between π_{tlp} and drought survival was mediated by Ψ_{MD}. These results provide strong evidence that desiccation avoidance mechanisms are the dominant driver of differential whole-plant drought survival in European temperate grassland species, rather than desiccation tolerance mechanisms. To our knowledge, this is the first time that π_{tlp} was related to comparatively assessed whole-plant drought survival across a sufficient number of species to directly test the relationship. Nevertheless, available pairwise comparisons of drought responses in herbaceous species with different π_{tlp} are consistent with our findings (Barnes, 1985; Braatne & Bliss, 1999; Holloway-Phillips & Brodribb, 2011; Torrecillas, Guillaume, Alarcón, & Ruiz-Sánchez, 1995).

Although it had been recognized that high π_{tlp} could allow plants to avoid desiccation and thus promote drought survival, this mechanism has so far received little attention (Bartlett, Scoffoni, & Sack, 2012). A positive relationship between whole-plant survival and π_{tlp} through desiccation avoidance could be based on early leaf senescence and plant dormancy which minimize transpiration under drought, as has been shown in Mediterranean grasslands (Ocheltree et al., 2016; Volaire et al., 1998). In this scenario, leaf level survival would be negatively related to π_{tlp} (i.e. lower leaf survival with higher π_{tlp}), and lead to the positive relation of π_{tlp} to whole-plant survival. However, we can exclude this possibility in our species because species with a high π_{tlp} exhibited less/later leaf necrosis, and species with less leaf necrosis, in turn, had higher drought survival (Jung et al., 2020). Thus, leaf level mechanisms that minimize water loss under decreasing water availability should underlie our findings. First, turgor loss can trigger the biosynthesis of abscisic acid, which leads to stomatal closure even at high leaf water potentials (McAdam & Brodribb, 2016). Positive correlations between π_{tlp} and stomatal closure in woody species (Bartlett, Klein, Jansen, Choat, & Sack, 2016) as well as in herbaceous species (re-analysed from Farrell et al., 2017) support this mechanistic linkage, and indeed the correlation also emerged in our focal species (S. Sun, B.M.J. Engelbrecht, unpubl. data). Second, in many species turgor loss induces leaf rolling or folding and vertical leaf orientation (Turner & Begg, 1981), which maximizes boundary layer resistance and thus minimizes the leaf-to-air water vapour deficit. Additionally, turgor loss leads to the shrinkage of cuticle waxes, which reduces cuticle permeability to water vapour, the main path of plant water loss after stomatal closure (Boyer, 2015). These mechanisms may individually or in combination link high π_{tlp} to the maintenance of high leaf water potentials, and consequently high survival under drought in temperate perennial grassland species.

π_{tlp} alone explained 22% of the variation of % survival across our focal species, and a few species with relatively low π_{tlp} nevertheless exhibited 100% drought survival, underlining that further mechanisms also contribute to desiccation avoidance and drought survival. Indeed, additional mechanisms of desiccation avoidance have also been shown to promote drought performance in perennial grassland species. For example, maximizing water uptake through high rooting depth and/or high root mass significantly contributed to high survival and forage production under drought (Barkaoui, Roumet, & Volaire, 2016; Volaire, 2008; Zwicke, Picon-Cochard, Morvan-Bertrand, Prud'homme, & Volaire, 2015). In contrast, relevant data on desiccation tolerance mechanisms for grassland species remain scarce. Xylem embolism resistance, one of the most important desiccation tolerance traits in woody plants (Anderegg et al., 2016; O'Brian et al., 2017), was unrelated to species whole-plant drought survival assessed in our study (13 species, analysed from Lens et al., 2016) or to habitat moisture (Ocheltree et al., 2016). Similarly, osmotic adjustment under drought was also unrelated to habitat moisture (Májeková et al., 2019). In summary, an important role of mechanisms of desiccation avoidance for the differential drought resistance of grassland species is supported by our own as well as previous results, while support for the relevance of mechanisms of desiccation tolerance is limited.

While we found a positive relationship of π_{tlp} with species whole-plant drought survival that held also within life forms, π_{tlp} was unrelated to species distributional association with habitat moisture. Drought survival or growth accessed in our common garden experiment was also not related to species local or large-scale moisture association (Jung et al., 2020). The result is also consistent with previous findings of a lack of a relationship between π_{tlp} and habitat moisture in European grassland species (Májeková et al., 2019) or the dry end of the rainfall niche in North American Prairie species (Griffin-Nolan et al., 2019). Similarly, high water potentials at stomatal closure (i.e. stomata close 'earlier' in a drought), which are related to high π_{tlp} (see above), were positively correlated with occurrence in dry habitats in some studies (Belluau & Shipley, 2017), while other studies showed the opposite trend (Craine et al., 2013; Tucker et al., 2011). These results suggest that processes other than the interplay between habitat moisture and species fundamental drought resistance are important in shaping habitat associations in grassland species and are overriding the direct effects of drought, for example nutrient relations or biotic interactions (Silvertown, Araya, & Gowing, 2015). However, drought resistance can vary between life stages (Cavender-Bares & Bazzaz, 2000), and although juvenile stages are generally considered a bottleneck in population dynamics (Harper, 1977), the drought resistance of older plants that dominate established perennial grasslands may be more important in driving moisture associations than the responses of the first-year plants studied here. Additionally or alternatively, the relatively coarse measures of species association with moisture (Ellenberg moisture index or rainfall niche) may not provide information on plant water availability and critical soil water potentials at a resolution fine enough to resolve the role of moisture and drought resistance for species distributions.

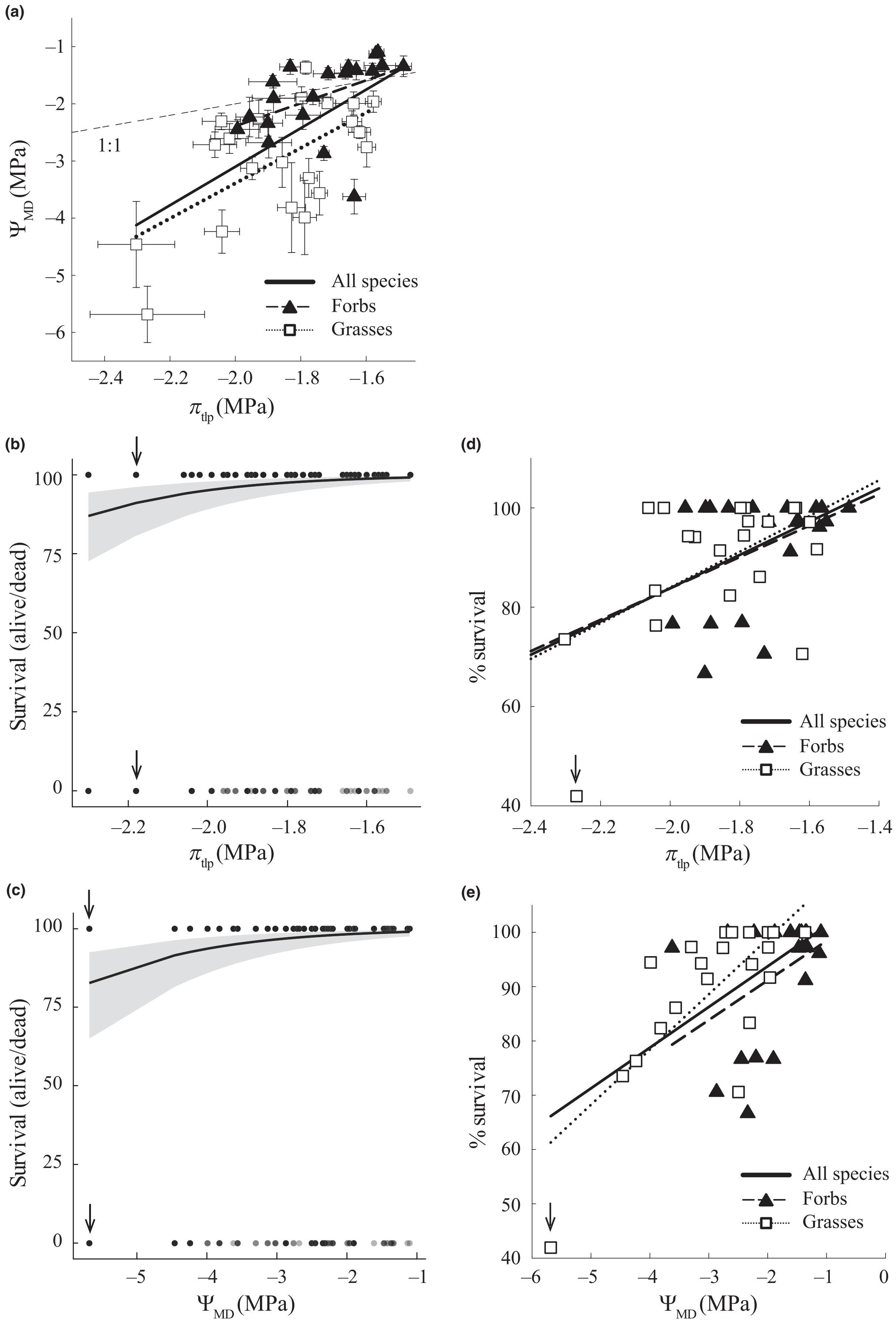
(a)
Ψ_{MD} (MPa)
−1
−2
−3
−4
−5
−6
1:1
All species
Forbs
Grasses
−2.4
−2.2
−2.0
−1.8
−1.6
π_{tlp} (MPa)
(b)
Survival (alive/dead)
100
75
50
25
0
−2.2
−2.0
−1.8
−1.6
π_{tlp} (MPa)
(d)
% survival
100
80
60
40
All species
Forbs
Grasses
−2.4
−2.2
−2.0
−1.8
−1.6
−1.4
π_{tlp} (MPa)
(c)
Survival (alive/dead)
100
75
50
25
0
−5
−4
−3
−2
−1
Ψ_{MD} (MPa)
(e)
% survival
100
90
80
70
60
50
40
All species
Forbs
Grasses
−6
−5
−4
−3
−2
−1
0
Ψ_{MD} (MPa)

FIGURE 3 Turgor loss point (π_{tlp}) was positively related to (a) midday leaf water potential under drought (Ψ_{MD}) and (b) species whole-plant drought survival. Higher Ψ_{MD} was also positively related to drought survival (c). Relations were significant across all 41 species, tested with Pearson's correlations in (a) ($r^2 = .36$, $p < .001$), and with generalized linear models (GLM) with a binomial distribution in (b) ($\chi^2 = 52.6$, $p < .001$) and (c) ($\chi^2 = 82.6$, $p < .001$). The relations stayed significant within forbs and grasses separately, as well as when the outlier (indicated with an arrow) was excluded. For details, see Table S3. For visual understandability, we additionally show in figures (d) and (e) the % survival fitted with Pearson's correlations, with $r^2 = .22$ and $r^2 = .36$, respectively. In (a), data points are averages ± *SE*. For species below the 1:1 line, Ψ_{MD} at the time of measurements were already below the π_{tlp} determined on well-watered plants. The grey areas in panels (b) and (c) represent the 95% confidence intervals, symbols are semi-transparent, that is, symbols are dark when the data points overlap

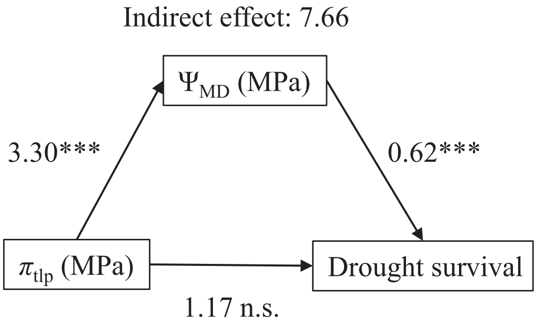

FIGURE 4 Schematic representation of results of the mediation test for the direct and indirect effects of turgor loss point (π_{tlp}) on whole-plant drought survival (alive/dead). Numbers adjacent to arrows indicate the effect size and the associated *p* value. ***$p < .001$, n.s. $p > .05$

4.2 | Contrasting mechanisms of drought resistance in herbaceous grassland versus woody species

The trend we found in herbaceous grassland species, that is, a *high* π_{tlp} associated with high drought survival, was opposite to woody species where a *low* π_{tlp} was associated with high survival under natural drought (Zhu, He, et al., 2018). At the same time, in woody species, a low π_{tlp} was also associated with species occurrence in dry habitats or biomes (Bartlett, Scoffoni, & Sack, 2012; Lenz et al., 2006; Maréchaux et al., 2015; Mitchell et al., 2008). These results imply that herbaceous species of temperate grasslands and woody species differ in drought resistance strategies, as well as in the ecological consequences of differential drought resistance. Mechanisms of desiccation tolerance generally dominate in woody species: high resistance to xylem embolism in leaves, stems, and roots, low lethal leaf water potentials and low water potentials at stomatal closure have been linked to high drought survival (Anderegg et al., 2015, 2016; Kursar et al., 2009; Urli et al., 2013; Zhu, He, et al., 2018). In turn, a low π_{tlp} was associated with these mechanisms of desiccation tolerance (Bartlett et al., 2016). On the other hand, in woody species Ψ_{MD} or maximum rooting depth was not related to drought survival (Hoffmann, Marchin, Abit, & Lau, 2011; Anderegg et al., 2016; B.M.J. Engelbrecht, M.T. Tyree, T.A. Kursar, unpubl. data), suggesting that the role of desiccation avoidance is limited. In summary, for woody species, there is plenty of evidence, including π_{tlp}, that mechanisms of desiccation tolerance are important for species differential drought survival, while a decisive role of mechanisms of desiccation avoidance is not supported. This is in stark contrast to our and other findings for herbaceous grassland species (see above).

Distinct strategies of drought resistance in herbaceous and woody species may be linked to the differences in biomass allocation patterns, functional and life-history characteristics. These include the generally much higher root:shoot ratios leading to higher water uptake capacity relative to water demand, and smaller stature reducing the length-dependent hydraulic resistance of the xylem in herbaceous compared to woody species (Mokany, Raison, & Prokushkin, 2006; Tyree, 2007). These traits of herbaceous species may facilitate the maintenance of high leaf water potentials, that is, desiccation avoidance, and release selection pressure for tissue tolerance to low water potentials, that is, desiccation tolerance, relative to woody species. To more fully understand differences in strategies to cope with drought between herbaceous and woody species, as well as among other life forms and life-history strategies, more studies are needed that directly link traits to whole-plant drought resistance.

5 | CONCLUSIONS

Our study showed that π_{tlp} contributes to driving differential drought survival, and that it is part of a desiccation avoidance strategy in European temperate perennial grassland species. While π_{tlp} turned out to be a promising trait to predict drought survival in grassland species, the relationship was relatively weak. Incorporating additional traits has the potential to improve predictions.

The relationship between π_{tlp} and drought survival we found in herbaceous grassland species was opposite to the one previously shown in woody species. These results highlight the need to directly establish the foundations of functional ecology (Shipley et al., 2016) in different plant life forms, before using traits for understanding the role of environmental factors for population and community dynamics and distribution patterns, and for making predictions for consequences of climate change.

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AUTHORS' CONTRIBUTIONS

B.M.J.E. and S.S. designed the research; S.S., E.J. and J.G. performed the experiments; S.S. and B.M.J.E. analysed the data; S.S., B.M.J.E. and E.J. wrote the manuscript; and all authors revised the manuscript.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.np5hqbzph (Sun et al., 2019).

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SUPPORTING INFORMATION

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