A meta-analysis of responses in floral traits and flower–visitor interactions to water deficit

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Abstract
Alterations in water availability and drought events as predicted by climate change scenarios will increasingly impact natural communities with effects already emerging at present. Water deficit leads to increasing physiological stress in plants, likely affecting floral development and causing changes in floral morphology, nectar and pollen production or scent. Understanding how these floral traits are altered by water deficit is necessary to predict changes in plant–pollinator interactions and how communities are impacted in the future. Here we employ a meta-analysis approach to synthesize the current evidence of experimental water deficit on floral traits and plant–pollinator interactions. Furthermore, we explore experimental factors potentially increasing heterogeneity between studies and provide ideas how to enhance comparability between studies. In the end, we highlight future directions and knowledge gaps for floral traits and plant–pollinator interactions. Furthermore, we explore experimental factors potentially increasing heterogeneity between studies and provide ideas how to enhance comparability between studies. In the end, we highlight future directions and knowledge gaps for floral traits and plant–pollinator interactions. Our analysis showed consistent decreases in floral size, number of flowers and nectar volume to reduced water availability. Other floral traits such as the start of flowering or herkogamy showed no consistent pattern. This indicates that effects of reduced water availability differ between specific traits that are potentially involved in different functions such as pollinator attraction or efficiency. We found no general decreasing visitation rates with water deficit for flower–visitor interactions. Furthermore, the comparison of available studies suggests that increased reporting of plant stress severity and including more hydraulic and physiological measurements will improve the comparability across experiments and aid a more mechanistic understanding of plant–pollinator interactions under altered environmental conditions. Overall, our results show that water deficit has the potential to strongly affect plant–pollinator interactions via changes in specific floral traits. Linking these changes to pollination services and pollinator performance is one crucial step for understanding how changing water availability and drought events under climate change will alter plant and pollinator communities.

KEYWORDS
climate change, drought, flowers, meta-analysis, plant–insect interaction, pollination
Climate change will likely alter rainfall patterns and increase the frequency and severity of drought events across ecosystems (Dai, 2011; IPCC, 2014; Naumann et al., 2018; Spini et al., 2014) with amplified impacts on terrestrial ecosystems already emerging in present times (Choat et al., 2018; Du et al., 2018; Schwalm et al., 2017; Vicente-Serrano et al., 2013). Such changes in water availability can affect plants and pollinators directly via decreased colonization, declining populations and extinctions in areas of non-suitable climate over time (Sgrò et al., 2016; Soroye et al., 2020) and indirectly via phenological mismatch (Forrest, 2015) or alterations of floral resources and phenotypes (Burkle & Runyon, 2016; Gallagher & Campbell, 2017; Phillips et al., 2018; Waser & Price, 2016). Despite being very subtle, intraspecific alterations in co-occurring floral phenotypes can be detected by pollinators and change their interaction patterns, flower visitation behavior or floral handling (Conner & Rush, 1996; Dormont et al., 2019; Galen & Newport, 1987; Hodges, 1995; Kuppler et al., 2016; Mitchell, 1993; Mothershead & Marquis, 2000). This can affect pollen transfer and pollination success for plants and foraging efficiency for pollinators and ultimately performance and reproductive success of both interacting partners. Therefore, exploring the responses of floral traits to reduced water availability will provide more accurate predictions of how climate change and drought impacts flower-visitor interactions.

Flowers have evolved as displays to attract pollinators and ensure successful pollination (Faegri & van der Pijl, 1979; Willmer, 2011). These functions are maintained by a combination of morphology, phenology, scent, color and resources (Junker & Parachnowitsch, 2015; Willmer, 2011), with traits differing in their relative importance for various aspects of plant-pollinator interactions. Scent, color, number of flowers and partially morphology are generally considered as important for the attraction of pollinators (Junker & Parachnowitsch, 2015; Raguso, 2008), whereas nectar, pollen and morphology are important for flower handling and efficiency of pollinators (Junker & Parachnowitsch, 2015; Sletvold & Gren, 2011; Willmer, 2011). Specific morphological traits, such as the position of stamen and stigma, are directly related to pollen receipt or removal and often critical for successful pollination (Campbell et al., 1996; Christopher et al., 2020; Harder & Barrett, 1993; Opedal, 2018). To maintain different functions under water stress traits may not change consistently or uniformly within these multi-trait displays.

From a physiological perspective, producing and maintaining flowers is energetically costly for plants as carbon, nutrients and water supplies are needed (Galen, 2000; Obeso, 2002; Roddy, 2019; Roddy et al., 2016, 2019; Teixido & Valladares, 2014). Under reduced water availability and physiological water stress, flowers are major drivers of water loss (Bourbia et al., 2020) and plants often produce smaller, fewer and/or short-lived flowers or reduce water stress by aborting flowers (Bourbia et al., 2020; Burke & Runyon, 2016; Carroll et al., 2001; Teixido et al., 2016). This indicates that plants can respond and adapt to unfavorable conditions of insufficient water supply by reducing overall floral area with a trade-off between floral size, longevity and number which has been shown in Mediterranean ecosystems (Dafni, 1996; Lankinen et al., 2017; Llorens & Peñuelas, 2005; Teixido et al., 2016).

Floral scent, color, nectar and pollen production are not directly linked to transpiration and water loss and thus, responses to reduced water availability are expected to be different than those of floral size. Floral scent compounds are derived from various biochemical pathways (Junker et al., 2017; Muhlemann et al., 2014) which may be affected in various ways by water availability and the plants’ stress responses. Thus, different compounds might be up- or downregulated resulting in changes in floral scent bouquet, similar to responses shown for floral scent to temperature (Farré-Armengol et al., 2014, 2020). Floral color can be directly affected by water availability due to changes in pigment concentrations, for example, flavonoids (Schemske & Bierzychudek, 2001; Strauss & Whittall, 2006; Vaidya et al., 2018; Warren & Mackenzie, 2001). Across species, flowers have been found to be more chromatic at the lower end of a precipitation gradient (Dalrymple et al., 2020), but within-species patterns are largely unknown. Furthermore, nectar production plays a key role in pollinator attraction across many species and can be extremely costly for plants (Pyke, 1991). As nectar consists of 50%–92% water, its provision is likely hampered under limited water supply. With decreasing nectar volume under drought conditions, nectar sugar concentration might increase if the same amount of sugar is produced. Similarly, pollen production, quantity and quality is often resource-limited (Ashman, 1994; Obeso, 2002) and has been shown to change with abiotic factors such as soil nutrients (Lau & Stephenson, 1994; Young & Stanton, 1990) or water availability (Rankin et al., 2020). Thus, under resource limitation including water supply, pollen production may decline. However, from an ecological perspective, all four trait groups are important for maintaining plant-pollinator interactions and pollination. Therefore, plants might reallocate additional water and resources to flowers to maintain trait expressions and functions in response to reduced water availability and drought.

How plants experience drought and respond to a reduction in water availability is a complex multidimensional process combining responses from a molecular, cellular, up to an organ and whole-plant level (Fang, 2015; Farooq et al., 2012; Gupta et al., 2020). Resulting strategies to escape, avoid or tolerate drought-induced water stress are likely to be influenced by species identity, on the one hand, and additionally modulated by environmental conditions of the habitat on the other hand (Levitt, 1980; Verslues et al., 2006). As water stress in the plants develops—a process which can be measured as decreasing water potential in the xylem—stomatal closure regulation in the leaves progressively restricts transpiration and consequently carbon assimilation (Berninger & Hari, 1993; Martin-StPaul et al., 2017). While plant water deficit is clearly defined as conditions when the rate of transpiration exceeds water uptake (Ritchie, 1998), drought, in contrast is a concept that encloses conditions where water availability is significantly below normal levels and which are “drier” in relation to the usual local site-specific context (Dai, 2011; Slette et al., 2019). Evidently, the ecological impact on the plant and the ecosystem are shaped by the duration, spatial extend and intensity
of the deficit. As the effect of drought stress on a plant encompasses the interaction among many factors including weather conditions (temperature, vapor pressure deficit, radiation and wind speed), soil physical and chemical factors, as well as biotic interactions with pathogens (Price et al., 2002), there is no single unique physical variable or index to quantify drought stress intensity across habitats and species (Mukherjee et al., 2018; Vicente-Serrano et al., 2013). In ecological literature, the term drought is often used in a more conceptual framework with studies rarely quantifying the magnitude of drought stress on the plant and relating it to the site-specific historical precipitation records (Slette et al., 2019). Therefore, within this meta-analysis, we will generally refer to drought only if it is presented in relation to site-specific historic precipitation patterns and otherwise use the terms reduced water availability or water deficit.

There are many studies addressing floral trait responses under water supply modification in various numbers of species, for mostly morphological traits and providing different measurements and documentation for the level of water stress the plants were subjected to. Recently, drought, as one of many extreme events, has been shown to have an overall negative on plants, pollinator and their interactions when summarizing various flower and flower–visitor interactions measurements (Nicholson & Egan, 2020; Walter, 2018). Therefore, with climate change and increasing extreme events (Erenler et al., 2015), water deficit and drought affect pollination. Here, we provide a comprehensive quantitative synthesis to generalize the observed patterns, to identify methodological differences and to highlight steps to increase comparability across studies to improve future study design. Therefore, we conducted a meta-analysis linking reduced water availability to changes in the multi-trait displays of flowers. The goals of our meta-analysis are fourfold: (1) to summarize the current knowledge on the effects of reduced water availability on floral traits and flower–visitor interactions; (2) to identify potential experimental factors increasing heterogeneity between studies; (3) to provide an overview of meta-data of experiments that could increase comparability of results between studies and (4) to highlight future directions and knowledge gaps in understanding the effects on water deficit and drought on flower–visitor interactions and pollination ecology.

2 | MATERIALS AND METHODS

We searched the Web of Science (ISI) database (Indexes = Web of Science Core Collection, BIOSIS Citation Index, Current Content Connect, Zoological Record, IC Timespan = All years) on April 9, 2020. Our search string was comprised of two substrings: One substring targeted the intervention, that is, any form of artificial reduced water supply treatment, and the other one the outcomes, that is, measured floral traits. We did not include a search string for plant–pollinator interactions as during initial optimizing of search strings such a string did not yield additional results (Koricheva et al., 2013). We used the following search string for our analysis:

\[ \text{TS} = (\text{"drought" OR "water availability" OR "reduced rainfall" OR "reduced precipitation" OR "rainfall variability" OR "dryness" OR "soil moisture" OR "water stress" OR "hydrol" gradient" OR "hydrol" regime" OR "rainout shelter") AND TS} = (\text{"floral trait" OR "flower trait" OR "floral volatile" OR "flower volatile" OR "floral scent" OR "flower scent" OR "flower reward" OR "floral reward" OR "floral resource" OR "flower resource" OR "food reward" OR "nectar production" OR "nectar amount" OR "nectar volume" OR "nectar" OR "pollen production" OR "pollen amount" OR "pollen grain" OR "floral morphol" OR "floral morphol" OR "floral display" OR "flower display" OR "flower size" OR "floral size" OR "flower display size" OR "floral display size" OR "floral diameter" OR "flower diameter" OR "inflorescence size" OR "inflorescence display size" OR "inflorescence diameter" OR "floral shape" OR "flower shape" OR "flower symmetry" OR "floral symmetry" OR "tube length" OR "tube width" OR "tube opening" OR "corolla" OR "nectar tube" OR "petal" OR "style" OR "stamen" OR "anther" OR "calyx") \]

Additionally, on June 4, 2020, we search Google Scholar with standardized title search; thus, the search history is not taken into account and only include the first 300 results as recommended by Haddaway et al. (2015). As Google scholar did not allow for the usage of the same long search strings as Web of Science, we did six separate searches:

1. ("drought" OR "water availability" OR "soil moisture") AND ("floral trait" OR "flower trait" OR "pollination" OR "nectar") AND ("calyx")
2. ("drought" OR "water stress") AND ("soil moisture") AND ("floral trait" OR "flower trait") AND "calyx")
3. ("drought" OR "water availability") AND ("soil moisture") AND ("floral trait") AND ("pollination") AND "calyx")
4. ("drought" OR "water availability") AND ("soil moisture") AND ("floral trait") AND ("pollination") AND "calyx")
5. ("drought" OR "water availability") AND ("soil moisture") AND ("floral trait") AND ("pollination") AND "calyx")
6. ("drought" OR "water availability") AND ("soil moisture") AND ("floral trait") AND ("pollination") AND "calyx")

2.1 | Study selection

Our initial search for Web of Science produced 1504 publications. First, publications were screened based on title and abstract using the abstract_screener() function of the metagear-package (Lajeunesse, 2016). For Google scholar, we screened 1800 publications (note that multiple publications were found in multiple of the six search strings) first on title, and then on abstract directly in Google scholar. For both searches, we included all studies that clearly did meet three criteria; ambiguous studies were included for further screening: (1) any Angiosperm herbaceous plant species; not wind pollinated, not a crop species, (2) any type of artificial/experimental drought treatment/reduced water availability for plant species including rain shelters reduced watering in pots, etc. including controls of the given treatments, that is, no reduced water availability or drought. Studies along natural environmental gradient were excluded, (3) changes in
any measurable floral traits and/or observed changes in flower visitors (if measured in the same studies as floral traits). After the initial screening, doubletons were removed, leaving 209 (Web of Science: 131, Google scholar: 78) potential suitable publications for which the full texts were screened. For all publications which we could not access full texts, we attempted once to acquire it by contacting the corresponding author and otherwise excluded the study. After full-text screening, 46 publications remaining from which we attempted to extract all necessary data. Study screening and inclusion was done by the first author. In total, we were able to extract necessary data from 39 publications. Screening results of different steps and included studies are given in Figure S1 and Table S1.

2.2 | Data collection and extraction

In an initial step, we extracted all measured floral traits, plant-pollinator interactions as well as plant reproductive success. Floral trait names and measurements were not consistent across studies but measured the same or were used as surrogates for comparable trait expressions. Therefore, we summarized measurements into following traits: plant height, calyx length, calyx width, corolla length, flower diameter, petal length, petal width, pistil length, stamen length and herkogamy (i.e. distance stigma–anther; morphology); days to flower, flower longevity and number of flowers (phenology including flower abundance); nectar sugar concentration, nectar sugar content, nectar volume and pollen number (resources); total floral scent emission (chemistry); visitation rate per flower and visitation rate per plant (interactions); seed/fruit set (reproductive output). Other traits measured were either excluded as these measurements were specific to plant species or only measured in one or two studies (Table S2).

Additionally, if available, we extracted measurements of plants and experimental conditions that could affect measured outcomes and could be used to describe the plant/soil water status and plant stress. Most studies described the watering scheme used to induce water stress in plant species, these differed from dry-down to differential watering (Table S3). These schemes are, however, difficult to compare between studies. Some studies assess the effectiveness of their scheme by comparing soil water content between treatment (n = 19), examine visually if plants are wilting and adjusting watering to it (n = 9) or no assessment (n = 12). Soil water content, however, is not directly comparable between studies as the water availability for plants for a specific soil water content is dependent on soil conditions, especially on soil particle size and composition forming silt, clay and sandy soils. Therefore, it could be the case that in some studies treatments may not induce a strong water stress. Given the reported meta-data, we separated the studies in three groups: visual examination of wilting (if plants wilted they should be at least under some stress), volumetric soil water content (differences are likely to indicate alterations in water availability for the plant) and no assessment. Any further separation was not possible given the data reported. For some studies, reported leaf water potential and water use efficiency were extracted as measure for plant water availability and plant water stress. Furthermore, if available, we extracted several modulators that describe the experimental design: Study type (growth/climate chamber, greenhouse, field experiment in pots or field experiment plants in soil), starting point of treatment (before or at flowering), duration of treatment (days, weeks, etc.), time point of trait measurement (days in treatment), soil conditions (pH, N, P, K) and abiotic conditions during experiment. From these measurements only study type and starting point of treatment was reported in a sufficient number of studies to conduct further analysis. Therefore, an increased reporting of the precise starting point of treatment and life stage of plants, duration of treatment and days in treatment at measuring in future study would be helpful for future analysis on heterogeneity in plant responses.

For each study, we extracted the mean, variation (standard deviation or error) and sample size for treatments and control separated for different populations/locations. If studies included multiple treatments of reduced water availability (n = 7), we used the most severe treatment instead of medium or moderated treatment. One study only included a time series, where we used time point one before treatment as control. If reduced water availability was tested in factorial combination with other factor, only drought treatments were used. Data were extracted from table, texts or graphics. In case, relevant data were not available from the paper, we contacted the corresponding author once and requested the additional data. Data from graphics were extracted using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/).

For measures of variation, the lower and upper error bar, if available, were extracted and the mean value was taken. Extracted results and sources are available from the published data files.

We were able to extract data out of 40 studies including 45 plant species from 36 genera and 22 plant families (Table S3). K refers to the number of measured effect size and n_{plant\ species} to the number of plant species: calyx length (k = 9, n_{plant\ species} = 6), calyx width (k = 4, n_{plant\ species} = 1), corolla length (k = 23, n_{plant\ species} = 15), flower diameter (k = 35, n_{plant\ species} = 24), herkogamy (i.e. distance stigma–anther; k = 15, n_{plant\ species} = 10), petal length (k = 19, n_{plant\ species} = 11), petal width (k = 5, n_{plant\ species} = 3), pistil length (k = 5, n_{plant\ species} = 5), plant height (k = 18, n_{plant\ species} = 9) and stamen length (k = 4, n_{plant\ species} = 3) [morphology]; days to flower (k = 20, n_{plant\ species} = 8), flower longevity (k = 2, n_{plant\ species} = 2) and number of flowers (k = 45, n_{plant\ species} = 21) [phenology including flower abundance]; nectar sugar concentration (k = 14, n_{plant\ species} = 12), nectar sugar content (k = 10, n_{plant\ species} = 6), nectar volume (k = 19, n_{plant\ species} = 15) and pollen number (k = 7, n_{plant\ species} = 3) [resources]; floral scent emission (k = 10, n_{plant\ species} = 6) [chemistry]; visitation rate per flower (k = 9, n_{plant\ species} = 3) and visitation rate per plant (k = 11, n_{plant\ species} = 5) [interactions]; seed set (k = 6, n_{plant\ species} = 3) [reproductive output].

Several traits were only measured in a low number of studies (n ≤ 5). Therefore, the effect sizes in the analysis are based on a limited number of plant species and experimental conditions. The results thus reflect the status of the current knowledge, while the inclusion of further species under various conditions potentially may result in different overall patterns and different patterns between species with varying ecology.
2.3 | Statistical analysis

All calculations and analysis were performed using functions of the metafor-package 2.4-0 and base R 4.0.2. (R Core Team, 2020; Viechtbauer, 2010). We used the standard mean differences between treatment and control groups (Hedges’ $g$) as measure for effect sizes calculated with the escalc-function(). Hedges’ $g$ is commonly used in ecological literature (Koricheva et al., 2013; Nakagawa & Santos, 2012) and includes a correction for small sample size (Koricheva et al., 2013). Values of Hedges’ $g$ larger >0 indicate a higher trait value under reduced water availability and $g < 0$ a lower trait value. For each trait, we fitted multi-level random-effect models with no moderator and plant species, study ID and effect size ID as random factors using the rma.mv-function with restricted maximum likelihood to estimate parameters. The mean effect size was considered different from zero if the 95% confidence interval did not overlap with zero. As there is no numerical benchmark in ecology (Lortie et al., 2015), we followed Cohen (1988) and interpreted the magnitude of effect sizes such that small $g \geq 0.2$, medium $g \geq 0.5$ and large $g \geq 0.8$. Heterogeneity was assessed by prediction intervals (IntHout et al., 2016). Total heterogeneity ($Q_p$) in effect sizes and proportion of heterogeneity between plant species, between- and within-studies ($I^2$), were calculated following Viechtbauer (2010). Significance of the $Q_p$ statistics suggests that differences between effect sizes are not an estimate of common population mean and vary because of factors such as environmental variability rather than sampling error. Meta-regressions were conducted to explore the effects of moderators (covariates) on the effect of drought treatment on different traits. We explore four moderators: stress assessment, study type (for nectar volume all included field experiments measured nectar production rate), start of treatment and water use efficiency. We used the between-group heterogeneity ($Q_m$) to test for the significance of each moderator. We took significance of $Q_m$ to show that the mean effect size differed between levels of the moderator, and further assumed that groups within the same moderator differed if their confidence intervals (CIs) did not overlap (Koricheva et al., 2013). For intrinsic water use efficiency, measured as photosynthetic rate $A$ [µmol m$^{-2}$ s$^{-1}$] divided by stomatal conductance $g_s$ [mol m$^{-2}$ s$^{-1}$], we used the mean difference between treatment and control as indicator of difference in plant water stress.

Publication bias was assessed using funnel plots displaying effect sizes against standard error (Notes S1). Publication bias creates asymmetric funnel with small non-significant studies and studies with directional effects are missing. We additionally calculated Egger regression by running the model with precision (1/standard error) as moderator (Viechtbauer, 2010). If a significant relationship is present, asymmetry is implied in the funnel plot. This can indicate publication bias but also other reasons such as heterogeneity (Nakagawa & Santos, 2012; Viechtbauer, 2010). We found evidence for publication bias for nectar volume, nectar sugar concentration, days to flower, calyx length, VOC emission, visitation rate to plants and flowers, seed set. The impact of publication bias was assessed by removing studies responsible for funnel asymmetry (Borenstein et al., 2009; Castro-Díez et al., 2019). Responsible studies were identified via the funnel plot itself and identification of influential data points via the cooks.distance()- and hatvalues()-function. The first calculates Cook’s distance and which is the leverages of the diagonal hat matrix and indicate strong influential points, if the hat values of effect sizes are two times the average hat values. If the new mean effect size still had the same sign and significance, we concluded that asymmetry is probably not a result of publication bias or that the impact of publication bias is modest. In case of the opposite publication bias may be substantial (Nakagawa & Santos, 2012). After removal of influential studies, no asymmetry was detected by egger tests and for all traits the sign and significance remained the same showing the robustness of the results. Only for seed set, the sign and magnitude switch to a negative sign different from zero indicating a substantial publication bias. This is not surprising as our data set only include studies that also measured floral traits.

3 | RESULTS

For 8 out of 10 morphological traits, effect sizes were negative and did not overlap with zero, except of pistil length and herkogamy (Figure 1; Table S4). The negative sign indicates that measures in the treatment are smaller than in the control. All effects were medium to strong, except for petal width ($g = −0.31$, 95% CI = (−0.57, −0.05), $k = 5$, $p < 0.01$). The strongest effects were found for plant height ($g = −1.18$, 95% CI = (−2.00, −0.35), $k = 18$, $p < 0.01$) and flower diameter ($g = −0.97$, 95% CI = (−1.37, −0.59), $k = 35$, $p < 0.001$). For phenology and flower abundance, the mean of number of flower per plant showed a medium decrease ($g = −0.62$, 95% CI = (−1.23, −0.01), $k = 45$, $p < 0.05$) but also a high heterogeneity in responses with several effect size above zero, indicating more flowers under reduced water availability. Furthermore, the mean effect size for days to flower was weakly positive ($g = 0.24$, 95% CI = (0.51, 1.00), $k = 20$, $p = 0.52$), but did not differ from zero. For floral resources, only nectar volume showed a strong negative decline with reduced water availability ($g = −0.82$, 95% CI = (−1.30, −0.33), $k = 19$, $p < 0.001$). Mean values for nectar sugar content, nectar sugar concentration and pollen number were all close to zero, including a few positive values (nectar sugar content: $g = −0.15$, 95% CI = (−0.38, 0.07), $k = 10$, $p = 0.18$; nectar sugar concentration: $g = 0.16$, 95% CI = (−0.07, 0.40), $k = 14$, $p = 0.16$; pollen number: $g = 0.14$ 95% CI = (−0.62, 0.89), $k = 7$, $p = 0.70$). Visitations rate, floral scent emission and seed set did not differ from zero and were all characterized by a high heterogeneity in the results. Overall, heterogeneity was high as indicated by overlapping prediction intervals with zero (Figure 1; Table S4).

Heterogeneity between studies may arise from differences in experimental design and procedures. Therefore, we assessed three different moderators describing differences in experimental design: status assessment, study type and treatment start. For status assessment, no consistent differences between assessments were found for flower diameter, petal length, number of flowers and days to flow- ers (Figure S2; Table S5). For flower diameter and number of flowers, the effect size differed between assessments (flower diameter: $Q_m = 29.23$, $p < 0.001$; petal length $Q_m = 26.35$, $p < 0.001$), but showed
opposite responses under which assessment a negative response was found (Figure S2). For days to flower and number of flowers, no differences between assessments were found (days to flower: $Q_m = 0.33, p = 0.95$; number of flowers: $Q_m = 5.75, p = 0.12$). For study type, plant height ($Q_m = 20.90, p < 0.001$), flower diameter ($Q_m = 24.20, p < 0.001$), corolla length ($Q_m = 12.34, p = 0.006$) and nectar volume ($Q_m = 14.46, p = 0.002$) differed between study type. Patterns between indoor and outdoor studies were inconsistent among morphological traits.
whereas for nectar volume indoor experiment showed a lower nectar volume in treatments and no differences between treatments in outdoor studies (Figure 2; Table S6). No differences were found for number of flowers \((Q_m = 4.81, p = 0.31)\) and days to flower \((Q_m = 5.28, p = 0.15)\). For start of treatment, plant height \((Q_m = 9.23, p = 0.03)\) and petal length \((Q_m = 16.63, p < 0.001)\) differed between treatments with an effect size different from zero for “before flowering” and no differences for “at flowering” (Figure 3; Table S7). Corolla length \((Q_m = 15.20, p < 0.01)\) and flower diameter \((Q_m = 36.78, p < 0.001)\) differed between treatments with higher effect sizes for “at flowering” than “before flowering.” VOC emission \((Q_m = 6.78, p = 0.03)\) differ between treatments and showed a higher emission in drought treatment for “at flowering.” Nectar volume differed between treatments \((Q_m = 8.42, p = 0.04)\), with a trend to lower volumes “at flowering,” but no differences for “before flowering.”

For corolla length \((Q_m = 8.73, p < 0.01, k = 6)\) and flower diameter \((Q_m = 31.70, p < 0.001, k = 6)\), sample sizes were adequate to compare studies that measured water use efficiency as measure of plant stress (Table S8). For both traits, the effect size increased with increased water use efficiency indicating that higher stress induces higher responses.

### 4.1 | Effects of water deficit on morphology and phenology

Under reduced water availability, plants produced smaller and fewer flowers while herkogamy and pistil length showed no consistent patterns. Pollination efficiency traits, for example, the relative position of female and male sexual organs (Barrett, 2002; Solís-Montero & Vallejo-Marín, 2017), can experience strong pollinator-mediated selection (Caruso et al., 2019) and can be adaptations to local pollinators (Newman et al., 2015). Pollinator attraction traits, on the other hand, may be under weaker pollinator-mediated selection than efficiency traits (Caruso et al., 2019). Thus, under opposing selection pressures by abiotic conditions and pollinators, effects may differ between specific efficiency and attraction traits. This may suggest

| Trait                      | Comparison | Start of Treatment | At Flowering |
|---------------------------|------------|--------------------|--------------|
| Plant height              | Q-m        | 9.23 p = 0.03      |              |
| Flower diameter           | Q-m        | 36.78 p < 0.001    |              |
| Corolla length            | Q-m        | 15.20 p < 0.01     |              |
| Flower diameter           | Q-m        | 31.70 p < 0.001    |              |
| Petal length              | Q-m        | 16.63 p < 0.001    |              |
| Number of flowers         | Q-m        | 4.81 p = 0.31      |              |
| Nectar volume             | Q-m        | 8.42 p = 0.04      |              |

**FIGURE 3** Standardized mean differences for floral trait responses to dry conditions separately for treatment start. Leaves represent before flowering, flowers = at flowering and question mark = unknown. Values are mean effect sizes (Hedges’ g, bordered) ±95% confidence intervals (CI, thick black bars) and predictions intervals (thin black bars). Colored points not bordered in the background show single effect sizes for each trait. Point size indicates its precision (1/standard error); \(k\), number effect sizes for each trait. Negative effect sizes indicate smaller values under dry conditions and effect sizes are considered significant when CIs do not overlap with zero (vertical dashed line). Different colors indicate different trait groups: Pink = morphology, dark blue = phenology, light blue = resources, green = floral scent, darkness gradients represent different assessments.
that a trait response to reduced water availability depends on its function and insurance of pollination success. Specific traits, such as corolla length or width, can affect pollination efficiency and pollinator attraction (Castellanos et al., 2004; Mitchell, 1994; Smith et al., 1996; Thompson, 2001) also declined on average with water deficit, indicating that the specific response of one trait depends on plant species identity. Thus, our conclusion needs to be tested for plant species for which the contribution to attraction and efficiency of one trait are known.

From pollinator perspective, relative to floral size, the body size of pollinators determines its pollination and foraging efficiency (Armbruster & Muchhala, 2009; Nagano et al., 2014). For example, some bumblebee species prefer larger flowers, which fit their tongue length, as their handling efficiency and resource intake is higher (Dohzono et al., 2011; Harder, 1983; Klumpers et al., 2019). On the contrary, hoverflies preferred smaller artificial flowers (Sutherland et al., 1999). This indicates that depending on pollinator species reduced flower size may change the foraging preferences and efficiency of pollinators. Such efficiency changes can result in decreased resource intake per time unit and consequently, affect pollinator reproduction, especially in combination with changes in resource availability.

4.2 Effects of water deficit on flower resources

Nectar volume declined under water deficit in indoor, but not outdoor studies. As there was no indication for differences in treatment strength, this might be explained by differences between plant species investigated or that in indoor studies no flower visitors were present. As nectar production is costly (Pyke, 1991), reducing nectar production under stressful conditions saves resources. However, in field experiments, pollinators are present and plants need to invest in nectar to maintain pollinator interactions (Willmer, 2011), especially if plants are at their optimum of nectar production, that is, maintaining interactions by minimal resource investment. Furthermore, under dry and warm conditions pollinators might prefer flowers with high nectar volume/water content. This highlights the importance of investigating drought impact under various conditions occurring in the wild/in-situ (Phillips et al., 2018) and the growing need for field studies.

Pollen number, nectar sugar concentration and content showed no consistent pattern which is in congruence with another study (Rering et al., 2020). Keeping sugar content and concentration relatively constant may be beneficial, as altered nectar amounts and viscosity may impair nectar intake by pollinators and lead to changes in visitation length and frequency (Harder, 1986; Kim et al., 2011; Thomson, 1988; Thomson & Plowright, 1980). The early determination of pollen quantity in flower development may explain consistent pollen numbers (Goldberg et al., 1993) and suggest investment by plants to maintain male reproduction (Minnaar et al., 2019). Anyhow, plant fitness might be reduced with water deficits as pollen viability and pollen germination are sensitive to temperature (De Storme & Geelen, 2014; Hedhly, 2011) and drought (Borghi et al., 2019; Descamps et al., 2018; Fang et al., 2010).

Overall, our data suggest that water insufficiency can be partially compensated at the flower level. Nonetheless, given the decreasing number of flowers resource quantity per plant will likely decrease for pollinators under water deficits.

4.3 Effects of water deficit on floral scent

Under water deficit, floral scent did not change in overall emission but in composition with following compounds often increased: (Z)-3-hexenol, 6-methyl-5-hepten-2-one, benzaldehyde, α- & β-pinene, (E)-β-ocimene, (E,E)-α-farnesene (Burkle & Runyon, 2016; Campbell et al., 2019; Glenny et al., 2018; Rering et al., 2020). Specific metabolic pathways of these widespread volatiles (Knudsen et al., 2006) maybe upregulated or downregulated, resulting in changes in scent composition as shown for temperature (Farré-Armengol et al., 2014, 2020). Higher emission of these volatiles may increase attractiveness (Raguso, 2008), potentially compensating decreasing attractiveness due to decreasing flower number. Thus, unless specific ratios are important for pollinator attraction, negative effects of changing floral scent might be weak, as generalist pollinators should experience these compounds in various concentrations.

4.4 Effects of water deficit on pollinator interactions

Overall, our results do not show a clear decrease in flower-visitor visitation rates, potentially due to differences in flower visitors observed. While for bumblebees, the response depended on air temperature (Descamps et al., 2018) or increased linearly along a soil moisture gradient (Kuppler et al., 2021), in studies with full flower-visitor communities, differences in visitation patterns were dependent on the plant species or showed nonlinear responses across a soil moisture gradients (Burkle & Runyon, 2016; Gallagher & Campbell, 2017; Glenny et al., 2018). Even though these observations were based only on four studies including visitation rates, it can be expected that prominent changes in floral traits may lead to alterations in visitation rates and consequently alter pollination success. The impact of drought on visitation rate is likely also dependent on the pollinator species and the relative changes of floral traits, where adverse effects of one specific floral trait to plant attractiveness might be counterbalanced by changes in another feature.

4.5 Assessment of water stress intensity and comparability among studies

The effects of water deficit on floral traits are likely to scale with treatment severity. The combined results from studies reporting water use efficiency, as surrogate for water stress, showed that for
flower size variables the reduction was indeed stronger under more severe water stress. Similarly, floral size and nectar volume increased linearly within species along a soil moisture gradient, assuming that soil moisture content scales with plant stress (Gallagher & Campbell, 2017; Kuppler et al., 2021).

Despite some clear patterns for floral traits, effects sizes were heterogeneous for all traits, potentially due to variation in study type, timing of stress imposition, stress assessment method, phylogenetical constrains or habitat type of plant species origin. Parts of the heterogeneity for different floral traits could be explained by the timing of stress imposition, while neither status assessment nor study type were relevant, besides for nectar volumes. For flower diameter, corolla length, number of flowers and nectar volume, we found a trend that a reduction in water availability at the beginning of flowering had a stronger impact than treatment application before flowering; only a single study had higher effect sizes for treatments before flowering as compared to ones at flowering. This may suggest that plants stressed earlier are able to adjust physiologically to the novel conditions, depending on intensity and duration and potentially save resources, for example, small height growth, to maintain floral integrity and seed production. Thus, the timing of drought can affect its impact on floral development and plant reproduction.

For a quantifiable measure of water stress intensity across plants, experiments and species, an accurate portrayal of state variables needs to be considered which describe the conditions the plant experiences in its immediate vicinity—at the boundary between plant and soil or plant and air (Tardieu, 1996). The non-uniform distribution of water in the soil makes the quantification of treatment intensity a challenge (Campbell & Gee, 1986; Or et al., 2002). Even using controlled manipulative approaches leads to plants experiencing different degrees of water deficit with time as individuals deplete soil water at different rates depending on plant size, leaf area and ambient microclimatic conditions (Granier et al., 2006). Soil and plant water potential and fraction of extractable soil water (e.g. Desclaux et al., 2000; Ray et al., 2002; Ritchie, 1981; Siddique et al., 2000; Tardieu, 1996) have been commonly used as measures to quantify the degree of drought stress a plant is subjected to. For another straightforward approach to describe the soil water status, the measurement of volumetric soil water content, a variety of methodologies and sensors are available (Bittelli, 2011). For the comparison of drought-treatment intensity across studies, the absolute and relative soil water contents as stand-alone variables are not very well suitable, as water-holding capacity in each soil depends on its texture and particle size distribution (Orr et al., 2002). Without relating these values to soil water potentials using, for example, water-release curves or pf curves obtained for each given substrate (Kern, 1995; Minasny et al., 1999), a comparison across studies remains problematic. We thus recommend the monitoring of soil water potentials at multiple times during the day using either tensiometers or heat dissipation matric potential sensors installed at different depths to avoid a steep moisture gradient in the soil particularly in potted plants. Often a dry soil surface deludes a successful treatment, while at the bottom of the pot—where most of the roots are curled up—the soil conditions can be still moist or even waterlogged. It is therefore advisable to evaluate the soil water status along the soil profile of the rooting zone weighted by root distribution within the depths.

Measuring physiological indicators of water stress in plants instead of soil water status is a methodological alternative to quantify soil water deficit (Granier et al., 2006; Sousa et al., 2006). Using this approach, it should be kept in mind that plant physiological responses to reduced water availability such as stomatal conductance, photosynthetic rate, plant water potential and osmotic adjustment can vary substantially across species and each of these physiological adaptations has its own partially uncoupled response to soil water status (Bray, 1997). Therefore, how "stressed" plants are under given conditions is thus most likely a nonlinear function of the soil water potential and the response relationship will be most likely also nonlinear (Carminati & Javaux, 2020). Despite these limitations, several approaches to better quantify water stress intensity within an experiment are available: Pre-dawn and midday leaf or shoot water potential can provide an integrated measurement of soil water potential as it is experienced by the plant (Ritchie, 1981; Tardieu, 1996). For comparisons across various habitats and species, water use efficiency measured either as δ13C or ratio of leaf photosynthesis to stomatal conductance (A/gs; Flexas & Medrano, 2002; Khan et al., 2007; Sousa et al., 2006), or leaf water potential at turgor loss point determined by either pressure-volume analysis or cell solute potential at full hydration by vapor-pressure osmometry can be used (Bartlett et al., 2012; Griffin-Nolan et al., 2019; Maréchaux et al., 2015). As future perspective, we emphasize the necessity to better monitor soil water status and to include a more comprehensive assessment of the severity of water stress that a plant is experiencing in studies involving drought effects on plant traits. With this in mind, there are great opportunities to extend our understanding of plant-pollinator interactions under altered environmental conditions, to improve reproducibility of our experiments and to sharpen our ability to quantitatively link physiological mechanisms to plant adaptation strategies.

4.6 | Caveats, future directions and conclusion

By better understanding the responses of prevalent plant species, we will increase the predictability of drought impacts on the interactions between pollinators and plants. However, our study only covers a restricted phylogenetic diversity (45 plant species from 36 genera and 22 plant families; Table S3) that may limit the results generality to other taxa growing under different climatic conditions. To provide recommendations on which plants are likely to maintain resources for pollinators under predicted increases in drought occurrence, severity and duration, a wider phylogenetic coverage is needed including more rare and common plant species. In the following, we want to further highlight four future research avenues.
At first, our current understanding of responses to water deficits within non-morphological plant traits is limited. In this context, only a few studies have explored floral scent emissions and floral color (Arista et al., 2013; Brunet & Van Etten, 2019). While the nutritional quality of nectar is essential for the reproductive success of pollen-collecting insects (Behmer, 2009; Vaudou et al., 2015), to our knowledge there are no studies exploring nectar sugar composition together with minor constituents such as amino acids and lipids, and only one study exploring pollen quality (Rankin et al., 2020), even though changes due to reduced water availability may lead to reduced pollinator reproduction and survival (Rankin et al., 2020).

Second, reduced water availability in combination with other biotic and abiotic factors such as herbivory, alteration in ambient CO₂ concentrations or temperature can modulate plant trait responses (Burkle & Runyon, 2016; Descamps et al., 2018; Glenny et al., 2018). Especially combining knowledge on the integrated effects of temperature and water deficit will increase our understanding of the impact and severity of drought conditions. Ideally, such different scenarios are based on site-specific historic climate values which frame the temperature and drought plant populations have been exposed to (Slette et al., 2019).

Third, consistent changes in flower morphology in response to drought emphasize the strong impact of abiotic conditions on flower traits and potential evolutionary consequences (Caruso et al., 2019; Strauss & Whittall, 2006). Therefore, water deficit can pose a strong selection pressure on floral size but may also constrain flower adaption to changes in pollinator communities (Caruso et al., 2019; Sletvold, 2019).

Finally, in addition to visitation rates, changes due to reduced water availability might also affect pollinator behavior on flowers (Höfer et al., 2021). Behavioral changes, such as increasing handling time, can impact pollen transfer to the stigma and pollen removal and can be better proxies for pollination efficiency than visitation rates (Wilcox et al., 2017; Willmer et al., 2017). To better understand the effects on plant fitness, we need to understand how drought-induced changes in floral traits relate to pollination, handling efficiency, pollen transfer and ultimately, plant fitness.

Overall, we are consistently increasing our understanding of the impact of reduced soil water availability and drought events on plant and flower traits, flower–visitor interactions and pollination. Available evidence shows that flowers become smaller under water deficit, but this is not necessarily the case for scent emission, resources or phenology. This can be partially attributed to small sample sizes and differences in water stress levels. Therefore, we encourage researchers to provide additional meta-data and physiological measurement in their studies (see above) to increase comparability between studies to aid a better understanding for drought effects on floral traits and plant–pollinator interactions. Plant–pollinator interactions are likely to be affected by changes in floral traits, due to reduced water availability, but we suggest that these changes are not manifested in overall visitations, but in visitations frequencies of specific species and changes in flower handling by pollinators and pollination efficiency.

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AUTHOR CONTRIBUTIONS
JK conceived the study and collected the data. JK and MK analyzed the data. JK wrote the first version which was revised and finalized by both authors.

DATA AVAILABILITY STATEMENT
All data extract from literature and the R Code used in this paper are available on Figshare https://doi.org/10.6084/m9.figshare.14221985.v1.

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