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Effect of water stress on weed germination, growth characteristics, and seed production: a global meta-analysis

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Abstract

Weeds compete with crops for soil moisture, along with other resources, which can impact the germination, growth, and seed production of weeds; however, this impact has not been systematically recorded and synthesized across diverse studies. To address this knowledge gap, a global meta-analysis was conducted using 1,196 paired observations from 86 published articles assessing the effect of water stress on weed germination, growth characteristics, and seed production. These studies were conducted and published during 1970 through 2020 across four continents (Asia, Australia, Europe, and North America). Imposed water stress was expressed as solution osmotic potential ($\psi_{solution}$), soil water potential (ψ_{soil}), or soil moisture as percent field capacity. Meta-analysis revealed that water stress inhibits weed germination, growth, and seed production, and the quantitative response intensified with increasing water stress. A $\psi_{solution}$ greater than −0.8 MPa completely inhibits germination of both grass and broadleaf weeds. A $\psi_{solution}$ from −0.09 to −0.32 MPa reduces weed germination by 50% compared with the unstressed condition. Moderate soil water stress, equivalent to 30% to 60% field capacity, inhibits growth characteristics (branches or tillers per plant, leaf area, leaves per plant, plant height, root, and shoot biomass) by 33% and weed seed production by 50%. Severe soil water stress, below 30% field capacity, inhibits weed growth by 51% and seed production by 88%. Although water stress inhibits weed growth, it does not entirely suppress the ability to germinate, grow, and produce seeds, resulting in weed seedbank accumulation. This creates management challenges for producers, because weed seeds can survive in the soil for many years, depending on weed species and environmental conditions. Quantitative information compiled in this meta-analysis can be instrumental to model the weeds' multidimensional responses to water stress and designing integrated weed management strategies for reducing the weed seedbank.

Introduction

Widespread precipitation deficits, as well as increased evaporative demands, have been recorded in the past, which resulted in drought conditions (i.e., soil moisture deficits), with further deficits projected for the future. According to the Intergovernmental Panel on Climate Change (IPCC 2021), the frequency and intensity of agricultural droughts will increase drastically over the 21st century. For example, in a future scenario of a 2 C increase in temperature, a once-in-a-decade drought event will occur twice in a decade (IPCC 2021). While irrigation is a common practice to alleviate crop water stress in water-limited agricultural regions (Kukal and Irmak 2019, 2020; Li and Troy 2018; Troy et al. 2015), benefits from irrigation are uncertain due to exacerbating freshwater limitations (Elliott et al. 2014) and the negative environmental and ecological impacts of irrigation (McDermid et al. 2021).

The resulting water-stress conditions negatively affect seed germination, plant growth and development, and seed production. For example, water stress can impede or delay germination by constraining water needed for seed hydration and/or during progressive germination and emergence phases (Koller and Hadas 1982). Similarly, water stress impacts plant growth and development, primarily by limiting photosynthetic capacity via stomatal closure (Chaves 1991; Chaves et al. 2009) and by reducing photosynthate assimilation via limited expansion of leaves (Boyer and McPherson 1975). Water limitation also induces numerous biochemical, molecular, and physiological changes that interfere with normal plant functions, growth, and development (Bhattacharjee and Saha 2014). Therefore, it is critical to synthesize existing information on how plants respond to water stress and provide evidence-based management recommendations for growers and land managers.

The effect of water stress on plant growth, photosynthesis, physiology, and survival has been studied extensively (Chaves et al. 2002; Pugnaire et al. 1999). Significant work has elucidated complex physiological and molecular mechanisms underlying plant adaptive responses to tolerate and/or avoid water stress (Osakabe et al. 2014; Shinozaki et al. 1998). Sun et al. (2020) used a meta-analysis approach to synthesize studies investigating plant morphology, physiology, and functionalities under water stress and found that stress significantly decreased plant growth and photosynthesis. Moreover, plants adjust their morphology and physiological responses as adaptation strategies for water stress over time. In managed cropping systems, water-stress conditions are more severe due to crop–weed competition for soil moisture among other resources. Weeds deplete soil moisture and reduce soil water availability in the crop root zone. Therefore, water stress in agricultural systems depends on crop–weed interactions and the degree to which crops and weeds extract soil water under water-stressed conditions.

Weeds have numerous similarities with crops, and sometimes even share a common origin and taxonomic classification (Harlan 1975; Holm et al. 1977). However, weeds have several competitive advantages over crops, in that they are phenotypically more plastic and can undergo morphological and physiological changes in response to environmental variations (Duke 2018). These short- and long-term adaptive mechanisms allow greater survival and fitness compared with crops in tolerating and/or avoiding environmental limitations such as water stress (Duke 2018). Owing to their extensive root systems, rapid root development, better drought tolerance, and water-use efficiencies, weeds can potentially extract a comparable or even greater amount of water from deeper soil layers than crops (Geddes et al. 1979; Patterson and Flint 1982; Stuart et al. 1984). Hence, weeds can be more competitive than crops under water-stressed conditions (Griffin et al. 1989; Orwick and Schreiber 1979). Some weeds are even characterized as "water wasters" as they transpire more water and maintain lower stomatal resistance compared with crops they compete with, and thus induce water stress for crops (Geddes et al. 1979; Patterson 1995; Scott and Geddes 1979).

Because of their multiple adaptive mechanisms, weeds have been found to tolerate moderate levels of water stress without significant effects on germination, survival, or seed production and thus manage to considerably increase the weed seedbank (Chahal et al. 2018). However, responses under crop–weed interactions are differential, unstable, and subject to change depending on the water-stress level, duration, and intensity; crop versus weed competitiveness; weed density; management practices; and other factors (Banks et al. 1986; Mortensen and Coble 1989). Moreover, weeds' response to water stress varies by species because of their innate/distinct characteristics, photosynthetic pathways, water acquisition and transport capacities, and favorable places of occurrence (Patterson 1995; Rodenburg et al. 2010; Wiese and Vandiver 1970). For example, weeds from humid regions, such as barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], crabgrass [*Digitaria sanguinalis* (L.) Scop.], and cocklebur (*Xanthium strumarium* L.), are more competitive in well-watered conditions, while weeds from semiarid or arid regions, such as buffalo bur (*Solanum rostratum* Dunal), kochia [*Bassia scoparia* (L.) A. J. Scott], and Russian thistle (*Salsola tragus* L.), are more competitive under drought conditions (Wiese and Vandiver 1970). The grass weeds have been reported to have less tolerance to water stress compared with broadleaf weeds within given agroecological regions (Mackie et al. 2019). Such differential responses of individual species to water stress can shift global weed distribution patterns by favoring deep-rooted over shallow-rooted species (Stratonovitch et al. 2012) and C_4 over C_3 weed species in regions with expected periods of long drought (Rodenburg et al. 2010). With these characteristics of competitive advantage and superior drought tolerance of weeds under drought conditions, it is vital to gather and synthesize information on the multidimensional responses of weed species to water stress.

Numerous studies have evaluated the response of individual weed species to water stress, and an abundance of quantitative information exists on these responses (Chahal et al. 2018; Kaur et al. 2016; Sarangi et al. 2016); however, no effort has been made to compile, integrate, and analyze results from these studies to infer how water stress impacts weed germination, growth characteristics, and seed production. The objectives of this global meta-analysis were to (1) determine the effects of water stress on weed germination, growth characteristics (radicle/root length, plant height, leaf area, branches/tillers per plant, leaves per plant, total biomass, root biomass, shoot biomass, and root:shoot ratio), and seed production (inflorescences per plant and seeds per plant); (2) determine how water-stress intensity impacts physiological responses; and (3) characterize differential responses of grass versus broadleaf weeds to water stress.

For the meta-analysis, studies with water stress expressed as solution osmotic potential ($\psi_{solution}$), soil water potential (ψ_{soil}), or percent field capacity are included. Studies that report stress imposition using $\psi_{solution}$ achieve these conditions using polyethylene glycol (PEG) or D-mannitol to adjust the water-stress levels of the solution (Ahmed et al. 2015; Chachalis et al. 2008; Evetts and Burnside 1972; Wilson and McCarty 1984). When soil is used as a test medium, water stress is induced and reported as either ψ_{soil} (Gealy et al. 1994) or soil moisture as percent field capacity (Bajwa et al. 2016; Khan et al. 2021). A major difference between two metrics is that while ψ_{soil} remains unchanged irrespective of what soil it is measured in, soil water content or soil moisture is a function of soil properties. Thus, from a transferability standpoint, reporting on a ψ_{soil} basis is preferable, especially when soil properties are not appropriately measured or reported. ψ_{soil} and soil moisture are related to each other via soil water retention or soil water characteristic curves, which are carefully measured soil-specific and nonlinear mathematical functions.

Materials and Methods

Literature Search and Data Extraction

The literature included in the meta-analysis was identified by searching specific terms in Google Scholar and three weed science journals of Weed Science Society of America (WSSA) (*Weed Technology*, *Weed Science*, and *Invasive Plant Science and Management*) published before April 2021. The search term included "weed" or the common and scientific names of the top 10 most common and troublesome weeds among all broadleaf crops, fruits, and vegetable crops based on the 2019 WSSA National Weed Survey Dataset (Wychen 2019) and the top 10 most common and troublesome weeds among all grass crops, pasture, and turf from the 2020 WSSA National Weed Survey Dataset (Wychen 2020) in the title of the publication in conjunction with ("AND") the search phrase ("water stress" OR "moisture stress" OR "moisture" OR "drought" OR "water reduction") in separate queries yielding 2,384 total search hits. We included the most common and troublesome weeds in our search terms, because they are the most extensively studied weeds and their inclusion was intended to broaden the search criteria. A multistep screening protocol was adopted to identify relevant literature for this meta-analysis (Page and McKenzie 2021; Figure 1). For the literature to be included, it had to meet the following criteria: (1) water-stressed and comparative control (i.e., well-watered) treatments were investigated under the same experimental conditions; (2) water stress was quantitatively expressed using one of three metrics: solution osmotic potential ($\psi_{solution}$), soil moisture in terms of soil water potential (ψ_{soil}), or percent field capacity (studies using vague terms such as "drought" to denote water stress were excluded); (3) means for at least 1 of the 12 response variables were reported for both water-stress and control treatments, and these response variables include indices related to weed germination (germination/emergence), weed growth characteristics (radicle/root length, plant height, leaf area, branches/tillers per plant, leaves per plant, total biomass, root biomass, shoot biomass, and root:shoot ratio), and seed production (inflorescences per plant and seeds per plant); (4) the weed was grown individually (i.e., in monoculture) and not in competition with the crop; and (5) water stress was maintained throughout the duration of the experiment.

A total of 86 relevant published papers were identified. From each selected paper, we extracted the following information (Table 1):

- *Weed-related information*: common name, scientific name, family name, and population/biotype.
- *Experiment-related information*: study location, study year, and number of replications.
- *Water stress–related information*: water-stress metrics ($\psi_{solution}$, ψ_{soil}, and percent field capacity) and their levels and test medium used (PEG or D-mannitol solutions, soil in pot studies).
- *Weed response–related information*: response indices (indices related to weed germination, growth characteristics, and seed production) and mean water-stress effects on corresponding indices for water-stress and control treatments.

When $\psi_{solution}$ or ψ_{soil} was reported in different units, units were standardized into a common unit of "MPa." Depending on the test medium and metrics used to express water stress across studies, a solution with $\psi_{solution}$ of "0 MPa" and soil with ψ_{soil} of ~ "−0.03 MPa" or "100% field capacity" were considered as comparative control treatments. If the information for given indices were reported over time, data were extracted from the last recorded observation. From each study, responses of different weed species (including distinct populations, biotypes, sex types, environmental occurrence, and seed sources) and at different water-stress levels were included as distinct observations in the database. The final data set had 1,196 observations from 86 articles published during 1970 through 2020 and spanned four continents (Asia, Australia, Europe, and North America).

Meta-analysis: Overall Water-Stress Effects

We used the natural logarithm of response ratios as effect sizes to calculate the overall effects of water stress on weed germination, growth characteristics, and seed production (Hedges et al. 1999).

$$\ln(\mathrm{RR}) = \ln(\bar{X}_{\mathrm{WS}}/\bar{X}_{\mathrm{C}}) = \ln(\bar{X}_{\mathrm{WS}}) - \ln(\bar{X}_{C}) \quad [1]$$

where ln(RR) is the natural log of response ratios, $\bar{X}_{WS}$ and $\bar{X}_{\mathrm{C}}$ are mean values of indices related to weed germination (germination/emergence), weed growth characteristics (radicle/root length, plant height, leaf area, branches/tillers per plant, leaves per plant, total biomass, root biomass, shoot biomass, and root:shoot ratio), and seed production (inflorescences per plant and seeds per plant) for water-stressed and control treatments, respectively. Under severe water-stress conditions, weeds did not germinate or died. In such cases, values for given indices were reported as zero. Because ln(RR) cannot be calculated when any of the treatment mean values are zero, we substituted zero with the minimum possible values (for example, 0.1% germination for 0% germination, 0.1 for other growth variables such as plant height, leaf area, total biomass, etc.) (Thapa et al. 2018a).

The bulk of the studies included in the meta-analysis did not report information that denotes within-study variabilities such as standard deviation (SD), standard error (SE), or the coefficient of variation (CV). Individual effect sizes could not be weighted by sampling variances as suggested by Hedges and Olkin (1985). Therefore, we weighted individual effect sizes based on experimental replications using the following equation (Adams et al. 1997):

$$w_i = (N_{\mathrm{WS}} \cdot N_{\mathrm{C}})/(N_{\mathrm{WS}} + N_{\mathrm{C}}) \quad [2]$$

where w_i is the weight for ith effect size, N_{WS} and N_{C} are the number of replications for water-stressed and control treatments, respectively.

More than one effect size was calculated from studies that reported results from multiyear experiments, and that tested multiple weed populations/biotypes and multiple water-stress intensities. This could lead to dependencies among effect sizes. Therefore, we modeled various sources of dependencies in effect sizes within and across studies by creating a multilevel mixed-effects meta-analytic model in the R *nlme* package (Pinheiro and Bates 2022; Thapa et al. 2018a, 2018b; Van den Noortgate et al. 2013). In this model, effect sizes were considered as a fixed effect, study/year/weed biotype/common controls were nested as random effects, and w_i values were included as weighting factors. Due to lack of actual measures of sampling variances, a cluster-based robust variance estimator was used to estimate robust SEs for mean effect sizes using the *clubSandwich* package in R (Pustejovsky 2022). Robust SEs were used to calculate 95% confidence intervals (CIs) for weighted mean effect sizes, that is, the natural log of response ratios [ln(RR)]. The overall water-stress effect on various indices related to weed germination, growth characteristics, and seed production was considered significant when the 95% CIs did not overlap zero ($P < 0.05$). For ease of interpretation, the mean effect sizes and their associated 95% CIs are exponentially back-transformed to the percentage change in responses using the following equation:

$$\%\text{ change in response} = \left[e^{\overline{\ln(\mathrm{RR})}} - 1\right] \times 100 \quad [3]$$

where $\overline{\ln(\mathrm{RR})}$ is the mean effect size for each index.

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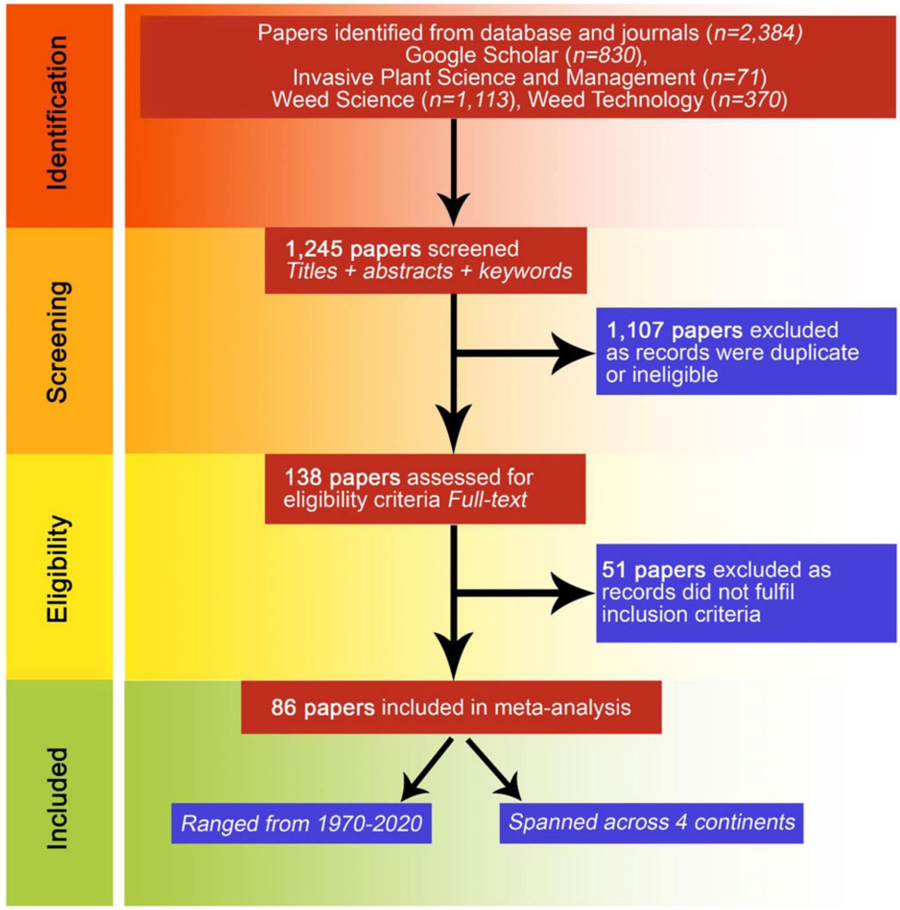

Figure 1. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Page and McKenzie 2021) flow diagram highlighting the selection procedure of 86 scientific published papers included in the meta-analysis.

Moderator or Subgroup Analysis: Effect of Weed Types, Families, and Water-Stress Intensity

A moderator analysis was conducted to determine whether or not the overall mean water-stress effects determined in this study were influenced by potential covariates. Covariates that were investigated included weed types (broadleaf vs. grass), families (Amaranthaceae, Asteraceae, Convolvulaceae, Fabaceae, Rubiaceae, and Poaceae), and the level of water stress. For this particular analysis on weed germination and seedling radicle length, we used studies in which water stress was expressed as $\psi_{solution}$, that is, studies conducted using PEG or D-mannitol solutions. Pot studies using soil as a test medium were not included due to a small number of pair-wise comparisons. For weed germination, $\psi_{solution}$ is categorized into seven subgroups ranging from low to severe water stress: 0 to −0.2, −0.2 to −0.4, −0.4 to −0.6, −0.6 to −0.8, −0.8 to −1.0, −1.0 to −1.4, and <−1.4 MPa. Shrestha et al. (2018) used exorbitantly greater levels of $\psi_{solution}$ (i.e., up to −5.56 MPa); therefore, it was excluded from the moderator analysis on weed germination. For seedling radicle length, $\psi_{solution}$ is categorized into five subgroups: 0 to −0.2, −0.2 to −0.4, −0.4 to −0.6, −0.6 to −1.0, and <−1.0 MPa. To investigate the moderating effect of water-stress intensity on indices related to weed growth characteristics and seed production, we only used pot studies that used soil as a test medium and expressed water stress in terms of "percent field capacity." We categorized effect sizes into three subgroups based on water stress: severe water stress (<30% field capacity), moderate water stress (30% to 60% field capacity), and low water stress (>60% field capacity). Due to small number of pair-wise comparisons, we did not use any studies that expressed water stress in terms of ψ_{soil} in any of the moderator analyses. Similarly, the germination response of broadleaf versus grass weeds to water stress was assessed.

Separate mean effect sizes and robust SEs were calculated for each subgroup using each one as a sole covariate in the original multilevel mixed-effects meta-analytic model described earlier. To safeguard against experiment-wise type I errors, 99% CIs were calculated for the subgroup analysis. The mean water-stress effect for each subgroup was considered significant ($P < 0.01$) if their 99% CIs leave out zero and significantly different if their 99% CIs did not overlap with one another. A four-parameter logistic model was fit to determine the quantitative relationship between water stress (expressed as $\psi_{solution}$) and mean water stress effect on moderating variables such as germination and seedling radicle length for grass versus broadleaf weeds:

$$\overline{\ln(\mathrm{RR})} = c + \frac{d - c}{1 + \exp[b \cdot (\psi_{solution} - \psi_{solution.50})]} \quad [4]$$

where $\overline{\ln(\mathrm{RR})}$ is the mean effect size for each subgroup, c is the lower asymptote, d is the higher asymptote, b is the slope at the inflection point, $\psi_{solution}$ is the solution osmotic potential, and

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Table 1. Summary of 86 published articles included in the meta-analysis.

Reference	Scientific names of weeds	Common names of weeds	Family	Country	Year	Weed type[a]	Water-stress metric[b]	Medium for water stress[c]
Ahmed et al. 2015	*Murdannia nudiflora* (L.) Brenan	doveweed	Commelinaceae	Philippines	2014	B	$\psi_{solution}$	PEG
Altom and Murray 1996	*Eclipta prostrata* (L.) L.	eclipta	Asteraceae	United States	1992	B	$\psi_{solution}$	PEG
Asgarpour et al. 2015	*Chamaesyce oncaten* (L.) Small	spotted spurge	Euphorbiaceae	Iran	2011	B	$\psi_{solution}$	PEG
Bai et al. 1995	*Artemisia frigida* Willd.	fringed sage	Asteraceae	Canada	1987,90-91	B	$\psi_{solution}$	PEG
Baird and Dickens 1991	*Diodia virginiana* L.	Virginia buttonweed	Rubiaceae	United States	1985	B	$\psi_{solution}$	PEG
Bajwa et al. 2016	*Parthenium hysterophorus* L.	ragweed parthenium	Asteraceae	Australia	2015	B	% field capacity	Soil
Bajwa et al. 2018	*Parthenium hysterophorus* L.	ragweed parthenium	Asteraceae	Australia	2016	B	$\psi_{solution}$	PEG
Blackshaw et al. 1981	*Setaria viridis* (L.) P. Beauv.	green foxtail	Poaceae	Canada	1980	G	$\psi_{solution}$	PEG (with soil)
Blackshaw et al. 2002	*Lamium amplexicaule* L.	henbit	Lamiaceae	Canada	2001	B	ψ_{soil}	Soil
Bolfrey-Arku et al. 2011	*Rottboellia cochinchinensis* (Lour.) W.D. Clayton	itchgrass	Poaceae	Philippines	2010	G	$\psi_{solution}$	PEG
Boydston 1989	*Cenchrus longispinus* (Hack.) Fernald	longspine sandbur	Poaceae	United States	1986	G	$\psi_{solution}$	PEG
Brecke 1995	*Euphorbia heterophylla* L.	wild poinsettia	Euphorbiaceae	United States	1994	B	$\psi_{solution}$	PEG
Brooks et al. 2018	*Clidemia hirta* (L.) D. Don *Miconia calvescens* DC. *Miconia nervosa* (Sm.) Triana	Koster's curse miconia melastome weed	Melastomataceae	Australia	2017	B	$\psi_{solution}$	PEG
Burke et al. 2003a	*Dactyloctenium aegyptium* (L.) Willd.	crowfootgrass	Poaceae	United States	2001	G	$\psi_{solution}$	PEG
Burke et al. 2003b	*Brachiaria platyphylla* (Munro ex C. Wright) Nash; syn.: *Urochloa platyphylla* (Munro ex C. Wright) R.D. Webster	broadleaf signalgrass	Poaceae	United States	2000	G	$\psi_{solution}$	PEG
Chachalis et al. 2008	*Hibiscus trionum* L.	Venice mallow	Malvaceae	Greece	2005	B	$\psi_{solution}$	PEG
Chadha et al. 2019	*Lactuca serriola* L.	prickly lettuce	Asteraceae	Australia	2018	B	% field capacity	Soil
Chahal et al. 2018	*Amaranthus palmeri* S. Watson	Palmer amaranth	Amaranthaceae	United States	2017	B	% field capacity	Soil
Chauhan 2013	*Rottboellia cochinchinensis* (Lour.) W.D. Clayton	itchgrass	Poaceae	Philippines	2011	G	% field capacity	Soil
Chauhan and Abugho 2012	*Ipomoea triloba* L.	threelobe morningglory	Convolvulaceae	Philippines	2011	B	$\psi_{solution}$	PEG
Chauhan and De Leon 2014	*Macroptilium lathyroides* (L.) Urb.	wild bushbean	Fabaceae	Philippines	2013	B	$\psi_{solution}$	PEG
Chauhan et al. 2006a	*Sisymbrium orientale* L.	oriental mustard	Brassicaceae	Australia	2006	B	$\psi_{solution}$	PEG
Chauhan et al. 2006b	*Galium tricornutum* Dandy	threehorn bedstraw	Rubiaceae	Australia	2005	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2008a	*Leptochloa chinensis* (L.) Nees	Chinese sprangletop	Poaceae	Philippines	2007	G	$\psi_{solution}$	PEG

(*Continued*)

Table 1. (*Continued*)

Reference	Scientific names of weeds	Common names of weeds	Family	Country	Year	Weed type[a]	Water-stress metric[b]	Medium for water stress[c]
Chauhan and Johnson 2008b	*Eleusine indica* (L.) Gaertn.	goosegrass	Poaceae	Philippines	2007	G	$\psi_{solution}$	PEG
Chauhan and Johnson 2008c	*Digitaria ciliaris* (Retz.) Koeler *Digitaria longiflora* (Retz.) Pers.	southern crabgrass India crabgrass	Poaceae	Philippines	2007	G	$\psi_{solution}$	PEG
Chauhan and Johnson 2008d	*Chromolaena odorata* (L.) R. M. King & H. Rob. *Tridax procumbens* L.	siam weed coat buttons	Asteraceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2008e	*Mimosa diplotricha* C. Wright; syn.: *Mimosa invisa* Mart., non Mart. Ex Colla	giant sensitiveplant	Fabaceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2008f	*Corchorus olitorius* L. *Melochia oncatenate* L.	nalta jute redweed	Tiliaceae Sterculiaceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2008g	*Borreria ocymoides* (Burm. F.) DC. *Heliotropium indicum* L.	purple-leaf button weed Indian heliotrope	Rubiaceae Boraginaceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2009a	*Amaranthus spinosus* L. *Amaranthus viridis* L.	spiny amaranth slender amaranth	Amaranthaceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2009b	*Synedrella nodiflora* (L.) Gaertn.	synedrella	Asteraceae	Philippines	2007	B	$\psi_{solution}$	PEG
Chauhan and Johnson 2009c	*Echinochloa colona* (L.) Link	junglerice	Poaceae	Philippines	2007	G	$\psi_{solution}$	PEG
Chauhan and Johnson 2010	*Echinochloa colona* (L.) Link	junglerice	Poaceae	Philippines	2007	G	% field capacity	Soil
Chejara et al. 2008	*Hyparrhenia hirta* (L.) Stapf	coolatai grass	Poaceae	Australia	2006	G	$\psi_{solution}$	PEG
Clewis et al. 2007	*Oenothera laciniata* Hill	cutleaf evening-primrose	Onagraceae	United States	2004	B	$\psi_{solution}$	PEG
Crowley and Buchanan 1980	*Ipomoea hederacea* Jacq. *Ipomoea hederacea* var. *intergruiscula* A. Gray *Ipomoea lacunosa* L. *Ipomoea purpurea* (L.) Roth *Jacquemontia tamnifolia* (L.) Griseb.	ivyleaf morningglory entireleaf morningglory pitted morningglory tall morningglory smallflower morningglory	Convolvulaceae	United States	1974	B	$\psi_{solution}$	PEG
Eslami 2011	*Chenopodium album* L.	common lambsquarters	Chenopodiaceae	Iran	2008	B	$\psi_{solution}$	PEG
Evetts and Burnside 1972	*Cynanchum leave* (Michx.) Pers.; syn.: *Ampelamus albidus* (Nutt.) Britton *Apocynum cannabinum* L. *Asclepias syriaca* L. *Bassia scoparia* (L.) A.J. Scott	honeyvine milkweed hemp dogbane common milkweed kochia	Asclepiadaceae Apocynaceae Asclepiadaceae Chenopodiaceae	United States	1970	B	$\psi_{solution}$	D-mannitol
Fernando et al. 2016	*Chloris virgata* Sw.	feather fingergrass	Poaceae	Australia	2015	G	$\psi_{solution}$	PEG
Florentine et al. 2018	*Echium plantagineum* L.	Paterson’s curse/vipers bugloss	Boraginaceae	Australia	2016	B	$\psi_{solution}$	PEG
Gealy et al. 1994	*Anthemis cotula* L.	mayweed chamomile	Asteraceae	United States	1993	B	ψ_{soil}	Soil
Ghorbani et al. 1999	*Amaranthus retroflexus* L.	redroot pigweed	Amaranthaceae	United Kingdom	1998	B	$\psi_{solution}$	PEG
Griffin et al. 1989	*Desmodium tortuosum* (Sw.) DC.	Florida beggarweed	Fabaceae	United States	1988	B	ψ_{soil}	Soil
Horak and Wax 1991	*Ipomoea pandurata* (L.) G. Mey.	bigroot morningglory	Convolvulaceae	United States	1988	B	$\psi_{solution}$	PEG

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Table 1. (*Continued*)

Hoveland and Buchanan 1973	*Crotalaria spectabilis* Roth	showy crotalaria	Fabaceae	United States	1972	B & G	$\psi_{solution}$	PEG
	Dactyloctenium aegyptium (L.) Willd.	crowfootgrass	Poaceae					
	Datura stramonium L.	jimsonweed	Solanaceae					
	Helenium amarum (Raf.) H. Rock	bitter sneezeweed	Asteraceae					
	Ipomoea hederacea Jacq.	ivyleaf morningglory	Convolvulaceae					
	Ipomoea lacunosa L.	pitted morningglory	Convolvulaceae					
	Rumex crispus L.	curly dock	Polygonaceae					
	Senna obtusifolia (L.) H.S. Irwin & Barneby	sicklepod	Fabaceae					
	Sesbania herbacea (Mill.) McVaugh	hemp sesbania	Fabaceae					
	Sida spinosa L.	prickly sida	Malvaceae					
	Taraxacum officinale F.H. Wigg.	dandelion	Asteraceae					
Iqbal et al. 2019	*Sesbania herbacea* (Mill.) McVaugh	hemp sesbania	Fabaceae	Australia	2016	B	$\psi_{solution}$	PEG
Johnston et al. 1979a	*Cardiospermum halicacabum* L.	balloonvine	Sapindaceae	United States	1978	B	$\psi_{solution}$	PEG
Johnston et al. 1979b	*Sesbania herbacea* (Mill.) McVaugh	hemp sesbania	Fabaceae	United States	1978	B	$\psi_{solution}$	PEG
Khan et al. 2021	*Amaranthus retroflexus* L.	redroot pigweed	Amaranthaceae	Australia	2018	B	% field capacity	Soil
	Amaranthus viridis L.	slender amaranth						
Kiemnec and Larson 1991	*Cardaria draba* (L.) Desv.	hoary cress	Brassicaceae	United States	1990	B	$\psi_{solution}$	PEG
	Centaurea diffusa Lam.	diffuse knapweed	Asteraceae					
Li et al. 2015	*Bromus arvensis* L. syn. *Bromus japonicus* Houtt.	Japanese brome	Poaceae	China	2014	G	$\psi_{solution}$	PEG
Loura et al. 2020	*Conyza bonariensis* (L.) Cronquist	hairy fleabane	Asteraceae	Australia	2018	B	$\psi_{solution}$	PEG
Lu et al. 2006	*Ageratina adenophora* (Spreng) R.M. King & H. Rob.; syn.: *Eupatorium adenophorum* Spreng.	crofton weed	Asteraceae	China	2005	B	$\psi_{solution}$	PEG
Macdonald et al. 1992	*Eupatorium capillifolium* (Lam.) Small	dogfennel	Asteraceae	United States	1989	B	$\psi_{solution}$	PEG
	Eupatorium compositifolium Walter	yankeeweed						
Mahajan et al. 2018	*Sisymbrium thellungii* O.E. Schulz	African turnipweed	Brassicaceae	Australia	2017	B	% field capacity	Soil
Mahajan et al. 2019	*Echinochloa colona* (L.) Link	junglerice	Poaceae	Australia	2017	G	% field capacity	Soil
Mahmood et al. 2016	*Galenia pubescens* (Eckl. & Zeyh.) Druce	green galenia	Aizoaceae	Australia	2015	B	$\psi_{solution}$	PEG
Mann et al. 1981	*Sicyos angulatus* L.	Burcucumber	Cucurbitaceae	United States	1979	B	$\psi_{solution}$	PEG
Maurice 1985	*Setaria glauca* (L.) P. Beauv.	yellow foxtail	Poaceae	Canada	1984	G	ψ_{soil}	Soil
	Setaria viridis (L.) P. Beauv.	green foxtail						
Mayeux 1982	*Xylothamia palmeri* (A. Gray) G.L. Newsom; syn.: *Ericameria austrotexana* M. C. Johnst.	false broomweed	Asteraceae	United States	1980	B	$\psi_{solution}$	PEG
Mobli et al. 2020	*Sonchus oleraceus* L.	annual sowthistle	Asteraceae	Australia	2018	B	% field capacity	Soil
Momayyezi and Upadhyaya 2017	*Cynoglossum officinale* L.	houndstongue	Boraginaceae	Canada	2016	B	% field capacity	Soil
Nandula et al. 2006	*Conyza canadensis* (L.) Cronquist	horseweed	Asteraceae	United States	2002	B	$\psi_{solution}$	PEG
Nosratti et al. 2018	*Sophora alopecuroides* L.	foxtail sophora	Fabaceae	Iran	2016	B	$\psi_{solution}$	PEG
Nosratti et al. 2019	*Picnomon acarna* (L.) Cass.	soldier thistle	Asteraceae	Iran	2017	B	$\psi_{solution}$	PEG
Reddy and Singh 1992	*Bidens pilosa* L.	hairy beggarticks	Asteraceae	United States	1990	B	$\psi_{solution}$	PEG
Roberts et al. 2021	*Eragrostis curvula* (Schrad.) Nees	African/weeping lovegrass	Poaceae	Australia	2020	G	$\psi_{solution}$	PEG
Scherner et al. 2017	*Apera spica-venti* (L.) Beauv.	silky windgrass	Poaceae	Denmark	2015	G	$\psi_{solution}$	PEG
	Poa annua L.	annual bluegrass						
	Vulpia myuros (L.) C.C. Gmel.	rattail fescue						

(*Continued*)

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Table 1. (*Continued*)

Reference	Scientific names of weeds	Common names of weeds	Family	Country	Year	Weed type[a]	Water-stress metric[b]	Medium for water stress[c]
Shrestha et al. 2018	*Echinochloa colona* (L.) Link	junglerice	Poaceae	United States	2015	G	$\psi_{solution}$	PEG
Singh et al. 2012	*Ipomoea purpurea* (L.) Roth	tall morningglory	Convolvulaceae	United States	2011	B	$\psi_{solution}$	PEG
Singh et al. 2021	*Brassica tournefortii* Gouan	African mustard	Brassicaceae	Australia	2019	B	$\psi_{solution}$	PEG
Stanton et al. 2012	*Solanum elaeagnifolium* Cav.	silverleaf nightshade	Solanaceae	Australia	2008	B	$\psi_{solution}$	PEG
Susko et al. 1999	*Pueraria lobata* (Willd.) Ohwi	kudzu	Fabaceae	United States	1999	B	$\psi_{solution}$	PEG
Teuton et al. 2004	*Urochloa subquadripara* (Trin.) R.D. Webster	tropical signalgrass/ smallflowered alexandergrass	Poaceae	United States	2003	G	$\psi_{solution}$	PEG
Thill et al. 1979	*Bromus tectorum* L.	downy brome	Poaceae	United States	1976-77	G	ψ_{soil}	Soil
Thompson et al. 2021	*Lolium rigidum* Gaudin	rigid ryegrass	Poaceae	Australia	2019	G	$\psi_{solution}$	PEG
Wang et al. 2016	*Galium aparine* L.	catchweed bedstraw	Rubiaceae	China	2015	B	$\psi_{solution}$	PEG
Wei et al. 2009	*Solanum rostratum* Dunal	buffalo bur	Solanaceae	China	2008	B	$\psi_{solution}$	PEG
Weller et al. 2021	*Amaranthus retroflexus* L.	redroot pigweed	Amaranthaceae	Australia	2020	B	% field capacity	Soil
Williams 1980	*Sesbania herbacea* (Mill.) McVaugh	hemp sesbania	Fabaceae	United States	1976	B	$\psi_{solution}$	PEG
Wilson 1979	*Cirsium arvense* (L.) Scop.	Canada thistle	Asteraceae	United States	1976	B	$\psi_{solution}$; ψ_{soil}	D-mannitol; soil
Wilson and McCarty 1984	*Cirsium flodmanii* (Rydb.) Arthur	Flodman thistle	Asteraceae	United States	1979	B	$\psi_{solution}$	D-mannitol
Yuan and Wen 2018	*Ageratum conyzoides* L. *Conyza canadensis* (L.) Cronquist *Crassocephalum crepidioides* (Benth.) S. Moore	billygoat weed horseweed redflower ragweed	Asteraceae	China	2017	B	$\psi_{solution}$	PEG
Yue et al. 2021	*Achnatherum inebrians* (Hance) Keng	drunken horse grass	Poaceae	China	2018	G	$\psi_{solution}$	PEG
Zollinger and Kells 1991	*Sonchus arvensis* L.	perennial sowthistle	Asteraceae	United States	1986	B	ψ_{soil}	Soil

[a]B, broadleaf weed; G, grass weed.
[b]$\psi_{solution}$: solution osmotic potential; ψ_{soil}: soil water potential; % field capacity: soil moisture as percent field capacity.
[c]PEG, polyethylene glycol.

$\psi_{solution.50}$ is the solution osmotic potential at the inflection point (i.e., $\psi_{solution}$ that produces a response midway between *c* and *d*).

Publication Bias and Sensitivity Analysis

As mentioned earlier, many studies included in this meta-analysis did not report sampling variances to create meaningful funnel plots. Therefore, publication bias was investigated indirectly by visualizing the distribution of individual effect sizes for each of the indices using density plots (Basche and DeLonge 2017; Thapa et al. 2018a). To create these density plots, we excluded the imputed effect sizes, that is, effect sizes in which weed response under water-stressed conditions was zero and was replaced with the minimum possible value. We also performed sensitivity analysis to identify studies that may have influenced results and hence, test the robustness of the overall effect size estimates obtained in this meta-analysis (Philibert et al. 2012). Overall effect sizes and their corresponding CIs for each of the indices were repeatedly calculated using the *Jackknife* sensitivity analysis procedure. Our approach involves rerunning the same multilevel mixed-effects multi-analytic model as described earlier, with each individual study excluded from the data set every time.

Results and Discussion

Database Description

The 86 studies included in the meta-analysis were conducted during the previous five decades (1970 through 2020) in nine countries across four continents: Asia (China, Iran, and the Philippines), Australia (Australia), Europe (Denmark, Greece, and the United Kingdom), and North America (Canada and the United States). More than one-third of the studies (79%; $n = 68$) were conducted in three countries: the United States (36%; $n = 31$), Australia (24%; $n = 21$), and the Philippines (19%; $n = 16$). China, Canada, and Iran had six, five, and four studies, respectively, whereas each European country (Denmark, Greece, and the United Kingdom) had one study.

Across all studies, a total of 102 weed species belonging to 24 families were investigated for their response to water stress (Supplementary Table S1). Most of the studies investigated water-stress effects on broadleaf weeds ($n = 62$) followed by grass weeds ($n = 23$). Only one study by Hoveland and Buchanan (1973) investigated both broadleaf and grass weed species (Supplementary Table S1). Most of the broadleaf weed species belonged to Asteraceae ($n = 22$), followed by Fabaceae ($n = 9$), Convolvulaceae ($n = 5$), Amaranthaceae ($n = 4$), and Rubiaceae ($n = 4$). Similarly, the investigated grass weed species belonged to the family Poaceae ($n = 24$). Among weed species, hemp sesbania [*Sesbania herbacea* (Mill.) McVaugh] was the most frequently investigated species in four studies, followed by junglerice [*Echinochloa colona* (L.) Link] and redroot pigweed (*Amaranthus retroflexus* L.), both of which were investigated three times. All other weed species were investigated once, except eight weed species that were investigated twice: crowfootgrass [*Dactyloctenium aegyptium* (L.) Willd.], green foxtail [*Setaria viridis* (L.) P. Beauv.], itchgrass [*Rottboellia cochinchinensis* (Lour.) W.D. Clayton], ivyleaf morningglory (*Ipomoea hederacea* Jacq.), pitted morningglory (*Ipomoea lacunosa* L.), ragweed parthenium (*Parthenium hysterophorus* L.), slender amaranth (*Amaranthus viridis* L.), and tall morningglory [*Ipomoea purpurea* (L.) Roth].

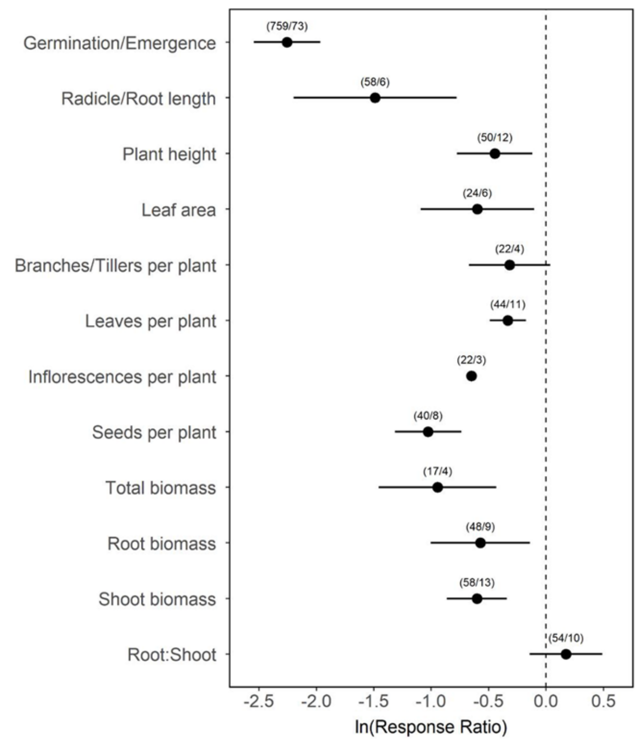

Figure 2. Overall water-stress effects on weed germination/emergence, growth characteristics, and seed production. The vertical black dashed line represents zero effect. The black dots are overall mean effect sizes, and the black lines are 95% confidence intervals (CIs). The values in parentheses are the number of observations followed by the number of studies for each pair-wise comparison. The mean effect sizes were considered significantly different when their 95% CIs did not include zero.

Effect of Water Stress on Weed Germination

Averaged across pair-wise observations, water stress reduced weed seed germination/emergence by 90% (95% CI = −92% to −86%; Figure 2). This effect of water stress on weed germination/emergence is likely because more than one-third of the observations (i.e., $n = 276$ out of 759) were exposed to severe water stress ($\psi_{solution}$ >−0.6 MPa), resulting in >97% germination inhibition. Seed imbibition is required for germination, and hydration levels vary by plant species (Hegarty 1978), although understanding of these levels in weeds is limited (Pérez-Fernández et al. 2000). We observed 86% to 95% inhibition in the germination of Amaranthaceae, Asteraceae, Convolvulaceae, Fabaceae, Rubiaceae, and Poaceae weed families (Figure 3). Although differences were nonsignificant, Asteraceae was the least responsive family with 86% (99% CI = −93% to −72%) germination inhibition, while Amaranthaceae was the most responsive family with 95% (99% CI = −99% to −65%) germination inhibition due to water stress.

Plant functional groups respond differently to moisture availability (Emanuel et al. 2007; Manzoni et al. 2011), as evidenced by greater negative responses of grasses than broadleaves to water stress (Emanuel et al. 2007). Overall, germination of grass weeds was inhibited by 93% (99% CI = −97% to −83%) compared with 90% (99% CI = −93% to −84%) for broadleaf weeds (Figure 3). Mackie et al. (2019) also noted a greater impact of summer drought on grasses than forbs in their experiments across eight sites. Similarly, we observed a general trend of grass weeds being more negatively affected than broadleaf weeds across water-stress levels (Figure 4). However, water-stress effects between broadleaf and

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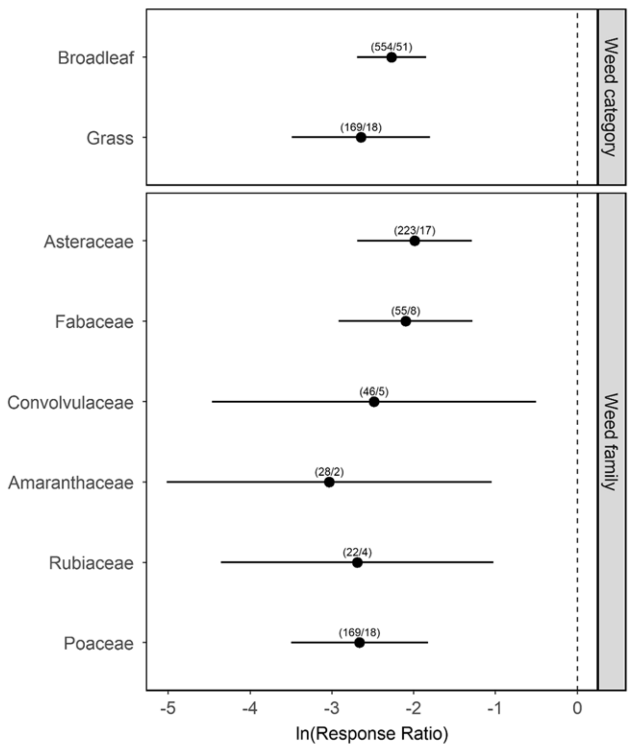

Figure 3. Overall water-stress effects on germination/emergence of grass and broadleaf weeds (top) and six weed families—Asteraceae, Fabaceae, Convolvulaceae, Amaranthaceae, Rubiaceae, and Poaceae (bottom). The vertical black dashed line represents zero effect. The black dots are overall mean effect sizes, and the black lines are 99% confidence intervals (CIs). The values in parentheses are the number of observations followed by the number of studies for each pair-wise comparison. The mean effect sizes were considered significantly different when their 99% CIs did not include zero.

grass weeds were not significantly different due to their overlapping 99% CIs across $\psi_{solution}$ subgroups.

At low water stress (i.e., $\psi_{solution}$ >−0.2 MPa), the mean water-stress effect on germination of broadleaf weeds was nonsignificant (mean = −18%, 99% CI = −41% to 14%), whereas grass weeds showed a negative effect (mean = −51%, 99% CI = −76% to −0.3%). At moderate water stress, the germination of broadleaves significantly decreased by 53% (99% CI = −69% to −29%) at $\psi_{solution}$ between −0.2 to −0.4 MPa and by 84% (99% CI = −92% to −70%) at $\psi_{solution}$ between −0.4 to −0.6 MPa. Similarly, the germination of grass weeds decreased by 73% (99% CI = −88% to −39%) at $\psi_{solution}$ between −0.2 to −0.4 MPa and by 92% (99% CI = −98% to −67%) at $\psi_{solution}$ between −0.4 to −0.6 MPa. At severe water stress, germination of broadleaf and grass weeds decreased by 97% (99% CI = −99% to −93%) and 98% (99% CI = −100% to −87%), respectively, at $\psi_{solution}$ between −0.6 to −0.8 MPa. With further decrease in $\psi_{solution}$ above −0.8 MPa, germination of both broadleaves and grasses was completely inhibited (i.e., >99% inhibition). We further modeled the effect of water stress on weed germination by fitting a four-parameter logistic model between mean effect sizes and mean $\psi_{solution}$ for each subgroup (Figure 4). The fitted model coefficients are presented in Table 2. For both broadleaf and grass weed types, weed germination decreased with a decrease in $\psi_{solution}$ (Figure 4). This indicates that the adverse effects of water stress on weed germination increased with increasing water stress.

Effect of Water Stress on Weed Growth Characteristics

Averaged across pair-wise comparisons, water stress negatively affected belowground weed growth characteristics (Figure 2). Water stress, on average, decreased seedling radicle/root length by 77% (95% CI = −89% to −54%) and root biomass by 44% (95% CI = −63% to −13%). A more intense effect of water stress on seedling radicle/root length was likely due to the use of PEG or D-mannitol solutions, with 35% of the observations (*n* = 19 out of 54) being exposed to severe water-stress (i.e., $\psi_{solution}$ >−0.6 MPa) conditions exhibiting > 97% inhibition (Figure 4). As $\psi_{solution}$ decreases, water stress increases, causing seedling radicle length to decrease progressively. At low to moderate water stress of $\psi_{solution}$ between 0 to −0.4 MPa, the mean decrease in seedling radicle length was not significantly different from zero. However, further decrease in $\psi_{solution}$ below −0.4 MPa resulted in a reduction in seedling radicle length compared with a no water stress condition. For instance, seedling radicle length decreased by 65% (99% CI = −82% to −31%) at $\psi_{solution}$ between −0.4 to −0.6 MPa, by 97% (99% CI = −99% to −84%) at $\psi_{solution}$ between −0.6 to −1.0 MPa, and by 99% (99% CI = −100% to −86%) at $\psi_{solution}$ below −1.0 MPa. Although the mean water-stress effects for each subgroup were not significantly different from zero, root biomass decreased from a mean positive effect of 2% (99% CI = −28% to 44%) at low (i.e., soil moisture >60% field capacity) to a mean negative effect of 39% (99% CI = −77% to 60%) and 69% (99% CI = −92% to 15%) at moderate (i.e., soil moisture at 30% to 60% field capacity) and severe (i.e., soil moisture <30% field capacity) water stress, respectively (Figure 5). The results suggest that belowground weed growth characteristics were negatively impacted by water stress, and the magnitude of the effect intensified with increasing water stress.

Water stress reduced most aboveground weed growth characteristics (Figure 2). Averaged across pair-wise comparisons, water stress decreased plant height by 36% (95% CI = −54% to −11%), leaf area by 45% (95% CI = −66% to −10%), leaves per plant by 28% (95% CI = −39% to −16%), and shoot biomass by 45% (95% CI = −58% to −29%). Although not statistically different, water stress decreased branches/tillers per plant by 27% (95% CI = −49% to 4%). Results were consistent with the findings from a recent meta-analysis by Sun et al. (2020), who reported a decrease in plant growth characteristics under water stress: for instance, they observed an overall decrease in plant dry biomass by 29% due to water stress.

Results from the moderator analysis indicated that the negative effects of water stress on aboveground weed growth characteristics intensified with increasing water stress (Figure 5). As soil moisture, expressed as percent field capacity, became more deficit, we observed a progressive reduction in the mean effect sizes for indices related to aboveground weed growth characteristics. For example, the mean effect on weed shoot biomass decreased from a nonsignificant effect of −15% (99% CI = −40% to 21%) at low (i.e., soil moisture > 60% field capacity) to a significant effect of −39% (99% CI = −56% to −14%) at moderate (i.e., soil moisture at 30% to 60% field capacity) and −61% (99% CI =-73% to −43%) at severe (i.e., soil moisture < 30% field capacity) water stress. Similarly, we found a nonsignificant effect of low water stress on other aboveground weed growth characteristics, including plant height, leaf area, leaves per plant, and branches/tillers per plant. Growth indices were reduced at moderate and severe water stress: plant height by −24% (99% CI = −34% to −12%) and −37% (99% CI = −46% to −26%), leaf area by −43% (99% CI = −60% to

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Table 2. Parameter estimates and SEs from a four-parameter logistic model fit to effect sizes for germination and seedling radicle length of broadleaf and grass weed species under water-stress gradients.[a]

Response variable	Weed type	*b*		*c*		*d*		$\psi_{solution.50}$		R^2
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	
Germination	Broadleaf	−3.568	1.193	−7.170	0.694	0.758	0.988	−0.737	0.073	0.991
Germination	Grass	−4.910	1.083	−6.909	0.347	−0.439	0.483	−0.742	0.050	0.991
Radicle length	Broadleaf	−6.239	0.432	−4.507	0.086	0.085	0.074	−0.758	0.015	1.000

[a]The model is fit to solution osmotic potential–based ($\psi_{solution}$) studies only. *c* is the lower asymptote, *d* is the higher asymptote, *b* is the slope at the inflection point, $\psi_{solution}$ is the solution osmotic potential, and $\psi_{solution.50}$ is the solution osmotic potential at the inflection point (i.e., the $\psi_{solution}$ that produces a response midway between *c* and *d*).

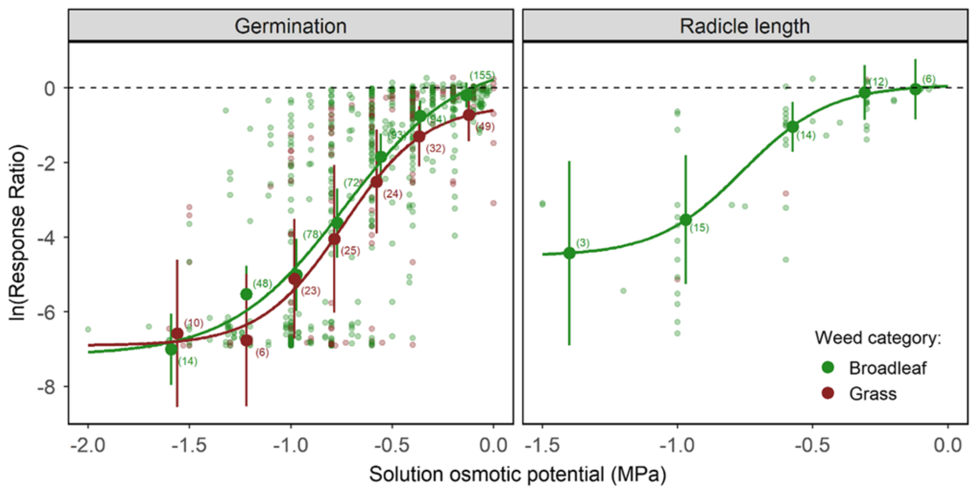

Figure 4. The log response ratio for germination and seedling radicle length of broadleaf (green dots/line) and grass (red dots/line) weed species as a function of water-stress intensity. Water stress increased as solution osmotic potential ($\psi_{solution}$) decreased and vice versa. The subgroups for germination are 0 to −0.2, −0.2 to −0.4, −0.4 to −0.6, −0.6 to −0.8, −0.8 to −1.0, −1.0 to −1.4, and <−1.4 MPa, while the subgroups for radicle length are 0 to −0.2, −0.2 to −0.4, −0.4 to −0.6, −0.6 to −1.0, and <−1.0 MPa. Only $\psi_{solution}$-based studies were used in this analysis. For each subgroup, the solid dots and lines represent mean effect sizes and their corresponding 99% confidence intervals (CIs). The mean effect sizes were considered significantly different when their 99% CIs did not include zero. Similarly, the water-stress effects were significantly different for each subgroup and among weed types only when their 99% CIs did not overlap with one another. The fitted lines represent a four-parameter logistic regression model, and the coefficients of the models are presented in Table 2.

−18%) and −44% (99% CI = −57% to −26%), leaves per plant by −30% (99% CI = −48% to −5%) and −47% (99% CI = −60% to −29%), and branches/tillers per plant by −23% (99% CI = −38% to −4%) and −52% (99% CI = −85% to 52%), respectively. Taken altogether, the adverse effects of soil moisture limitations on weed growth intensified with increasing water stress, as reported in a recent meta-analysis (Sun et al. 2020). Growth reduction is not only a direct effect of water stress but also an important adaptive mechanism (Skirycz and Inzé 2010). Plants rapidly inhibit their growth at the onset of water stress before gradually recovering and adapting to stressed conditions (Skirycz and Inzé 2010). Additionally, plants have similar multiple adaptive responses, such as generating antioxidants (Nayyar and Gupta 2006), regulating hormones (Peleg and Blumwald 2011), inducing stress proteins (Poolman et al. 2002), and improving water-use efficiency by increasing root ducts (Lee et al. 2016). Hence, although water stress will reduce weed growth, timely established weeds that can utilize soil moisture from the early onset of precipitation or soil water storage can be more competitive owing to lower resource competition (Hanson 2015).

Averaged across pair-wise comparisons, water stress reduced total weed biomass by 61% (95% CI = −77% to −35%; Figure 2). Although not significantly different from zero, root:shoot ratio was the only index that increased under water stress (mean = 19%; 95% CI = −13% to 63%; Figure 2). A moderator analysis further indicated that the positive effect on root:shoot ratio was mostly observed when soil moisture was maintained above 60% field capacity, that is, at low water stress (mean = 27%, 99% CI = −0.2% to 61%; Figure 5). Even under moderate and severe water stress, that is, when soil moisture was below 60% field capacity, the root:shoot ratio of weeds remained unaffected. These results indicate root growth is generally less sensitive to water stress relative to shoot growth (Sharp and Davies 1989). Plants allocate a greater portion of assimilated dry matter to roots under water stress (Delfin et al. 2021; Xu et al. 2015), and the resultant increase in rooting depth allows for water extraction from deeper layers, maintaining a higher root water influx for longer durations (Chaves et al. 2002). Osmotic adjustment (Saab et al. 1992), higher soluble sugars and dry matter in roots (Xu et al. 2015), increased cell wall loosening ability (Hsiao and Xu 2000), and water stress–induced abscisic acid and ethylene (Sharp and LeNoble 2002; Spollen et al. 2000) are the primary mechanisms assuring greater root resilience under water stress relative to shoots. Considering plant adaptive mechanisms and the abilities of weeds to extract more water and tolerate water stress, weeds are thus expected to further intensify water-stressed conditions for crops (Griffin et al. 1989; Patterson and Flint 1982; Stuart et al. 1984).

Effect of Water Stress on Weed Seed Production

Water stress decreased weed seed production or fecundity. Averaged across pair-wise comparisons, water stress decreased inflorescences per plant by 48% (95% CI = −49% to −46%) and

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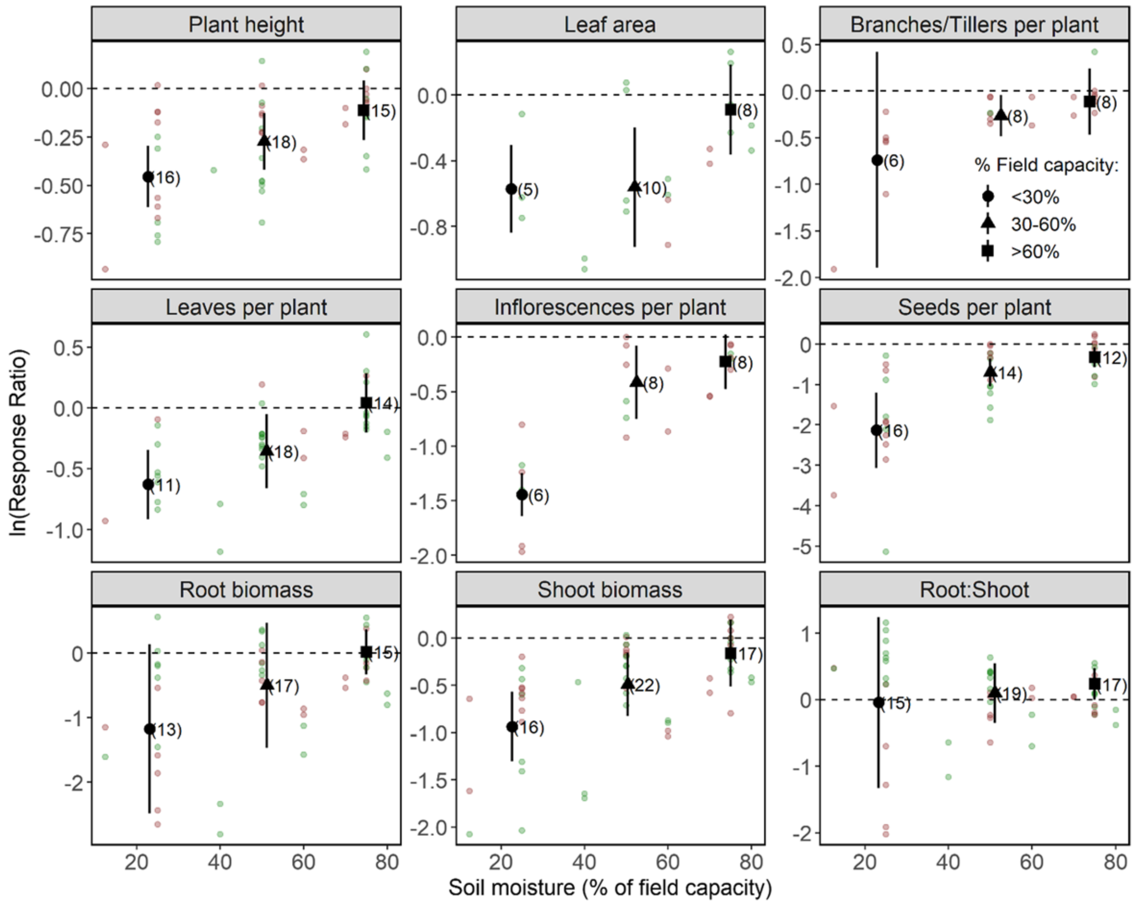

Figure 5. The log response ratio for weed growth characteristics (plant height, leaf area, branches/tillers per plant, leaves per plant, root biomass, shoot biomass, and root:shoot ratio) and seed production (inflorescences per plant and seeds per plant) as a function of water-stress intensity. Water stress increased as soil moisture (% field capacity) decreased and vice versa. The green and red dots represent broadleaf and grass weed species, respectively. The solid black points and the lines represent mean effect sizes and their 99% confidence intervals (CIs) for low (>60%), moderate (30%–60%), and severe (<30% field capacity) water-stress subgroups. The mean effect sizes were considered significantly different when their 99% CIs did not include zero. Similarly, the water-stress effects were significantly different for each subgroup and among weed types only when their 99% CIs did not overlap with one another.

seeds per plant by 64% (95% CI = −73% to −52%) relative to the unstressed condition (Figure 2). A moderator analysis indicates that both inflorescences and seeds per plant decreased with increasing water stress (Figure 5). The inflorescences per plant decreased by 76% (99% CI = −81% to −71%) at severe water stress of <30% field capacity to 34% (99% CI = −53% to −8%) at moderate water stress of 30% to 60% field capacity, and 20% (99% CI = −38% to 2.5%) at low water stress of >30% field capacity. Similarly, the seeds per plant decreased by 88% (99% CI = −95% to −70%) at severe water stress of <30% field capacity to 50% (99% CI = −65% to −31%) at moderate water stress of 30% to 60% field capacity, and 27% (99% CI = −43% to −7%) at low water stress of >30% field capacity. These results suggest that weeds can continue to produce flowers and seeds to some extent under water-stressed conditions. When water is limited, plants often shorten their vegetative growth and accelerate to rapid flowering and seed production to attain senescence (Bernal et al. 2011; Franks et al. 2007; Sherrard and Maherali 2006).

Publication Bias and Sensitivity Analysis

The distribution of individual effect sizes for various indices related to weed germination, growth characteristics, and seed production is shown as density plots in Figure 6. All indices had narrow distributions and slightly offset from zero, indicating a negative effect, except root:shoot ratio, which showed a slightly positive effect of water stress. Nonetheless, density plots for all indices show nearly symmetrical distribution, indicating no publication bias for any of the indices considered in the meta-analysis (Light and Pillemer 1984; Sterne and Harbord 2004).

Sensitivity analysis identified a few influential studies for some of the indices investigated (Figures 7 and 8). For example, an exclusion of Zollinger and Kells (1991) from the data set increased overall effect size estimates from −36% (95% CI = −54% to −11%) to −23% (95% CI = −29% to −15%) for plant height and from −45% (95% CI = −66% to −10%) to −33% (95% CI = −46% to −17%) for leaf area. Similarly, with the exclusion of Chauhan (2013), the magnitude of overall effect size estimates increased from −27% (95% CI = −49% to 4%) to −15% (95% CI = −28% to −0.2%) for branches/tillers per plant and from −28% (95% CI = −39% to −16%) to −15% (95% CI = −28% to −0.2%) for leaves per plant. This was likely because these studies reported drastic impacts of water stress on weed growth characteristics; for example, Chauhan (2013) observed a 56% reduction in leaf area at 12.5% field capacity compared with the control (i.e., 100% field capacity). Therefore, the exclusion of these studies caused a deviation in the overall effect size estimates. In contrast, the exclusion of Chadha et al. (2019) decreased the magnitude of

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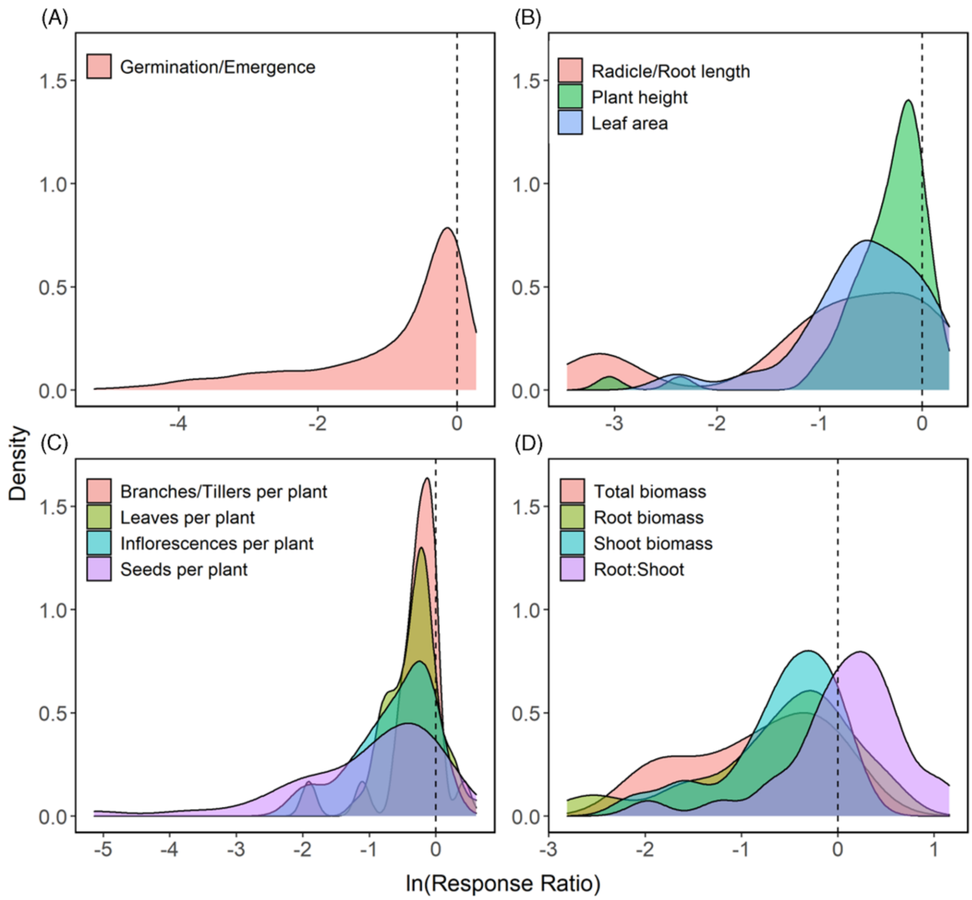

Figure 6. Density plots depicting the distribution of the individual effect sizes for all 12 response variables considered in this meta-analysis: (A) weed seed germination/emergence; (B) radicle/root length, plant height, and leaf area; (C) branches/tillers per plant, leaves per plant, inflorescences per plant, and seeds per plant; and (D) total biomass, root biomass, shoot biomass, and root:shoot ratio.

the overall effect size estimates for weed total biomass by 9% from −61% (95% CI = −77% to −35%) to −70% (95% CI = −72% to −68%). However, we determined that the main conclusions of this meta-analysis are robust, because (1) overall effect sizes for all other indices (germination/emergence, radicle/root length, inflorescences per plant, seeds per plant, root biomass, shoot biomass, and root:shoot ratio) were not sensitive to any given study, (2) overall effect sizes estimated using the *Jackknife* procedure after excluding influential studies fall within 95% CI of their original overall effect size estimates, and (3) drastic effects of severe water stress on plants are not uncommon, and these effects have caused the resultant change in magnitude of the aforementioned overall effect sizes.

Lessons Learned, Evidence Gaps, and Future Research Considerations

The meta-analysis based on 1,196 observations from 86 studies accomplished in this study is the first to assess the integral and quantitative response of 102 weed species to water stress. This is also the first study to evaluate the holistic effect of water stress on 12 response variables associated with germination, growth, and seed production of weeds, and concurrently differentiate germination response of grasses and broadleaf weeds. We found a generally negative response of weeds to water stress, and our findings underscore and strengthen the previously held notion that water stress inhibits plant growth and performance. The germination of grass weeds might be slightly more sensitive to water stress compared with broadleaf weeds. Moreover, weed germination is completely inhibited at $\psi_{solution}$ below −0.8 MPa, and a minimum of −0.09 MPa for grass weeds and −0.32 MPa for broadleaf weeds is required to inhibit their germination by half. Similarly, a minimum of −0.50 MPa is required to reduce seedling radicle length of broadleaf weeds by half. Plant height demonstrates inhibition by about one-fourth, inflorescences per plant by one-third, and seeds per plant by one-half under moderate water stress of 30% to 60% field capacity. In general, weed fecundity was found to be suppressed to a larger degree than growth morphology under water stress. For instance, weed root biomass and shoot biomass were inhibited by 61% to 69%, whereas fecundity (inflorescences per plant and seeds per plant) was inhibited by 76% to 88% under severe water stress of <30% field capacity relative to unstressed (i.e., 100% field capacity) conditions. Our findings that weeds will germinate, survive, grow, and reproduce and will continue to be competitive and problematic in managed agronomic systems, even under intense drought or water-stressed conditions, cannot be ignored. As cropping systems continue to experience extreme weather events more than at any time in the past, future studies should investigate, evaluate, and promote the adoption of multiple diverse strategies aimed at effectively managing weeds under water-limited conditions as an integral component of integrated weed management programs. This study identifies distinctive, adaptive behavior (i.e., ability to compete for water) of weeds that

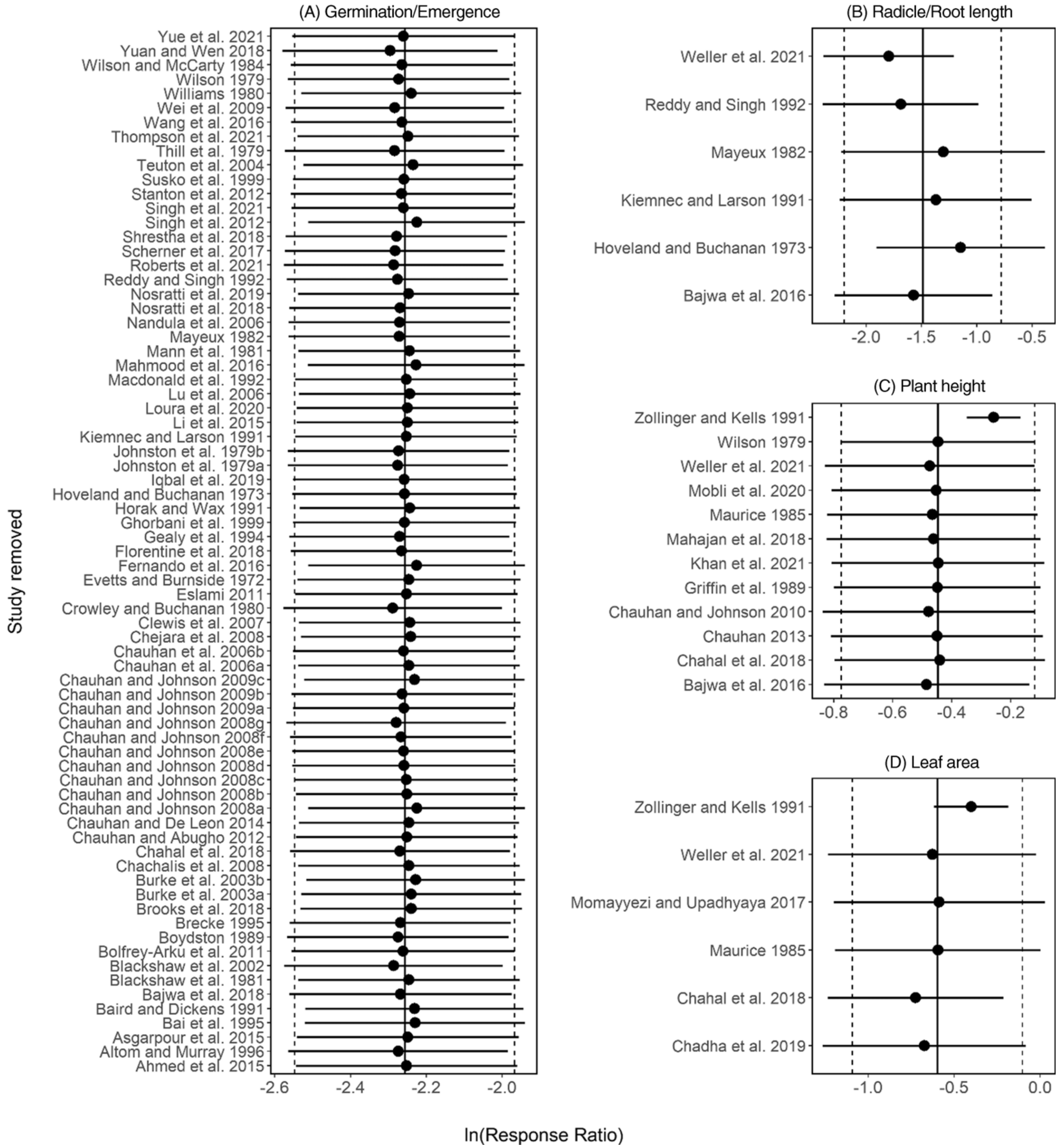

Figure 7. Results from the sensitivity analysis depicting variations in the overall effect size estimates (mean ± 95% confidence intervals [CIs]) of water-stress effects on (A) weed germination/emergence, (B) seedling radicle/root length, (C) plant height, and (D) leaf area when a particular study is omitted from the analysis. The vertical black solid and dashed lines represent overall effect sizes (mean ± 95% CIs) with all studies included.

can inform predictions of emergence, survival rate, and possible shifts in weed communities in water-limited regions and periods. Finally, quantitative information gathered in this meta-analysis will be helpful in modeling and/or predicting multidimensional responses of weeds to water stress.

This current meta-analysis identified critical gaps in the existing evidence base and provides directions for reporting data standards and future research avenues:

- Numerous studies included in the meta-analysis lack information on variability within sampling populations such as SD, SE, CV, or LSD. Within-treatment uncertainty statistics are critical for the robust characterization of confidence in reported effect size estimates. Therefore, we ask researchers to report these statistics along with replication size and treatment means in each study. Such a practice will allow reasonable quantitative analysis and information integration.

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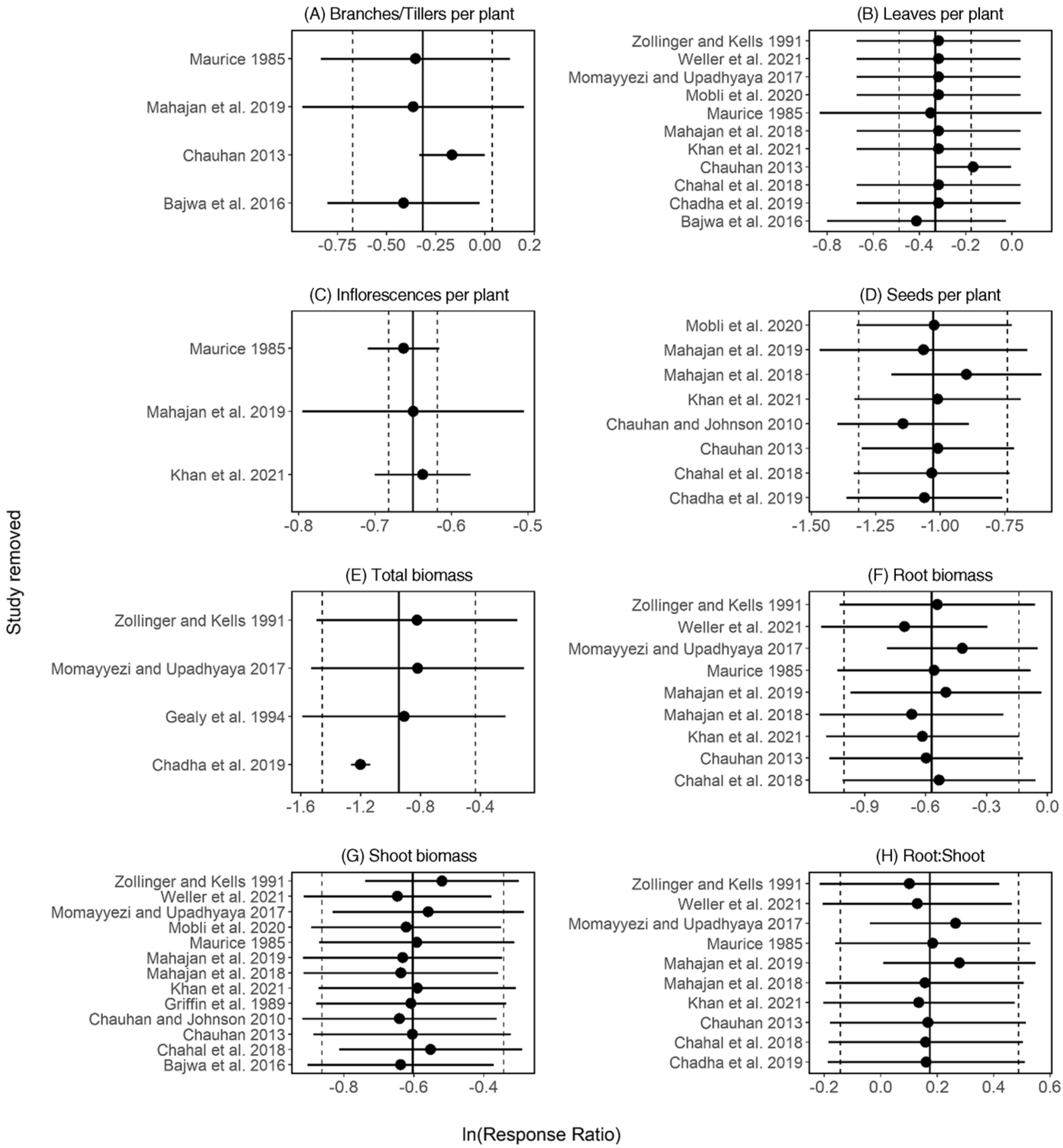

Figure 8. Results from the sensitivity analysis depicting variations in the overall effect size estimates (mean ± 95% confidence intervals [CIs]) of water-stress effects on (A) branches/tillers per plant, (B) leaves per plant, (C) inflorescences per plant, (D) seeds per plant, (E) total biomass, (F) root biomass, (G) shoot biomass, and (H) root:shoot ratio, when a particular study is omitted from the analysis. The vertical black solid and dashed lines represent overall effect sizes (mean ± 95% CIs) with all studies included.

- Meta-analyses require independence, and quantitative results from the same group of researchers/programs/collaborator networks are treated as a possible source of dependence (Stevens and Taylor 2009). Certain authors/research groups might be more likely to find certain results due to their use/preference of specific methodological elements (protocols, populations, experimental environments, instrumentation, etc.) or bias in performing the experiment, analyzing data, or reporting results (Danchev et al. 2019). This can violate the assumption of independence between effect sizes, potentially distorting the results of the meta-analysis (Moulin and Amaral 2020). In the present study, we found that two investigators conducted 69% ($n = 11$ out of 16) of studies in the Philippines, and one of those investigators was involved in 75% ($n = 3$ out of 4) and 81% ($n = 17$ out of 21) of studies in Iran and Australia, respectively. In total, one investigator authored or coauthored 41% ($n = 36$ out of 86) of the studies included. Therefore, there might be a potential source of systemic dependence due to the heavy contribution by a single research group in the meta-analysis. Authorship dependence has been reported to impact effect sizes (Abou-Setta et al. 2019; Moulin and Amaral 2020; Singh et al. 2013). We therefore encourage the global community of weed scientists to assess water stress effects on weeds (using local water availability regimes, soil types, cropping systems, etc.). This will ultimately help to develop a more diverse, robust, reliable, and conclusive understanding of weeds' performance, population dynamics, and potential weed shift patterns in an altered climate.

- Water-stress effects on weed seed germination and seedling radicle length were mostly studied using PEG or D-mannitol solutions of varying osmotic potential in petri dishes. However, such solutions may not realistically represent soil–water–seed interactions occurring in fields. As a result, the observed effects on weed seed germination and seedling radicle length with PEG or D-mannitol solutions may not necessarily translate in field conditions. Thus, field-sampled soils are more suitable as test media compared with potting mix or solutions, in the interest of transferability. Supporting this hypothesis, Camacho et al. (2021) observed varying responses of seed germination of multiple weed and crop species between PEG versus soil test media as well as among different soil textural groups under the same water potentials. They further indicated that total seed germination is better characterized as a function of soil hydraulic conductivity rather than soil water potential. Therefore, if the goal is to test field seed germination with regard to soil moisture availability rather than determining the relative susceptibility of multiple weed or crop species to drought stress, future research should use soils of varying textures as test media.
- A systematic search of studies for meta-analysis identified most of the evidence base toward water-stress effects on weed seed germination/emergence. In total, water-stress effects on weed germination/emergence were investigated in 84% of the studies (i.e., $n = 73$ out of 86) accounting for 60% of the total observations (i.e., $n = 759$ out of 1,196) included in this meta-analysis. We only found a few studies that investigated water-stress effects on weed growth characteristics and seed production, thereby limiting detailed quantitative synthesis. For example, data were insufficient to elucidate how water-stress intensity expressed as soil water potential (ψ_{soil}) will impact weed seed germination, growth morphology, and fecundity under field conditions. We only found four ψ_{soil}-based water-stress studies that resulted in 77 observations for 12 weed indices. Out of 1,196 total observations, 62 studied root and shoot, and 77 studied inflorescence and weed seed production. Roots and shoots are important in assessing the impacts of water stress on plant functioning and seed production is important to assess the ability to reproduce; hence, we suggest conducting more ψ_{soil}-based water-stress studies (Singh et al. 2022) for investigating weed growth and especially seed production. Such studies will essentially unveil the relative fitness and adaptability of weeds to water stress compared with crops and will predict weed seedbank size and infestation in water-limited field conditions.
- Seed size and depth of occurrence in soil (burial depth) are the other important factors that influence the relative effect of water stress on weed germination/emergence (Cordeau et al. 2018; Tanveer et al. 2013). Larger seeds can have a greater advantage over smaller seeds, as they have higher food reserves, leading to greater emergence, rooting depth, and survival under increasingly dry conditions (Harrison et al. 2007; Leishman and Westoby 1994; Tanveer et al. 2013). Likewise, weed seeds that are buried deeper can exhibit a considerably greater emergence rate than seeds closer to or on the surface during dry soil conditions (Cordeau et al. 2018). Although we did not quantitatively address these factors in our meta-analysis due to limited consideration given to these factors in the included studies, exploring the role of covariates such as the average seed size of weed species and their burial depth could be a promising avenue for future research that supplements existing lessons from this meta-analysis.
- Plant functional characteristics such as leaf/root/seed traits govern their differential response to water stress across plant functional groups (Lopez-Iglesias et al. 2014). Leaf traits such as lower specific leaf area (Pérez-Ramos et al. 2013), and seed traits such as heavy and rapidly germinating seeds (Merino-Martín et al. 2017) favor drought survival. Similarly, the response of root traits to drought varies among plant functional groups, for example, grass weeds can increase their root diameter and specific root surface area and decrease root tissue density to produce thicker roots for better nutrient and water acquisition, while herbs can decrease their specific root surface area and root length to increase root carbon allocation and water uptake (Lozano et al. 2019). Essentially, droughts can modify plant communities, species distribution, diversity, and richness (Evans et al. 2011; Garssen et al. 2014; Olivares et al. 2015), and the magnitude of response to drought is determined by the distribution and composition of plant species and functional groups (Kuiper et al. 2014; Zweifel et al. 2009). It is therefore important to highlight, acknowledge, and understand the role of plant functional traits and their intraspecific as well as interspecific variations in mediating drought response. The existing literature has limited data on water-stress response of broadleaf versus grass weeds to their below- and aboveground growth characteristics as well as seed production. Future studies in weed science research communities should prioritize understanding the differential response of these general weed types to water-stress gradients. This is needed for the accurate and robust characterization of the shift patterns among weed species/functional groups in water-limited environments, thereby enabling us to design effective weed management programs for sustainable farming.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2022.59

Data Availability Statement. The raw data from this study are available upon request from the corresponding author.

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