BIOLOGY AND MANAGEMENT OF WEEDS AND INVASIVE PLANT SPECIES UNDER CHANGING CLIMATIC AND MANAGEMENT REGIMES

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BIOLOGY AND MANAGEMENT OF WEEDS AND INVASIVE PLANT SPECIES UNDER CHANGING CLIMATIC AND MANAGEMENT REGIMES

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EDITORIAL
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Editorial: Biology and Management of Weeds and Invasive Plant Species Under Changing Climatic and Management Regimes

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Keywords: climate change, weed biology, weed ecology, invasive plants, weed management

Editorial on the Research Topic

Biology and Management of Weeds and Invasive Plant Species Under Changing Climatic and Management Regimes

The global climate is changing rapidly. Rising levels of atmospheric carbon dioxide, erratic precipitation, and warmer temperatures have significant effects on biology and distribution of plant species. These climatic changes are also known to alter biology, distribution, interference potential, and management of weeds and invasive plant species (Varanasi et al., 2016; Ziska, 2016; Matzrafi, 2018; Chauhan, 2020; Rice et al., 2021). The objective of this Research Topic is to advance our understanding of the impact of rapidly changing climatic and management regimes on biology, ecology, and management of weeds and invasive species. We accepted five research articles and four review articles contributed from six countries of Asia-Pacific, Europe, and North America. The key focus of these contributions is on how climatic changes impact emergence, establishment, adaptive evolution, and management of some of the most problematic weeds and invasive species.

The ability to successfully germinate and establish early under harsh conditions was recognized as a key adaptive strategy for many weeds and invasive species under changing climate in this Topic. For instance, Yair et al. investigated the germination ecology and growth behavior of three *Ambrosia* weed species under temperature stress in Israel. They reported that *Ambrosia confertiflora* showed a dramatic shift from a naturalized to invasive species status and it outperformed other species under high temperature stress. Further, rapid growth and fast sprouting were suggested to be the contributing factors for superior competitive ability and stress tolerance in this species. In another study, Matzrafi et al. documented the current invasion status of *Parthenium hysterophorus* in Israel and they also studied the life cycle and biology of a local population of this species. New invasions were recorded in several locations across the northern part and Mediterranean coastal plain of Israel. The optimal temperature range (15–25°C) and soil depth (0–3 cm) for germination were also reported in this study. Shading was found to be a limiting factor for biomass accumulation, height, and flowering in *P. hysterophorus*. From Australia, Wu et al. studied the seed biology of *Panicum capillare* and found that germination was stimulated by light and was better at both constant and alternating temperatures over 20°C. They found that seeds of *P. capillare* were fairly persistent in the soil seedbank (up to 4 years) and can germinate under high moisture stress/low water potential (-0.48 MPa). These studies suggest that weeds can quickly adapt to changing environmental conditions to ensure their successful emergence and establishment which contributes toward their invasion success.

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The role of different ecological, physiological, and genetic traits in adaptive evolution of weeds under changing climate is also well-explored in this Research Topic. In a review article, Clements and Jones argued that accelerated climate change is causing rapid evolution in many weeds through multiple evolutionary mechanisms such as genetic modifications, changes in plant morphology, phenology and physiology, and niche shifts. The authors suggested that this rapid evolution could enable range expansion of many weeds and invasive plants while making their management a challenge. In another review, Rutland et al. suggested that future climatic changes may favor polyploid species; however, limited data are available for weedy species to make meaningful speculations in this regard. Thus, authors proposed that understanding of genomics and molecular biology of polyploid species will help elucidate weed adaptation to climate change. In recent years, several agronomically important weed species have been sequenced and the data are made publically available. Such data will help decipher the genes that help weedy species to cope with harsh climatic conditions. Stallworth et al. screened a mini germplasm collection of weedy rice/red rice (*Oryza sativa* spp.), and found that certain accessions may possess traits to withstand heat stress as well as perform well under submerged conditions, enabling this problematic weed to thrive under severe conditions. They proposed that these accessions could be used in breeding programs to develop cultivated rice varieties suitable for future climate. Adhikari et al. assessed the variability and heritability of different phenotypic functional traits within distinct populations of *Anthemis cotula* (from different land-use and geographic conditions) in the Pacific Northwest region of the USA. The authors noted significant variations within populations with high heretability, suggesting that weed populations can adapt quickly under different climatic and management regimes, making the task of management more difficult.

There is reasonable literature available on generalistic impacts of climate change on weed dynamics in agroecosystems, but the region-specific information for some of the most vulnerable areas has been scarce. Marambe and Wijesundara reviewed the current and potential impacts of climate change on spread, interference and management of numerous weeds and invasive plants in an agricultural context in Sri Lanka. They stressed that agroecosystem of the Island nation are under extreme pressure of biological invasions in the wake of rapid climatic changes and therefore, comprehensive risk assessment systems and coordinated management efforts are urgently needed. Finally, a collaborative article by weed scientists from Switzerland and Iran addressed the contentious, yet important topic of the lack of collaboration between the disciplines of weed science and invasion ecology in addressing the climate change impacts (Sun et al.). They argued that a more inter-disciplinary approach with better knowledge sharing could help mitigate the climate-mediated biological invasions and failing weed management crises.

In conclusion, weed scientists across the world, recognize the impacts of climate change on weed management and invasion. There is a need to further understand the fundamental biological mechanisms which enable weeds' success as well as future proofing for integrated weed management programs. In recent years, considerable emphasis has been given to understand basic aspects of biology and ecology of weedy and invasive species. However, the need for further work in a climate change context is imminent.

AUTHOR CONTRIBUTIONS

AB, MM, and MJ contributed equally in organizing this Research Topic and writing this editorial based on the contributed articles. All authors contributed to the article and approved the submitted version.

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ORIGINAL RESEARCH
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Differential Germination and Growth Response to Temperature of Three *Ambrosia* Weed Species—Implications for Future Spread

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Three main *Ambrosia* species (Ragweed) grow in Israel; the most abundant invasive *Ambrosia confertiflora* DC, whereas *A. artemisiifolia* L. and *A. tenuifolia* Spreng., are of restricted distribution. The present research was aimed to study the effect of temperatures regimes on the development and growth of these *Ambrosia* species, to elucidate the environmental conditions and plant traits that affect their growth and infestation patterns. All three *Ambrosia* species germinate best in light from the soil surface with no prerequisite of a stratification period. *A. confertiflora* seed emergence is inhibited at high temperature regimes (28/34°C). *A. artemisiifolia* at low temperature regimes (10/16°C), while *A. tenuifolia* is less affected by the temperature regimes. *A. confertiflora* plant height increases with increasing temperatures, and at lower temperatures develops a rosette. Root and rhizome biomass were less affected by the different temperatures regimes; *A. artemisiifolia* aboveground mass was not affected by temperature regimes while *A. tenuifolia* aboveground mass was reduced only at lower temperatures. *A. confertiflora* fast invasion and establishment are due to the combined effects of prolific seed dispersal, rapid sprouting and growth, and its phenotypic plasticity.

Keywords: *Ambrosia artemisiifolia*, *A. confertiflora*, *A. tenuifolia*, invasive weeds, plant biomass, plant emergence, ragweed, seed germination

INTRODUCTION

Biological invasions are a main threat to biodiversity in terrestrial, freshwater, and marine ecosystems, requiring extensive research and management efforts (Mačić et al., 2018). Invasive species are defined as animals, plants, or other organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species. *A. artemisiifolia* is known throughout the world as an invasive weed and in many countries it causes severe damages to agriculture and substantial health effects to millions of people, due to its high allergenic properties (Makra et al., 2005, 2014; Bullock et al., 2012; Montagnani et al., 2017; Schaffner et al., 2020). In Israel there are five Ambrosia species, but only *A. confertiflora* is defined as an invasive species (Dufour-Dror, 2016; Yair et al., 2019).

The origin of most Ambrosia species is in the Americas and they spread mainly by global commerce to Europe, Asia and Australia. The genus Ambrosia belongs to the Asteraceae family (Compositae) and includes 42 species (Strother, 2006). *Ambrosia* plants are annual or perennial monoecious with wind-pollinated flowers producing achenes. The wind-borne pollen grains cause severe allergenic response in humans and animals. The perennial species propagate by achenes and by underground rhizomes.

There are five *Ambrosia* species in Israel, which were detected in the early 1990's (Danin, 1994; Yair et al., 2017). Species details and characteristics are summarized in **Table 1**. The invasive perennial species *A. confertiflora* DC (Burr ragweed), is the most abundant in Israel, mainly found in Central Israel; Three naturalized perennial species *A. tenuifolia* Spreng; (Lacy ragweed) is found in several locations but its spread is limited; *A. psilotachya* DC (Cuman ragweed or Perennial ragweed and *A. greyi* (wooly leaf bur ragweed) are restricted to one location only. The fifth species *A. artemisiifolia* L. (short ragweed, common ragweed) an annual casual plant that appears in several sites but manages to survive only in the Hula Lake Natural Reserve in northern Israel. The causes of *Ambrosia* spp. invasions in Israel are mainly anthropogenic and are believed to originate with shipments of grain for food, feed and oil production from the USA. *A, confertiflora* is hardly studied. This perennial species originated in South-West US to Central Mexico and is invasive in Australia (Watt, 1987) and Israel (Yair et al., 2019), and may have a spread potential in south Europe (Tanner et al., 2017). *A. confertiflora* is a highly variable and complex erect plant, reaching up to 3 m in height, (Payne, 1964; Whisenant, 2018), which produces both achenes and rhizomes that create dense sprouts. The plant produces numerous viable hooked prickled achenes (1-2 mm long, as described in Yair et al., 2019) that are easily dispersed by animals and humans. *A. tenuifolia* produces rhizomes and achenes but the latter are non-prickled, hardly viable and thus their low dispersion potential (Yair et al., 2019).

Research regarding biological invasions and traits is mainly related to the *A. artemisiifolia* species that produces many achenes, 3,000–62,000 per plant (Dickerson and Sweet, 1971; Fumanal et al., 2007). Germination of seeds is optimal at soil level, decreases between 2 and 8 cm depth while in 10 cm depth no germination is observed, thus seed burial by deep tillage can reduce seed germination (Bassett and Crompton, 1975; Guillemin and Chauvel, 2011). Seeds of *A. artemisiifolia* require stratification at 4°C for 8 weeks or more and for maximum germination there is a preference for alternating temperatures and light (Willemsen and Rice, 1972; Willemsen, 1975). The minimum temperature requirement for germination is 5°C (Baskin and Baskin, 1980) and at optimal conditions, germination begins at 2 days (Ortmans, 2016). Seeds possess secondary dormancy (Bazzaz, 1970, 1979) and can germinate even after 40 years (Baskin and Baskin, 1977; Telewski and Zeevaart, 2002).

The aim of this research was to study the effect of temperature on the development and growth of *A. confertiflora* compared to the other *Ambrosia* species present in the Israeli flora, to elucidate the environmental conditions and plant traits that may explain the rapid distribution and vast infestation of *A. confertiflora* in Israel.

MATERIALS AND METHODS

Germination and Emergence Experiments

Plants and seeds of the three *Ambrosia* species *A. confertiflora*, *A. artemisiifolia,* and *A. tenuifolia*, were collected from various open field areas between the years 2009–2014 and kept dry in paper bags at 4°C until use. For germination experiments, seeds were germinated in Petri dish on various substrates: Whatman No. 1 filter paper, sea sand, vermiculite, perlite, Rehovot sandy soil, and commercial potting soil (Tuff Merom Hagolan). Following the finding that the best substrate for germination was Whatman No. 1 filter paper, all experiments were conducted on two layers of this filter paper in 9 cm Petri dish, moistened with 500 microliter tap water, sealed with Parafilm and placed in a 25/18°C 16d/8n growth chamber. No germination in Petri dishes wrapped with aluminum foil to prevent light penetration was recorded hence all other experiments were conducted under light condions. Seeds were determined germinated once the radicle length reached the length of the achene.

For depth emergence experiments, plastic boxes (18 × 14 × 10 cm L/W/H) filled with sieved Rehovot sandy soil (1.2% clay, 3.3 % silt, 95.5% sand, 0.2% organic matter, pH 7.5) were used. For each box seeds of fifty *A. confertiflora*,

TABLE 1 | Ambrosia species present in Israel and their characteristics.

Ambrosia species	Common name	Origin	Annual/ perennial	First identified in Israel	First HUJI herbarium collection*	Invasive stage in Israel
A. confertiflora DC.	Burr ragweed	South-West USA and Mexico	Perennial	1990	1990	Invasive
A. tenuifolia Spreng.	Lacy ragweed	South- America	Perennial	1990	1951	Naturalized
A. artemisiifolia L.	Common/short ragweed	North America	Annual	1999	1925	Casual
A. psilostachya DC.	Western/perennial ragweed	North America	Perennial	2017	2007	Naturalized
A. grayi Shanner	Wooly leaf bur ragweed	South USA	Perennial	2017	2017	Naturalized

**The Herbarium of The Hebrew University of Jerusalem, Israel.*

or 20 *A. artemisiifolia* or *A. tenuifolia* were separately sown in rows at 0, 1, 2, 3, 4 cm soil depth, and placed in the phytotron under the following temperature regimes: 10/16°C, 16/22°C, 22/28°C, and 28/34°C night/day temperatures which represent the four seasons in the Mediterranean region. Pots were randomly placed, watered by hand with no fertilizer for 55 days. Emerging seedlings were recorded on a weekly basis.

Plant Development

For *Ambrosia* biomass experiments, four to six leaf *A. confertiflora*, *A. artemisiifolia,* and *A. tenuifolia* seedlings from

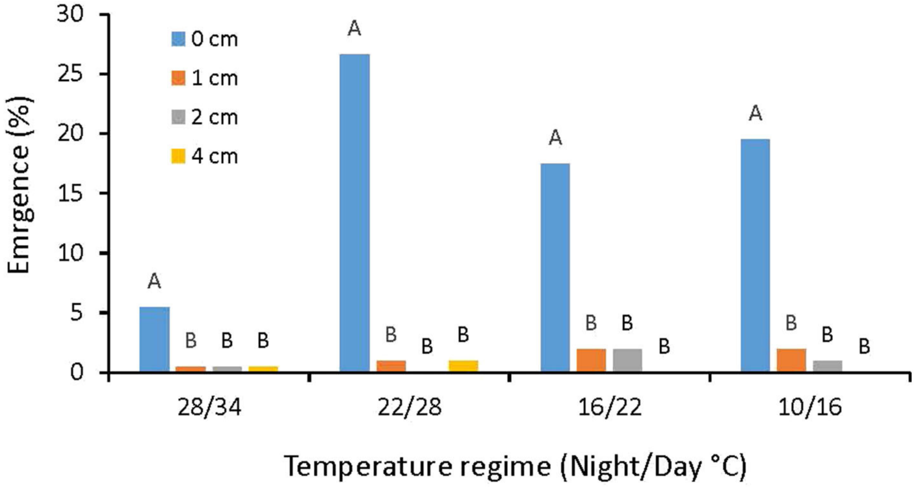

FIGURE 1 | *A. confertiflora* emergence rate at four temperature regimes, 55 DAS. Columns within each temperature regime topped by different letters are significantly different according to Tukey-Kramer HSD, $p = 0.05$.

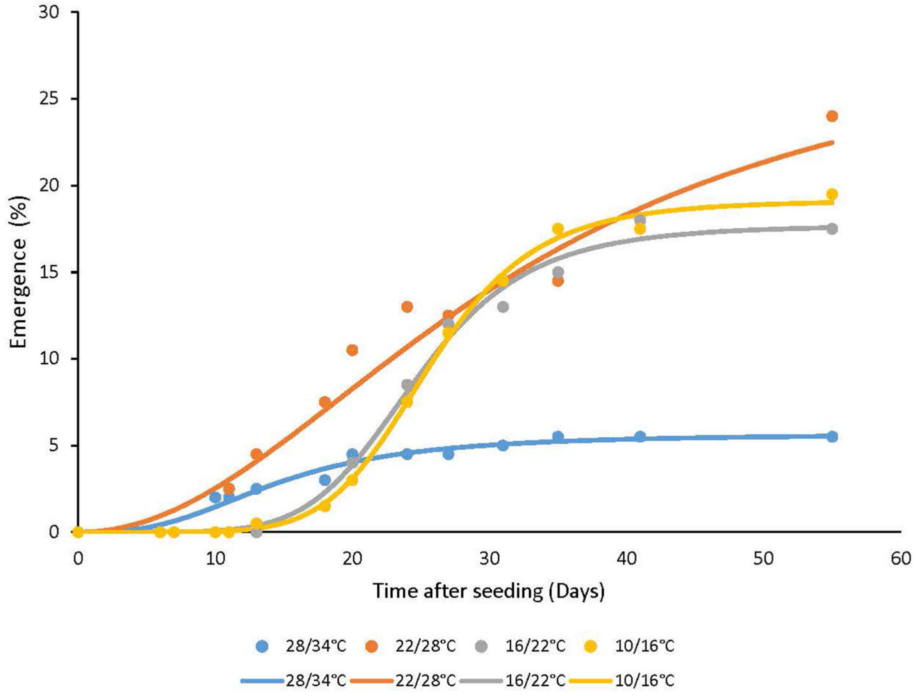

FIGURE 2 | The effect of temperature regimes on the seedling emergence rate of *A. confertiflora.* Seed placed on the soil surface (0 cm seeding depth), 55 DAS. Three-parameter logistic nonlinear regressions between *A. confertiflora* emergence and time (days) were used. Parameters of the equations of four temperatures regimes are presented in **Table 2**.

each species, were transplanted into 3.9 L plastic pots filled with potting soil and placed in the phytotron under four temperature regimes as described above. Eight pots (= 8 replicates) were transferred to each temperature regime. Pots were randomly placed and watered by hand for 121 days. Weekly measurements of plant height, sprout number, inflorescence development and final plant mass (shoot, root, and rhizomes) were conducted. The fresh weight of plants parts was determined at harvest and the dry weight after placing the plants in an oven for 3 days at a temperature of 60°C. For convenience all results are presented in fresh weight.

Rhizome Development

To determine rhizome sprouts development of the two perennial species *A. confertiflora* and *A. tenuifolia,* 10 replicates of a single 6–8 leaf stage plant were transferred into the center of 50 × 30 × 6.5 cm plant trays containing potting soil, trays placed in the Faculty of Agriculture net-house in Rehovot, Israel. The Number of sprouts was recorded weekly until 111 DAS.

We conducted two experiments in the net-house at the same time of year- August to November in two subsequent years. The average of the two experiments is presented in the results.

Statistical Analysis

All experiments were conducted in a complete random design, repeated at least twice with five to six replications. The results were combined and analyzed as 10–12 replications. Analysis of variance was computed and means were compared using Tukey Kramer HSD test ($P \leq 0.05$) using JMP ver. 13.0 (SAS Institute Inc. USA). When data were naturally quantative, a three-parameter nonlinear logistic equation was fitted using Sigma Plot 10 (SYStat Software, Inc. California, USA) (Ephrath et al., 2012):

$$f(x) = a/\left[1 + \left(\frac{x}{x_{50}}\right)^{b}\right]$$

Where f (x) represents the number of *Ambrosia* spp. emergence, a represents the upper asymptote (maximum emergence), x_{50} represents the time when Y is 50% of maximum, and b represents the slope at x_{50}.

RESULTS

Germination and Emergence Rates

In our Petri dish study, both *A. artemisiifolia* and *A. confertiflora* did not show a dormancy period thus do not require stratification. Attempts to enhance seed germination by physically cracking the seed coat, soaking in sodium

TABLE 2 | Three-parameter logistic nonlinear regressions between *A. confertiflora* emergence and time (days).

Temperature regime (°C)	Coefficient parameters									Regression	
	a^{a}	SE(a)	P(a)	b^{b}	SE(b)	P(b)	x_{50}^{c}	SE(x_{50})	P(x_{50})	*p*	RMSE
28/34°C	5.6579	0.3523	<0.0001	−2.8431	0.4969	0.0001	14.5239	1.1303	<0.0001	<0.0001	0.4058
22/28°C	29.832	6.8958	0.0012	−2.0522	0.4415	0.0007	31.9	8.1417	0.0024	<0.0001	1.6267
16/22°C	17.7054	0.5545	<0.0001	−6.0252	0.6007	<0.0001	24.6885	0.4946	<0.0001	<0.0001	0.653
10/16°C	19.1307	0.3158	<0.0001	−6.6298	0.3587	<0.0001	25.6337	0.2524	<0.0001	<0.0001	0.3773

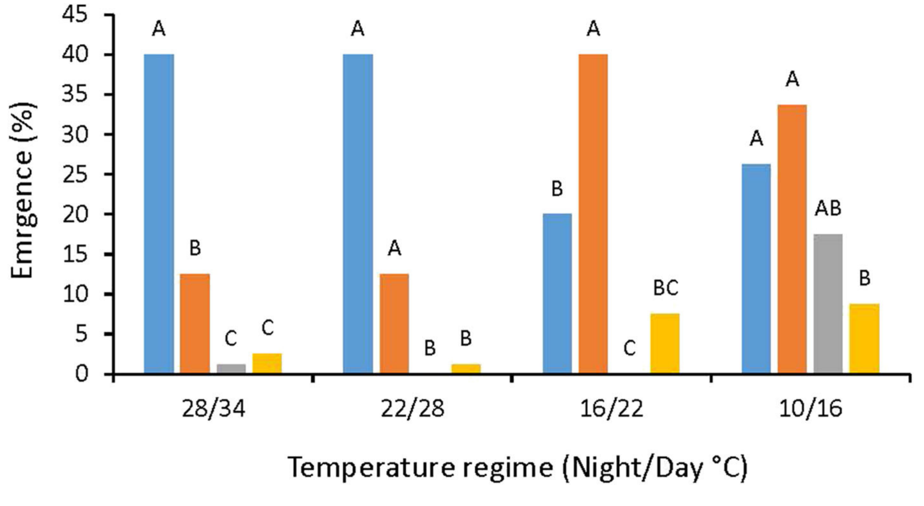

FIGURE 3 | *A. artemisiifolia* emergence rates at four temperature regimes, 55 DAS. Columns within each temperature regime topped by different letters are significantly different according to Tukey-Kramer HSD, $p = 0.05$.

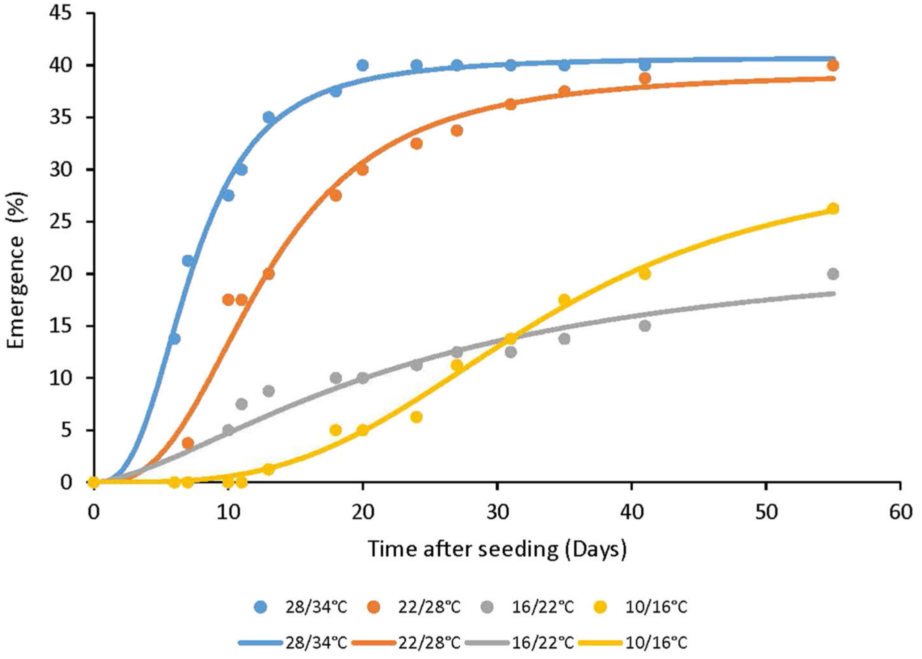

FIGURE 4 | The effect of temperature regimes on the seedling emergence rate of *A. artemisiifolia.* Seeds were placed on the soil surface (0 cm seeding depth), 55 DAS. Three-parameter logistic nonlinear regressions between *A. artemisiifolia* emergence and time (days) were used. Parameters of the equations of four temperatures regimes are presented in **Table 3**.

TABLE 3 | Three-parameter logistic nonlinear regressions between *A. artemisiifolia* emergence and time (days).

Temperature regime (°C)	Coefficient parameters									Regression	
	a^{a}	SE(a)	P(a)	b^{b}	SE(b)	P(b)	x_{50}^{c}	SE(x_{50})	P(x_{50})	*p*	RMSE
28/34°C	40.7651	0.545	<0.0001	−2.8342	0.2305	<0.0001	7.3104	0.1745	<0.0001	<0.0001	1.0761
22/28°C	39.374	1.7054	<0.0001	−2.7855	0.3875	<0.0001	12.7226	0.732	<0.0001	<0.0001	2.1861
16/22°C	23.0644	6.5453	0.0048	−1.5515	0.4687	0.0069	23.9257	10.1024	0.0373	<0.0001	1.7498
10/16°C	30.9158	2.253	<0.0001	−3.3108	0.3165	<0.0001	33.109	1.8343	<0.0001	<0.0001	0.8146

hypochlorite, ethanol or gibberellic acid, were not successful. Seed germination initiated 2–3 days after seeding (DAS) and reached the maximum rate at 10 DAS. The average germination rate of *A. confertiflora* in Petri dish in light conditions was 40 and 56% for *A. artemisiifolia*. In dark conditions, *A. confertiflora* germination rate was only 0.4% and for *A. artemisiifolia* only 22%, indicating that both *Ambrosia* species require light for germination as was found at (Baskin and Baskin, 1980).

The achenes of these species do not require stratification for germination and stratification did not increase germination rate. Achenes of the plant germinated immediately after maturing and harvest. Dry achenes maintained viability for a long period. Three out of four *A. confertiflora* achenes collected by A. Danin in Yamit, Sinai in 1981 and kept at the Jerusalem Herbarium, successfully germinated in our studies 35 years later and produced viable plants.

The emergence of *A. confertiflora* achenes (seeds) in the pot experiment started 6 days after seeding and the highest emergence rate of 30% was recorded in the 10/16°C regime when the achenes were placed on the soil surface exposed to light. At this temperature regime, the burial of seeds at 1 cm depth was sufficient to drastically reduce seed emergence to 2% and at 4 cm depth, no emergence was recorded at all, indicating the importance of light for *A. confertiflora* emergence (**Figure 1**).

Seed emergence of *A. confertiflora* placed on the soil surface was inhibited at the highest temperature regime resulting in ca 5% emergence after 55 DAS, whereas at the lower temperature regimes the accumulated seed emergence rate reached a maximum of 28% at 55 DAS (**Figure 2**).

The other perennial species, *A. tenuifolia,* that under field conditions produces a very low number of viable seeds, which in pots poorly germinated mainly from the soil surface (data not shown). *A. artemisiifolia* achenes which are bigger than those of other tested *Ambrosia* species, were less affected by the depth of seeding and germinated even from 4 cm depths (**Figure 3**). *A. artemisiifolia* achenes emergence rate from the soil surface was higher in high temperatures regimes (28/34°C, 22/28°C) as compared to lower temperatures regimes (10/16°C and 16/22°C), and started 6 days later than in the higher temperature regimes (**Figure 4**).

Ambrosia Plant Development

Ambrosia species respond differently to different temperature regimes. Stem elongation differences were most evident in *A. confertiflora* as compared to *A. tenuifolia* and *A. artemisiifolia*, particularly at the two highest temperature regimes (**Figure 5**). Hence, at 100 DAS and 28/34°C regime *A. confertiflora* plants reached an impressing height of more than 180 cm (average height of 140 cm), whereas at the lowest temperature regime (10/16°C), the stem elongation was dramatically inhibited remaining at the rosette stage. Plant height of *A. tenuifolia* and *A. artemisiifolia* was less affected by the temperature regimes (**Figure 5**). *A. tenuifolia* plants were significantly shorter only at the lowest temperature regime, while in the *A. artemisiifolia* there was almost no effect to changes in temperature. *A. confertiflora* and *A. artemisiifolia* plants reach their maximal height at 60-80 DAS while *A. tenuifolia* maximal elongation was recorded at 100 DAS (data not shown).

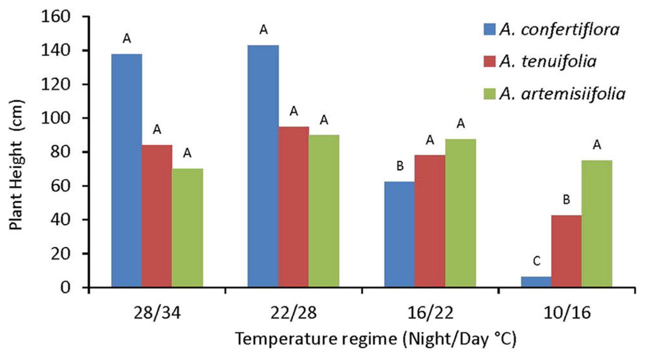

FIGURE 5 | The effect of temperature regimes on plant height of *A. confertiflora*, *A. tenuifolia* and *A. artemisiifolia* at 121 DAS. Within a species (color), columns topped by different letters are significantly different according to Tukey Kramer HSD, $p = 0.001$.

The perennial species (*A. confertiflora* and *A. tenuifolia*), did not flower under long-day conditions throughout the current study. In contrary, flowering and fruit set were recorded in *A. artemisiifolia* as early as 25 DAS, in spite the fact that it is a short-day plant (Ziska et al., 2011), perhaps due to the reported short juvenile period in which it is not affected by day length (Deen et al., 1998).

Shoot biomass of the annual *A. artemisiifolia* was not affected by temperature, whereas the shoot biomass of *A. confertiflora* and *A. tenuifolia* was significantly reduced by the coldest temperature regime (**Figure 6**).

In the perennial species, underground biomass (roots and rhizomes) was not affected by the temperature regimes, while the underground biomass (roots only) of the annual species was dramatically increased when grown under the coldest regime (10/16°C) (**Figure 7**). Thus, in order to elucidate the effect of temperature on resource allocation, we compared the effect of temperature on the ratio of underground/aboveground biomasses of the different species. The data presented in **Figure 8** demonstrate that all tested species directed more resources to the underground organs as temperatures decline. This phenomenon was most evident in the annual *A. artemisiifolia* grown in the coldest conditions (10/16°C) that diverted 6-fold more resources to the roots than to the shoot. For *A. confertiflora* and *A. tenuifolia* the temperature effect was more moderate: the ratio was 2-3 in the coldest temperature regime and decreased to 0.5 in the warmest temperature regime (**Figure 8**).

Sprout Development

Sprouts develop from rhizomes in the perennial species *A. confertiflora* (**Figure 9**) and *A. tenuifolia* only, and not in the annual *A. artemisiifolia.* In the net-house experiments conducted during the summer and fall (August-November),

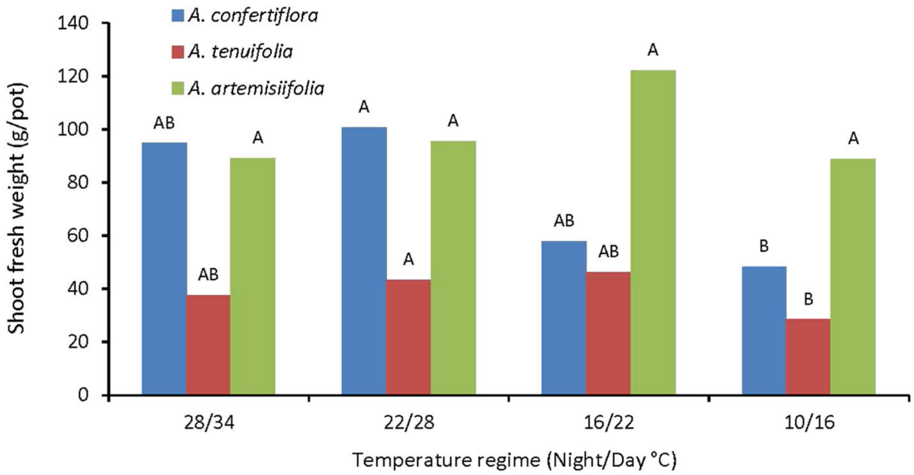

FIGURE 6 | The effect of temperature regimes on the shoot fresh weight of *A. confertiflora*, *A. tenuifolia,* and *A. artemisiifolia* 121 DAS. Within a species (color), columns topped by different letters are significantly different according to Tukey Kramer HSD, $p = 0.001$.

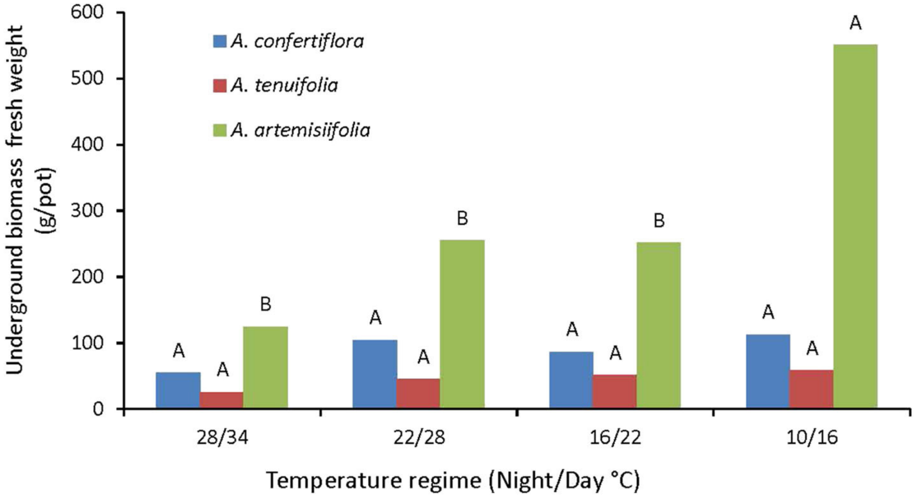

FIGURE 7 | The effect of temperature regimes on the underground biomass accumulation of *A. confertiflora*, *A. tenuifolia,* and *A. artemisiifolia* 121 DAS. Within a species (color), columns topped by different letters are significantly different according to Tukey Kramer HSD, $p = 0.001$.

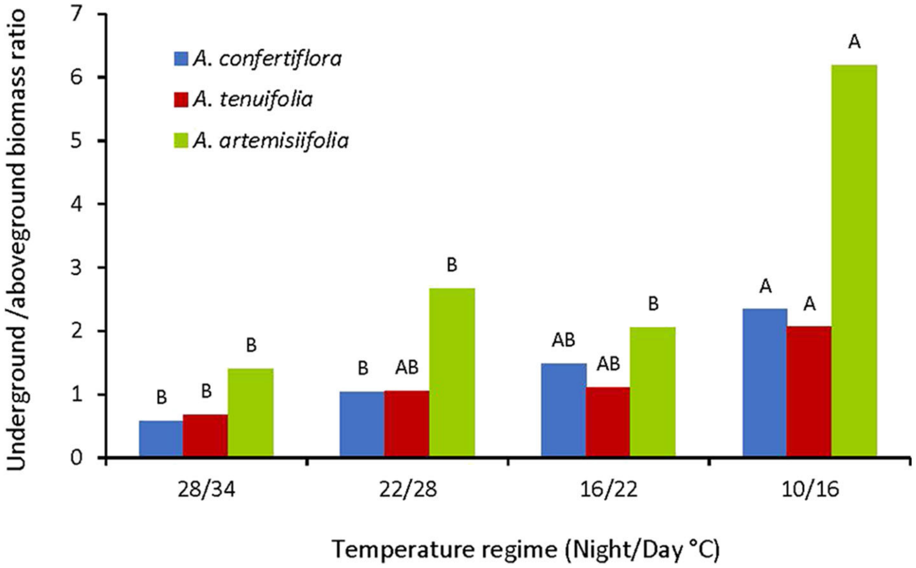

FIGURE 8 | Effect of temperature regimes on underground/aboveground biomass ratio of *A. artemisiifolia, A. confertiflora,* and *A. tenuifolia* 121 DAS. Same colored bars topped with a same letter are not significantly different according to Tukey-Kramer HSD, $p = 0.05$.

sprouts first emerged from soil 25 DAS in both species. The average accumulated number of *A. tenuifolia* sprouts that developed from one mother plant at the end of the experiment (111 DAS) was five-fold higher than the number of sprouts that developed in *A. confertiflora*, 250 and 50, respectively (**Figure 10**).

DISCUSSION

This research elucidates the effect of temperature regimes on the early development and growth of three *Ambrosia* species that are in various distribution-status in Israel. The depth of seed placement in the soil strongly affects the germination and emergence of the three species: the seeds germinate well from the soil surface and up to 2 cm depth, as found also by Martínez et al. (2002). As these small seeds are placed deeper than 2 cm their emergence rate decreases accordingly (Farooq et al., 2019). The germination of *A. confertiflora* seeds are exceptionally sensitive to burial depth and they hardly emerge from more than 1 cm depth, while the bigger seeds of *A. artemisiifolia* possess more resources enabling them to emerge from deeper soil levels (2–4 cm), but as reported earlier they cannot emerge from depths >10 cm (Bassett and Crompton, 1975; Guillemin and Chauvel, 2011; Farooq et al., 2019). In contrast with other reports (Bazzaz, 1970, 1979; Willemsen and Rice, 1972; Willemsen, 1975; Baskin and Baskin, 1977, 1980; Leiblein-Wild et al., 2016), our germination studies showed that there is no need for stratification or other procedure to break the dormancy of *A. artemisiifolia*.

The two invasive species, *A. confertiflora* in Israel and *A. artemisiifolia* in Europe, demonstrate a higher phenotypic plasticity response to different temperatures, a common trait of invasive species. The effect of different temperatures on *A. confertiflora* and *A. artemisiifolia* seed germination is inverse: high temperatures reduce *A. confertiflora* germination rate and percentage, while the opposite occurs in *A. artemisiifolia* seeds as reported also by Gentili et al. (2019). As an annual plant, *A. artemisiifolia* is dependent mainly on the efficacy of seed germination and emergence for further favorable vegetative and reproductive growth (Gentili et al., 2019). The three examined *Ambrosia* species exhibit retarded growth in response to low temperatures, but *A. confertiflora* response to these low temperatures is the most extreme, leading to an increase in underground organs build-up, rosette formation and sprouting, while as temperature increases the stem elongates but the leaf number remains unchanged.

FIGURE 9 | Sprouts of a single *A. confertiflora* rhizome that developed from a plant grown in a tray in the summer in the net-house 121 DAS.

The two invasive *A. artemisiifolia* and *A. confertiflora* species have an interesting strategy of energy allocation following low temperatures to their underground plant parts (roots in *A. artemisiifolia* and rhizomes in *A. confertiflora*). In both *A. confertiflora* and *A. artemisiifolia* underground biomass increases 2 and 6-folds, respectively, in comparison to their above-ground mass. This ensures that plant resources are directed for supporting the establishment in soil under cold temperature periods. The annual short-day *A. artemisiifolia* plant grew rapidly, produced inflorescences and flowered 25 DAS, whereas *A. confertiflora*, did not flower throughout the four-month-long experiment. The high necessity to flower is not surprising as flowering is the sole way of reproduction of this annual plant, whereas the perennial *Ambrosia* species that reproduces also by sprouting is less dependent on seed production.

A. tenuifolia is not an invasive plant in Israel albeit the very high number of sprouts it rapidly produces. This is probably due to its less aggressive development in comparison to *A. confertiflora* and the fact that it produces a very low number of seeds, probably due to self-incompatibility (Friedman and Barrett, 2008). Furthermore, the seeds that are produced lack spines and are not dispersed by animals.

The naturalized *A. artemisiifolia* species is rapidly invading and spreading in Europe, Asia, and Australia. This annual invasive species successfully competes with local plant species due to its resistance to abiotic stresses, and its effective production and dispersion of viable achenes. Despite the sporadic detection of this species in Israel, *A. artemisiifolia* does not survive due to the dry summer in which the

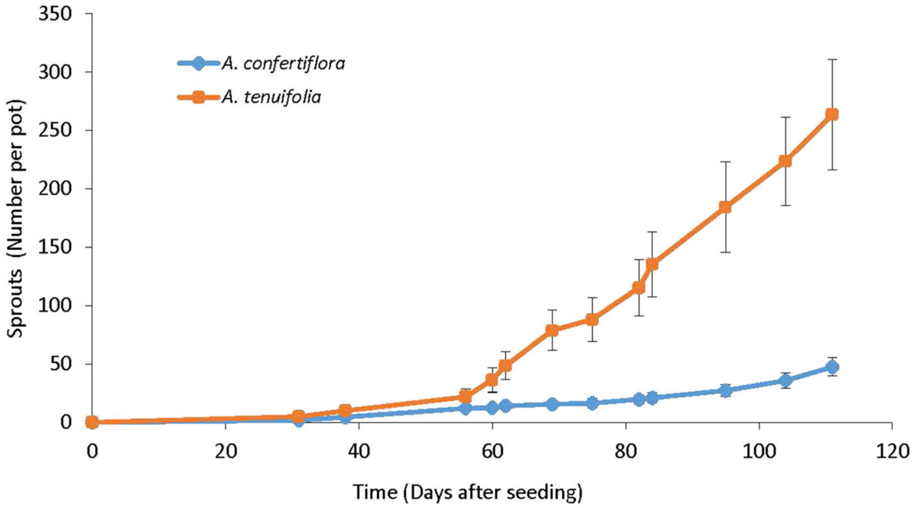

FIGURE 10 | Accumulated number of *A. confertiflora* and *A. tenuifolia* rhizome sprouts that developed over time in pots in the net house from August to November, 111 DAS. Error bars represent the Standard Error of the means.

seedlings dry up and die. These plants can fit themselves to reduced moisture (Leiblein-Wild et al., 2014), but not to complete dryness such as the arid conditions in the Israeli summer. In highly moist conditions as in the reclaimed Hula Valley natural reserve in North-East of Israel, *A. artemisiifolia* grows rapidly and produces viable achenes, endangering the natural reserve and the neighboring irrigated agricultural fields (Yair et al., 2019).

The *A. confertiflora* species was first recorded in Israel in 1990 (Danin, 1994) and underwent a population explosion in less than 15 years (Yair et al., 2019), thus shifting from a naturalized to an invasive plant status. Several plant characteristics are responsible for this dramatic shift: fecundity, with the production of a vast number of viable achenes, easily caught on animal fur and other objects; ease of dispersion by man, farm equipment and the transportation of contaminated soil as well as rapid and long-distance seed transportation through water canals, streams and rivers (Yair et al., 2017). Additionally, rapid growth and fast sprouting contribute to its high competition with neighboring plants, resistance to temperature stress and growth plasticity may explain its rapid distribution and its establishment on river banks and fields adjacent to waterways.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BR, YY, and HE conceptualized and designed the overall study. YY, YG, and MS conducted the experimental work. YY, YG, MS, HE, and BR analyzed the data, wrote, and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Addressing Climate Change: What Can Plant Invasion Science and Weed Science Learn From Each Other?

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Plant invasion science and weed science, both dealing with harmful plants, have historically developed in separation. This may also be true for how the two fields are addressing the consequences of future climate change. Here, we first conducted a literature survey to explore how researchers in these two disciplines study the effects of climate change, and then identified their characteristic approaches to determine what the disciplines can learn from each other to better understand, predict, and mitigate the outcomes of responses of harmful plants to climate change. Over the past 20 years, we found a much steeper increase in publications dealing with climate change for invasive alien plants (IAP) than for weeds. However, invasion scientists have to date only rarely investigated climate change effects at the local scale, such as on functional traits and population dynamics. In contrast, weed science could benefit from studies at larger scale, such as using a modeling approach to predict changes in weed distributions. Studies assessing the impacts of the target plants on ecosystem properties and on society, and on their management under climate change are important components of weed studies but remain neglected for IAP. This is despite an urgent need, especially because under climate change, abandoned cropland, and areas of high conservation value are facing increasing risk from IAP. We argue that the strengths and diversity of approaches of these two disciplines in studying the effects of climate change are complementary and that closer ties between them would be highly beneficial for both.

Keywords: impact, invasive alien plants, literature survey, management, publication metrics, research questions, study method, weeds

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INTRODUCTION

Plant invasion science is a relatively new research field dealing with the causes and consequences of organisms introduced into and invading areas outside their native range, and in the case of plants, mostly on species that conquer semi-natural and natural ecosystems. It is mainly driven by fundamental scientific questions and ecological theories, also by the practice of conservation, with a focus on community, ecosystem, and biogeography (Kueffer et al., 2013). In contrast, weed science has a long tradition supported by agronomy with good links to the private sector, and is mainly driven by practical management and control questions, and innovations in agricultural engineering (Hall et al., 2000; Fernandez-Quintanilla et al., 2008; Jordan et al., 2016). Its main focus is on cultivated land (i.e., the land used for producing major food and animal feed, including perennial crops and managed grassland) and the reduction of biomass at a site. This distinct history, focus, and approach between the two disciplines have recently been further elaborated by Müller-Schärer et al. (2018). Here we hypothesize that these differences between the two disciplines might also be evident on how consequences of future climate change for harmful plants and their management are being addressed. We acknowledge that both invasion and weed science also deal with harmful plants at historical places, in cities, and along linear transport structures, such as roads, railway tracts, and rivers, although not being their main focus. To account for and repeal this overlap, we excluded these habitat types in our literature survey.

Anthropogenic climate changes driven by greenhouse gas emissions include increases in temperature and CO_2 emissions, changing patterns of precipitation and the severity, and frequency of extreme climatic events (i.e., drought, flood, fires, intense storms, and heat waves). These changes are predicted to select on means and plasticities of plant traits and vital rates to better cope with these changing environmental conditions, with consequences for competitive interactions, local abundances, spread and impact on plant communities and ecosystems, and ultimately on ecosystem services and people's livelihoods (Vilà et al., 2007). Climate change, especially effects of increased CO_2 and temperature have been postulated to affect weed germination, emergence pattern, their competitive ability, and thus, also crop yield, but yet few studies experimentally addressed climate change effects on weed growth, water limitations, or herbicide efficiency (Ziska, 2016). Decreasing efficiency of herbicides under climate change may lead to an increased risk for the evolution of herbicide-resistant weeds (Matzrafi et al., 2016). Thus, for both invasive alien plants (IAP in the following) and weeds, these changes will also create a need for adapted control strategies as part of mitigation planning (Chauhan, 2020). This offers a wide range of climate features to elaborate upon, a variety of study questions and methods, and a multitude of impacts and outcomes to study, ranging from changes in functional traits, population dynamics, and distribution of the harmful plants up to their consequences for crop yield and ecosystem services. Here, we first conduct a literature survey to explore if and how studies on IAP differ from crop and grassland weeds when considering effects of climate change. These findings allow us then to identify the strengths and gaps, as well as the commonalities and differences when studying climate change effects in these disciplines, and to derive what can be learnt from each other for understanding, predicting, and mitigating outcomes of climate change.

STUDY PROCEDURE

For our literature survey, we used the search term combinations "{AB = [(climate change OR climatic change OR warming) AND (invasive plant OR plant inva*)] AND TS = (introduced OR exotic OR alien)} *AND* DOCUMENT TYPES: (Article) Timespan = 2000–2020" and "{AB = [(climate change OR climatic change OR warming) AND (weed)] AND TS = (crop OR grassland)} *AND* DOCUMENT TYPES: (Article) Timespan = 2000–2020" on the ISI Web of Knowledge database on July 23, 2020 for relevant articles on IAP and weeds, respectively. In our search, we found no studies of alien weeds in grassland ecosystems matching our criteria, but a total of 21 out of 65 studies on alien crop weeds, thus delimiting the studies of the two disciplines mainly based on the habitat type where the harmful species occur i.e., semi-natural and natural vs. cultivated habitats (cf. e.g., Holzner and Glauninger, 2005; Follak et al., 2017; Fried et al., 2017). In the following, we therefore mainly use the term disciplines for the separation of the two searches.

Our survey resulted in an initial set of 616 and 407 articles for IAP and weeds, respectively. To minimize assessor biases (González-Moreno et al., 2019), all co-authors first reviewed and classified the same 100 publications. Discrepancies between the assessors were discussed to reach a consensus and to establish a standard protocol for each category before the main assessor examined each publication to first decide whether it is meeting the selection criteria for inclusion in the review. The main criterion for our selection was that the studies quantitatively address the effects of climate change features on the target plant species, on the target plant's impact on ecosystem properties and the society, and on their management interventions. A total of 179 articles representing 204 case studies of IAP and 45 articles representing 65 case studies of weeds across 47 plant families met our criteria. For these, we assessed a total of seven categories with each 5–7 sub-categories (cf. **Figures 1B**, **2**): publication metrics (publication year, impact factor of the published journal, number citations, publication activity, country of the first author, research area, number of institutions listed in authors' affiliation), climate features studies [modeled data using multiple climate features, experimentally testing temperature, CO_2, precipitation, fire, and others (i.e., salinity, shade, and nitrogen)], taxonomic classification of IAP and weeds, research question (i.e., effects of climate change on target IAP/weed: functional and morphological traits, population dynamics, distribution or niche, abundance and evolutionary changes), study method (observation/interview, field manipulative experiment, common garden experiment, omics tool, modeling, and meta-analysis), impact of the target plants (on resident community, trophic interaction, crop yield, infrastructure, human welfare, and economy), and management of the target plants (prevention, competition, eradication, physical control, chemical control, and biological control). Uncertainties of the main assessor (BPK) in doing these classifications were discussed as they came up with two co-authors (YS and HM-S) to reach a consensus score.

All statistical analyses were done in R version 3.6.0 (R Development Core Team, 2019). The relative similarity of the studies in two disciplines was compared using a non-metric multidimensional scaling (NMDS) ordination on Bray Curtis distance among the study characteristics using the dissimilarity for mixed variables, obtained from *gowdis* function in *FD* package (Laliberté et al., 2014) that implements Podani (1999) extension to ordinal variables. To determine whether the ordination obtained by NMDS was significantly correlated with the two disciplines, we fit discipline as a factor to all ordinations by the "envfit" function in the *VEGAN* package (Oksanen et al., 2007). We used $n = 9,999$ permutations for the envfit permutation testing procedure. We then performed chi-square tests to analyze

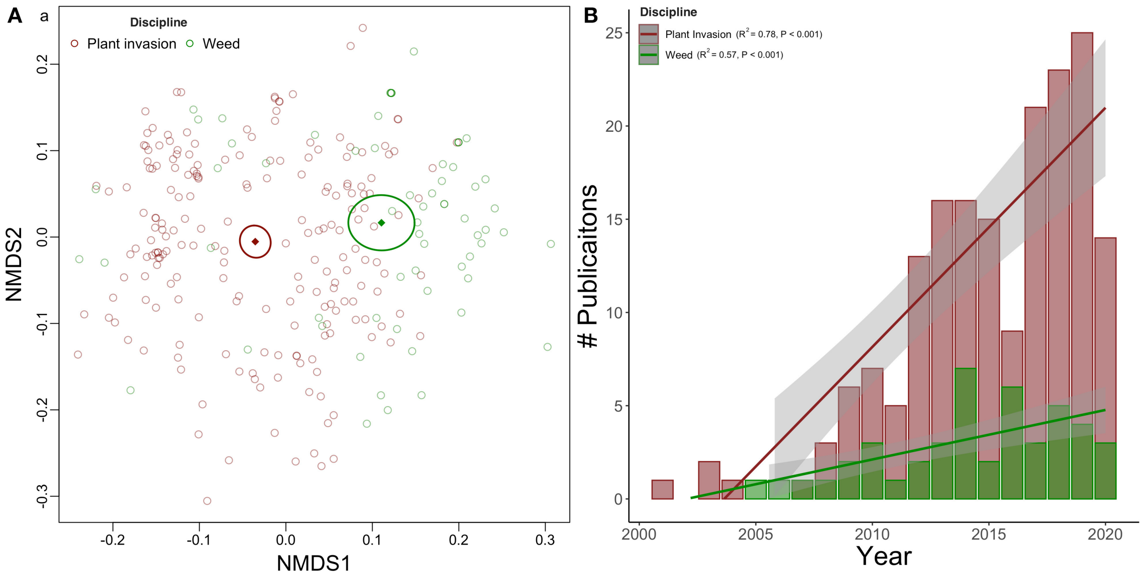

FIGURE 1 | (A) Non-metric multidimensional scaling (NMDS) ordination of the overall compositions of the study categories and sub-categories of the two disciplines based on Bray–Curtis dissimilarities (stress = 0.15). Points represent individual studies, and ellipses represent standard errors (SE) around the mean centroid of each discipline. **(B)** Number of publications per year that address climate change features for the two disciplines with their linear regression line.

the differences in categories/subcategories between the two disciplines. We analyzed the continuous data (e.g., cited time, activities) with linear mixed models, using the *lmer* functions in the R package *lme4* and maximum likelihood to estimate model parameters (Bates et al., 2014), which include discipline as a fixed factor and publication year as a random factor.

STUDYING INVASIVE ALIEN PLANTS VS. WEEDS UNDER CLIMATE CHANGE

Based on all pairwise rank order comparisons for all study categories and their sub-categories, NMDS ordination allows for a visualization of the overall distance between the two disciplines in studying climate change effects. The NMDS plot shows a clear separation along the first dimension ($P < 0.001$; **Figure 1A**), thus indeed, plant invasion science and weed science use different research methods to address different aspects of the target plants when studying consequences of future climate change. The publication metrics significantly differ between the two disciplines (**Figure 1B**). Over the past 20 years, there is an overall increase in publications per year studying climate change effects in both disciplines, but a much steeper increase in publications dealing with IAP than with weeds, reaching 25 publications per year for the former as compared to only four for the latter in 2019 (**Figure 1B**). Linked to this, average citations per publication over this period (20.5 vs. 16.9, $P = 0.03$) and overall activities (number of times the full text of a record has been accessed or a record has been saved since February 1, 2013; 58.86 vs. 39.45, $P < 0.001$) were also much higher for IAP than for weeds. In line with this, also the average impact factor of the publication journal was higher for the plant invasion than the weed science discipline (3.67 vs. 2.81, $P = 0.009$). The average number of authors per publication did not differ between the two disciplines (4.72 vs. 4.75, $P = 0.82$), but the average number of institutions per publication was higher for the plant invasion than the weed science discipline (3.41 vs. 2.65, $P = 0.03$).

For all other categories and sub-categories, we then compared the relative contribution of sub-categories within each category for both IAP and weeds, and the relative numbers of studies within each category between the two disciplines. Based on the continent given for the first author, the relative number of climate change studies in the various continents did not differ between the two disciplines ($P = 0.12$), with first authors in both disciplines more often coming from Europe and America, and least often from Africa (**Figure 2A**). Moreover, only 10 studies dealt with non-angiosperms (four Pinaceae, five Salviniaceae, and one *Caulerpaceae*), all IAP. Among the angiosperms, monocots, compared to dicots are less often studied in plant invasion than in weed science ($P = 0.006$; **Figure 2B**). The relative numbers of the various climate features studied differed between disciplines ($P = 0.008$), with the highest proportion of modeling studies for IAP, and with relatively more studies investigating effects of experimentally testing temperature, CO_2, and fire in weeds than in IAP (**Figure 2C**). The research questions ($P = 0.002$) and study methods ($P < 0.001$) also differed between the two disciplines, with traits and population dynamics being relatively more often assessed for weeds than for IAP, while plant distribution is more often studied for IAP. Among all study methods, a modeling approach using multiple climate features was most often used in both disciplines, but the relative importance within disciplines was higher for IAP with 57% of the methods used as compared to 38% for weeds (**Figures 2D,E**). Climate change effects was assessed in only 31 studies of IAP and 23 studies of weeds, thus

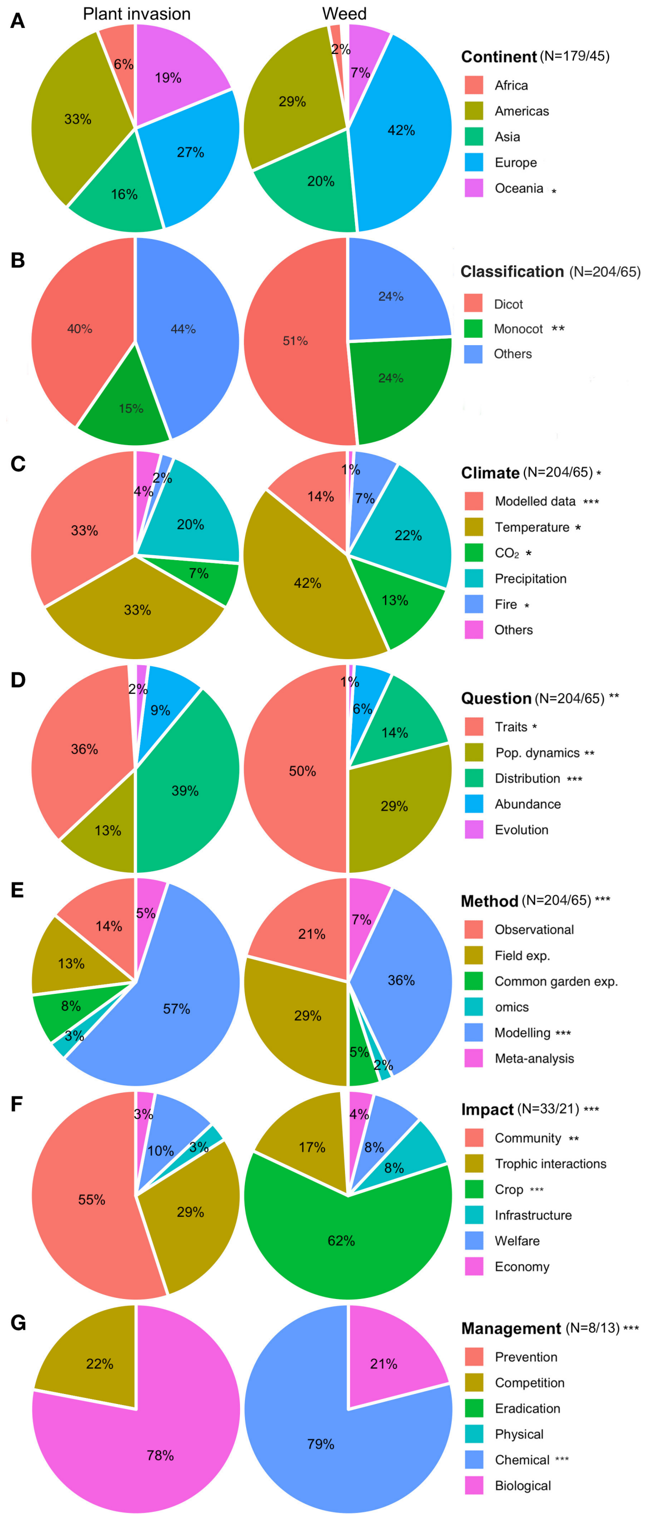

FIGURE 2 | Relative abundance of subcategories within each category for both plant invasion and weed science, and number of studies and comparisons between the disciplines, with ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$, empty: $p > 0.05$. **(A)** Continent of the first author, **(B)** study plant classification, **(C)** climate feature studied, **(D)** research question, **(E)** main method used, **(F)** assessed impact, and **(G)** evaluated management intervention.

yet twice as often in weeds (32%) than in IAP studies (16%). Not surprisingly, community impact of the target plant was studied most often in IAP (55%), whereas impact on crops most often in weeds (58%). Trophic interactions were also studied twice as often in IAP (31%) than in weeds (15%), but this difference was not statistically significant (**Figure 2F**). Finally, effects of climate change on management still remains only little studied, but relatively more often in weeds (18%) than in IAP (4%), with studies addressing climate change of chemical control dominating the management interventions of weeds (**Figure 2G**).

SYNERGIZING THE STRENGTHS OF THE TWO DISCIPLINES TO THE BENEFIT OF BOTH

We are well aware that the distinction between plant invasion and weed science is getting blurred in many countries as the two disciplines are coming increasingly closer together, but our survey yet confirmed, clear differences between them on how they study the effects of climate change. Identifying knowledge gaps in the two disciplines resulting from our literature survey will help to guide discipline-specific future (experimental) research in order to better predict, understand, and hence mitigate climate change effects mediated by potentially favoring harmful plants.

We found distinct differences in the publication metrics between the two disciplines with regard to how often climate change is being addressed. The higher number of publications over the past 20 years on IAP as compared to weeds (179 vs. 45) that address climate change may reflect on the one hand the increased interest of the society due to the ever increasing number of IAP worldwide, and their huge impact on the economy and ecosystems (Seebens et al., 2017), and of researchers in basic ecology and evolution studying the specific features that plant populations offer when introduced to novel abiotic and biotic habitats (Callaway and Maron, 2006). This is mirrored, e.g., in dedicated sessions on plant invasions at nearly every international symposium in ecology, conservation biology, biogeography, and evolution, and also explains the increased activities and impact factor of the journals in which studies of the IAP compared to weeds are being published. On the other hand, weed science, especially in Europe, has experienced a steady decline of active weed scientists over the past few decades (Fernandez-Quintanilla et al., 2008; cf. Müller-Schärer et al., 2018 for more details). Opening-up the scope in weed science from close ties to agriculture to address new issues such as global warming, invasive alien species, and client diversification is presently ongoing (Chauhan, 2020; https://www.ewrs.org/en/pages/Weed-Research-Themes). This may lead to the initiation of more interdisciplinary studies on weeds that will result in increased visibility also through enhanced coverage in more highly cited journals. In this respect, the higher average number of institutions per publication for the plant invasion science than the weed science discipline addressing climate change features may indicate larger and already better-established interdisciplinary networks in plant invasion science as compared to weed science.

The fact that climate change studies are predominantly headed by researchers from Europe, followed by America and Asia, and least in Africa, as based on continent of the first author (**Figure 1A**), may reflect that the re-orientation in weed science toward including, among others, climate change issues, is still less advanced in Asia and Africa (Ward et al., 2014).

Our finding that monocots are relatively more often studied in weed science than in invasion science is not surprising given the high number of monocot weeds in crop and grassland habitats as compared alien monocot species in non-crop habitats (Daehler, 1998). Main plant traits and responses driving population dynamics range from seed fate in the seed bank (Walck et al., 2011), physiological seed dormancy (Ooi et al., 2012), and accordingly seedling emergence pattern (Classen et al., 2010), relative growth rate (Bütof et al., 2012), morphological characteristics (Guerin et al., 2012) up to canopy structure (Pangga et al., 2013), seed production (Nguyen et al., 2017), environment maternal effects (Dwyer and Erickson, 2016), and shifts in the weed flora (Peters et al., 2014), all being sensitive to climate change effects. Climate change is expected to also highly influence herbicide effects via changing herbicide uptake, translocation, and metabolism (Varanasi et al., 2016). This may also break herbicide selectivity and cause crop damage (Jursík et al., 2020). Furthermore, resistant populations are expected to arise via changes in herbicide effects under climate change conditions (Refatti et al., 2019). However, climate change features on weed biology often have been studied in isolation, focusing on increase in temperature or CO_2 only, and although such basic knowledge is getting more readily available, so far only few studies are addressing practical implementations to mitigate climate change effects. Invasion scientists so far only rarely investigated processes at a local range, such as plant traits and the population dynamics of IAP. On the other hand, modeling studies, often based on latitudinal or altitudinal climate gradients, have been used more often in plant invasion science, but could also be explored more often by weed scientists to address expected outcomes of climate change at a larger spatial scale.

Studies on the impact of the target plants and on their management must be an important component of weed studies under climate change, as weed science, fundamentally, has been founded on the basis of weed management. Any study on biology, evolution, ecology, physiology, and population genetics is eventually looking for an approach to managing weeds (Zimdahl, 2018). In line with this, the main conclusions in weed science publications are expected to end up with a recommendation to manage undesirable vegetation (https://www.cambridge.org/core/journals/weed-science/information/instructions-for-authors). On the other hand, impact and management studies remain greatly neglected in plant invasion science (**Figure 2G**). Invasion science has recently made significant progress in classifying and conceptualizing invasion processes (Wilson et al., 2020) and in documenting the increasing number of invasions worldwide coupled with ever increasing costs for the society, but these achievements are of little help to practitioners confronted with alien invasive plants (Plank et al., 2016; Nkambule et al., 2017; Zhang et al., 2020). Thus, an increased focus on specific ecosystem and society impacts of the target plant and on its management is greatly in need when exploring outcomes of climate change for IAP, especially to mitigate climate change effects for areas of high conservation value presently under great risk from IAP (Slodowicz et al., 2018).

Clearly, both disciplines could greatly benefit from more evolutionary studies investigating changes in the genetic composition within and among populations, thus both at the local and larger regional scale. Rapid increases in herbicide resistance have highlighted the ability of weeds to undergo rapid evolutionary change, but as shown in a recent review by Ziska et al. (2019), genetic changes in weed populations in response to the rapid rise in atmospheric carbon dioxide (CO_2) and other associated changes in climate are only rarely studied, but most likely to occur, with consequences for the distribution, community composition, and herbicide efficacy. Similarly, Müller-Schärer et al. (2020) and Sun et al. (2020b) reviewed the increasing yet limited evidence of rapid post-introduction evolution in IAP, and Sun et al. (2020c) and Sun et al. (2020a) reviewed and discussed the potential ecological and evolutionary outcomes for biological control management, and its efficacy under present and future climate conditions. A better understanding of such evolutionary processes will improve our prediction of the adaptive potential, future spread and management outcomes of harmful plants under climate change.

It remains to be further explored on how the recipient communities may also be affected by climate change, either directly (e.g., drought stress) or indirectly (e.g., change in land use), which in turn will affect their susceptibility to, or impact on, weeds and IAP. For instance, some of the worst weed invasions in Wyoming (Cramer et al., 2008) and Ethiopia (Dong et al., 2011; Degefa and Soromessa, 2015) occurred in areas where a reduction in rainfall during the twentieth century led to the abandonment of crop production; these habitats with a history of soil disturbance were then overrun by invasive alien plants. Also, crop species or varieties that use less water now being used to mitigate climate change effects might also differently respond to, or being impacted by, weed species. Under climate change, populations of IAP may either migrate to follow suitable environmental conditions in space without evolving, or they might locally adapt to novel climatic conditions, with or without migrating (Polechová et al., 2009; Sun et al., 2020b). The relative importance of these two scenarios is still unclear. In weed management, the expected accelerated evolution of herbicide resistance under climate change, increased herbicide regulations (e.g., the ban of numerous acting ingredients of herbicides) and a reduction in the discovery of new active ingredients of herbicides, is presently moving the field from herbicide dominated weed management to Integrated Weed Management (IWM). How the outcome of such changes will be modulated by climate change, still needs to be explored (Neve et al., 2009). To answer these pressing questions in view of mitigating the expected increasing impact of harmful plants on the environment and economy under climate change, joint efforts across disciplines and country are urgently needed.

Presently, in most countries, the two research fields are indeed coming closer together, also as typical IAP are increasingly reported from crop fields and native crop weeds are invading adjacent non-crop land that, under climate change, may become more suitable to the growth and development of certain weed species. Thus, target habitats will increasingly overlap, which earlier separated the two disciplines (Müller-Schärer et al., 2018). This offers increased opportunities to jointly address issues of harmful plants and by this, to synergize the strength of the two disciplines. Only this joint effort may bring real advances in understanding, predicting, and mitigating climate change effects for both IAP and weeds.

AUTHOR CONTRIBUTIONS

YS, HM-S, and MO designed the study. BK did most of the data retrieval. YS did the statistical analyses. YS and HM-S wrote the first version of the manuscript. All authors contributed to the final version.

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Within-Population Trait Variation in a Globally Invasive Plant Species Mayweed Chamomile (*Anthemis cotula*): Implications for Future Invasion and Management

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Quantification of variation for phenotypic traits within and among weed populations facilitate understanding of invasion mechanisms and management tactics. In the Pacific Northwest (PNW), USA, in response to climate change and to improve sustainability, producers are increasingly adopting broadleaf crops and cover crops, but Mayweed chamomile (*Anthemis cotula* L.) is a significant barrier to diversifying cropping systems because of its abundance and lack of herbicide options for its control. To quantify within-population phenotypic trait variation and heritability, plants ($n = 300$) from six half-sib families (i.e., seed source plants or mother plants) from each of 10 *A. cotula* populations (infested farms or sites) in the PNW were grown from seed through the flowering stage in the greenhouse common garden experiment. We measured percent seedling emergence, the initial date of flowering, flowering duration, plant biomass, number of flower heads, floral scent profiles, and other traits on individual plants. Trait variation was high among half-sib families within each population. For example, in two of the populations, percent seedling emergence within 30 days of planting ranged from 5 to 41% and 3 to 53%, respectively. As another example, initial date of flowering in two other populations ranged from 61 to 93 days and 58 to 92 days, respectively. Differences among half-sib families were greatest for flowering period, which differed by a month in most populations, and floral scent profiles. Heritability estimates were higher than 1.0 for most phenotypic traits, indicating that the study plants were more closely related than half-sibs (i.e., included full-sibs or products of selfing). These patterns of phenotypic trait variation are potentially caused by local edaphoclimatic factors and within-field farm management practices, suggesting that management of *A. cotula* might be challenging and differ within and across farms.

Keywords: cropping system, floral scent volatile, half-sib family, heritability, phenotypic trait, selection pressure, weed management

INTRODUCTION

Mayweed chamomile (*Anthemis cotula* L.; Asteraceae) is an annual, bushy, ill-scented, and globally invasive weed that originated in Eurasia to have a wide geographic range and long invasion history (Kay, 1971; Adhikari S. et al., 2020). It has been introduced worldwide, presumably as a contaminant of crop seed and other plant materials (CABI, 2018), and has become abundant especially in Mediterranean-like climates such as in the Pacific Northwest (PNW), USA. It can be aggressively weedy in croplands and pastures, significantly reducing crop yields and forage quality (Kay, 1971; Adhikari S. et al., 2020). *Anthemis cotula* has been present in the PNW for more than 143 years, but it has recently become much more problematic (Adhikari S. et al., 2020). Despite increases or stable crop production in recent decades, uncertainties caused by climate change and pest challenges have threatened low-input cereal-based cropping systems and, progressive farmers are responding by adopting climate-change-resilient practices including intercropping and cover crops, fall- and spring-seeded pulses and oilseed *Brassica* crops into cereal rotations (Eigenbrode et al., 2013; O'Leary et al., 2018). These new crops, however, are vulnerable to *A. cotula* because it can outcompete them and there is a lack of compatible herbicides for its management (Lyon et al., 2017). As a result, PNW growers indicate anecdotally that *A. cotula* is more severe in broadleaf cover crops than in cereal crops and presents a substantial barrier to diversifying their cropping systems. To help understand *A. cotula* and the management challenges it presents, there is a need to assess systematically the phenotypic traits that contribute to its invasiveness and weediness.

Invasive species like *A. cotula* have adapted and colonized habitats with diverse ecological conditions worldwide and are a threat to native biodiversity, a threat which is expected to be exacerbated by anthropogenic disturbance and global environmental change (Lee and Gelembiuk, 2008; Richardson and Pyšek, 2012; Downey and Richardson, 2016). Cropping systems are particularly vulnerable to plant invasion. Modern monoculture-based intensive farming practices fragment agricultural landscapes and disturb or displace native flora (Tilman et al., 2011; Chaudhary et al., 2016; Adhikari et al., 2019), enabling invasion by plant species that colonize and evolve rapidly (Williams et al., 2016). Under climate change, not only are the adverse effects of modern agriculture expected to intensify (Bradley et al., 2010; Giejsztowt et al., 2020) but widely distributed invasive weeds with long invasion histories are expanding their range and becoming more invasive (Adhikari A. et al., 2020; Sharma et al., 2020). These ecological challenges necessitate additional study to understand invasion drivers and avenues to improve weed management. Invasive species, usually with limited population sizes when initially colonizing novel environments, frequently adapt, accumulating phenotypic traits that facilitate their success in the new environment (Baker, 1974). For agricultural weeds, abiotic and biotic conditions created by edaphoclimatic variables and within-field management practices may exert localized selection pressure, causing adaptation to the site with implications for management practices (Gunton et al., 2011; Fried et al., 2012; Gaba et al., 2017; Yvoz et al., 2020). Traits such as seed germination, duration of flowering, and fecundity (i.e., abundant flowers or seeds) are known to contribute to invasiveness of plant populations (Pyšek and Richardson, 2008). Variation in traits such as seedling emergence rates within a weedy plant population could complicate management decisions (Sterling et al., 2004). Hence, identifying and quantifying variation in traits of adaptive significance could help improve management, reducing the potential long-term economic and environmental impacts of invasive weeds (Kueffer et al., 2013; Travlos, 2013).

Traits must be heritable for adaptation to occur, and heritability estimates help explain the phenotypic (i.e., underlying genetic) trait variation within a population. Heritability is a useful concept for evaluating and understanding invasive populations' evolutionary dynamics (Visscher et al., 2008; Zas and Sampedro, 2015). Heritability is the proportion of the total phenotypic variance due to genetic variance (Falconer and Mackay, 1989; Zhao et al., 2018) relative to the total phenotypic variance, so heritable traits are less controlled by the environment. Narrow-sense heritability is the proportion of phenotypic variance due to additive genetic variance only.

Anthemis cotula is an important, model, globally-invasive annual agricultural weed that has yet to be assessed for its phenotypic variation in any part of its invaded range. We delineated phenotypic trait variation among half-sib families (i.e., pooled seed from individual mother plants) collected from 10 *A. cotula* PNW populations using a common garden greenhouse experiment. We compared the traits seedling emergence, number of branches, initial day of flowering, number of flower heads, biomass production, plant height, flowering duration, and floral scent volatile organic compound (VOC) profiles (abundance, richness, diversity, evenness) among half-sib families from each of the 10 *A. cotula* populations. The study objectives were: (1) To assess the extent of phenotypic trait variation within *A. cotula* populations and determine if half-sib families explain more variation in traits than populations; and (2) Evaluate the extent of genetic variation (as estimated by heritability) of phenotypic traits within populations. We expected to find within-population (i.e., among half-sib families) variation in phenotypic traits in all of the populations.

MATERIALS AND METHODS

Seed Collection and Greenhouse Common Garden Experiment

In the summer of 2018, seeds were harvested from six different individual plants from each of 10 *A. cotula* infested farms (names are based on nearest towns or farm name: Genesee, Kambitsch, Palouse, Parker, Potlatch, Spillman, St. John, Tensed, Thornton, and Troy) across a precipitation gradient (see **Supplementary Table 1** for farm details) in the PNW. Seeds from each individual were kept separate, each constituting a half-sib family. *Anthemis cotula* is an obligate outcrossing species (Adhikari S. et al., 2020), and the seed from individual plants were assumed to be half-sibs for this analysis.

To measure phenotypic traits of individuals among half-sib families of 10 populations (i.e., sampling locations or farms), an experiment was conducted from February 27 to August 25, 2019. *Anthemis cotula* plants were grown in a common garden greenhouse under a 15-h photoperiod of sunlight and supplemental artificial light (high-pressure sodium lights of photosynthetic photon flux = 595 μmol m^{-2} s^{-1}; model MVR1000/U, General Electric Company, Cleveland, OH) with an average temperature of 22.9 ± 0.26 (mean ± SE) °C and ambient humidity of 43.7 ± 9.5% (mean ± SE). Individual plants were grown in 2.3 L pots filled with a commercial greenhouse soil mix (PRO-MIX BX containing 75–80% Canadian sphagnum peat moss along with perlite and vermiculite; produced by Premier Tech Horticulture Ltd, Alberta, CA). From each of six families of the 10 populations (i.e., 60 seed source plants), 20 seeds were planted in each pot for a total of 300 pots, which were distributed on the greenhouse bench in a randomized complete block design with five replications. Pots were regularly watered as needed and not fertilized. Thirty days after seeding, seedlings were either thinned to a single plant per pot. If there was no emergence from any pot within a family, extra seedlings were transplanted into those pots to ensure within-family replication.

Phenotypic Traits

Data on 13 phenotypic traits were collected from plants in the study. The phenotypic traits assessed were percent seedling emergence in the first 30 days, days to first bud (time spent in vegetative growth), anthesis (days from the first bud to first opening or early flowering), the initial date of flowering (days to the first opening of bud), plant height (cm), number of branches, the final date of flowering (days to flower mature and wilting), flowering duration, the total number of flower heads, plant life (days from emergence to harvest), aboveground dry biomass (g) at harvest, and floral scent profiles. All traits were measured on every plant in the study except for floral scent characterization (see below).

Floral Scent Analysis

Four populations (Genesee, Kambitsch, Palouse Farm, and Thornton), that had at least three half-sib families each with three plants with five flowers blooming at the time of volatile collection, were selected for floral scent characterization among half-sibs of a subset of families. As an obligate out-crosser and a generalist species (Kay, 1971; Adhikari S. et al., 2020), *A. cotula* floral scents could be important to attract diverse pollinators and maximize seed production, contributing to invasiveness. When the plants were blooming abundantly, solid-phase microextraction ["SPME": field sampler with 100-μm polydimethylsiloxane coated fiber; Supelco (Sigma-Aldrich) Bellefonte, PA, USA] was used to collect VOCs (volatile organic compounds) from eight or nine individual plants of each population. To collect VOCs, five live flowers, still attached to plants, were carefully inserted into a 90 mL (30 mm diameter) glass tube, and cotton was pushed in around the stems at the base of the tube to contain the airspace (**Supplementary Figure 1**). SPME fibers were then inserted through a 1 mm hole of a septum (PTFE silicon septum; 10 mm diameter) in the top of the tube and exposed for an hour. After exposure, the fibers were retracted and sampler was held on ice for 5 min while samples were transported to the laboratory for gas chromatography/mass spectrometry (GC/MS). An Agilent 7890A gas chromatograph/5973 Mass Selective Detector (Santa Clara, CA, USA) equipped with an EC-WAX polar column (30 m long, 0.25 mm × 0.25 μm film thickness: Grace, Deerfield, IL, USA) was used for analysis. Helium was used as the carrier gas at a constant flow rate of 1 mL min^{-1}, and the injector temperature was held at 250°C. While analyzing samples, starting oven temperature was 60°C with a 3-min holding period, which later reached to a maximum temperature of 260°C after ramping 10°C per minute for 20 min. Compounds were provisionally identified based on match (≥80%) between their spectra and NIST-11 spectral library (National Institute of Standards and Technology, Gaithersburg, MD, USA) linked to Agilent Mass Hunter software. Compounds present in empty-tube controls were excluded as contaminants. Along with the abundance (total chromatogram *m/z*; mass-to-charge ratio) and richness (expressed as the number of compounds), Simpson's diversity (Simpson, 1949) and Pielou's evenness (Pielou, 1966) were calculated for VOCs.

Statistical Analysis

To assess phenotypic trait variation among half-sib families within each *A. cotula* population, linear mixed models were used for plant height and dry biomass:

$$
\begin{aligned}
y_{ijk} &= \mu + \alpha(\eta)_{ik} + \eta_k + \beta_j + \epsilon_{ijk} \qquad (1)\\
\text{Family within-population} &\sim N(0,\ \sigma^2_{\alpha(\eta)})\\
\text{Population} &\sim N(0,\ \sigma^2_{\eta})\\
\text{Block} &\sim N(0,\ \sigma^2_{\beta})\\
\text{Error} &\sim N(0,\ \sigma^2_{\varepsilon})\\
y_{ij} &= \mu + \alpha_i + \beta_j + \epsilon_{ij} \qquad (2)\\
\text{Family} &\sim N(0,\ \sigma^2_{\alpha})\\
\text{Block} &\sim N(0,\ \sigma^2_{\beta})\\
\text{Error} &\sim N(0,\ \sigma^2_{\varepsilon})
\end{aligned}
$$

Where y_{ijk} and y_{ij} are the response variables, μ is the mean, $\alpha(\eta)_{ik}$ is the random effect for half-sib family within the population, η_k is the random effect for population, α_i is a random effect due to half-sib family, β_j is a random effect of the block, and ϵ_{ij} is the error term. The R package "lme4" was used for analysis (Bates et al., 2015). Residuals were examined for homogeneity of variance, and Q-Q-plots were used to check for normality. For traits quantified as count variables, a generalized linear mixed model with a Poisson distribution and log link function was used, following the model framework described above. The count variables were days to seedling emergence, days to first budding, days to anthesis, days to first and last flowering, flowering duration (days), number of branches, number of flower heads, and plant life (days). For generalized linear models, the residual plots were also examined for homogeneity of variance. For percent emergence data, mixed-model beta regression with

TABLE 1 | Mixed effect model results for 11 phenotypic traits comparing among half-sib families across 10 *Anthemis cotula* populations[a].

Phenotypic traits	Statistics	Genesee	Kambitsch	Parker	Palouse	Potlatch	Spillman Farm	St. John	Tensed	Thornton	Troy
Percent seedling emergence	DF	5, 24	5, 20	5, 24	5, 20	5, 20	5, 20	5, 20	5, 20	5, 24	5, 20
	F	2.08	9.01	21.47	19.51	9.40	3.97	16.02	2.43	21.58	12.09
	P	0.10	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.01**	**<0.001**	0.07	**<0.001**	**<0.001**
Plant height	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	3.23	2.75	5.73	0.72	4.95	1.26	9.96	2.65	2.41	0.71
	P	**0.03**	**0.05**	**0.002**	0.62	**0.006**	0.32	**<0.001**	**0.05**	0.074	0.63
First budding date	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	14.35	3.64	15.65	3.52	3.32	9.96	5.53	2.31	6.95	3.1
	P	**<0.001**	**0.003**	**<0.001**	**0.004**	**0.006**	**<0.001**	**<0.001**	**0.045**	**<0.001**	**0.01**
First flowering date	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	13.568	3.37	14.21	3.76	3.29	8.56	5.07	1.93	6.37	2.24
	P	**<0.001**	**0.006**	**<0.001**	**0.003**	**0.007**	**<0.001**	**<0.001**	0.09	**<0.001**	**0.05**
Anthesis (budding to flowering)	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	0.75	1.11	0.28	0.74	0.44	0.41	0.23	0.21	0.27	0.31
	P	0.59	0.36	0.92	0.59	0.82	0.84	0.95	0.96	0.93	0.91
Total number of branches	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	2.07	0.97	1.02	0.71	1.03	0.68	3.57	1.16	3.35	1.73
	P	0.07	0.44	0.41	0.62	0.4	0.64	**0.004**	0.33	**0.006**	0.13
Flowering period	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	7.38	7.87	7.44	7.94	4.77	4.54	9.5	6.1	11.68	5.04
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Total number of flower heads	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	3.08	3.93	20.67	3.79	0.95	15.6	3.97	12.48	22.29	6.75
	P	**0.01**	**0.002**	**<0.001**	**0.002**	0.45	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**
Last day of flowering	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	6.04	5.54	1.97	2.59	1.62	2.83	5.75	7.64	2.97	2.78
	P	**<0.001**	**<0.001**	0.08	**0.026**	0.16	**0.02**	**<0.001**	**<0.001**	**0.01**	**0.02**
Plant life (days of harvest from seeding)	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	4.41	5.33	2.39	2.56	1.86	2.78	1.15	3.99	0.65	1.28
	P	**<0.001**	**<0.001**	**0.04**	**0.03**	0.1	**0.02**	0.33	**0.002**	0.66	0.27
Plant dry biomass (g)	DF	5, 24	5, 21	5, 20	5, 19	5, 19	5, 24	5, 21	5, 24	5, 23	5, 22
	F	3.47	1.27	0.8	2.78	3.12	0.9	1.85	0.38	0.58	2.75
	P	**0.02**	0.32	0.57	0.06	**0.04**	0.49	0.15	0.86	0.72	**0.05**

[a] *P-values ≤ 0.05 are bolded. Numerator degrees of freedom were five for each population (n = 6 half-sib families for each population), but the DDF (Denominator degrees of freedom) varied across population as some plants of certain half-sib families of certain population did not germinate.*

function "glmmTMB (generalized linear mixed model using template model builder)" was used (Brooks et al., 2017). In addition to the univariate analysis, using populations and half-sib families in the models, we also performed the variance partitioning to estimate the percentage of variation explained by half-sib families within populations for each trait, and the significance of variation was tested by using a likelihood ratio test. For floral VOC diversity and evenness, simple linear models were used and for VOC abundance and richness generalized linear models with a Poisson distribution and log link function were used. All data analyses were performed using R 3v.5.1 (R Development Core Team, 2018).

To assess if the overall composition of phenotypic traits were different among half-sib families in each population, we conducted a permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) of 10 phenotypic traits [plant height, the total number of branches, first budding date, first flowering date, anthesis, plant life, flowering period, last day of flowering, the total number of flower heads, and plant dry biomass (g)]. The results were visualized with Non-metric Multidimensional Scaling (NMDS) ordination. The package "vegan" was used for conducting PERMANOVA and NMDS (Oksanen, 2019).

Heritability

We calculated narrow-sense heritability (h^2) on each phenotypic trait of 10 populations using mixed-effect models [Equation (2); see details in *Statistical Analysis*], with half-sib family and block as random effects.

$$\text{Heritability } (\text{h2}) = \frac{\text{Va } (\text{additive variance})}{\text{Vp } (\text{phenotypic variance})} = \frac{4 \text{ x V(half} - \text{sib family)}}{\text{Vp } (\text{phenotypic variance})} \qquad (3)$$

Because half-sibs are expected to share ¼ of their genetic information by descent, four times the intraclass correlation of half-sib families can be used as an estimate of narrow-sense heritability (Equation 3) although maternal half-sib families may have an upward bias due to maternal environmental effects (Falconer and Mackay, 1989). In plants, maternal environmental effects are especially prevalent in seed traits such as seed weight or germination rate (Hendrix, 1984).

RESULTS

Phenotypic Traits

The first day of budding and flowering periods varied among and within half-sib families within each of the 10 *A. cotula* populations or sampling locations (**Table 1**, **Supplementary Table 2**). Phenotypic variation among half-sib families was observed in nine populations for first flowering day and total flower heads, eight populations for seedling emergence within 30 days of planting and last day of flowering, six populations for plant life, four populations for plant height, two populations for total branches and plant dry biomass, and zero populations for anthesis (**Table 1**, **Supplementary Table 2**). For example, percent seedling emergence within 30 days of planting among half-sib families ranged from 2 to 35% in Parker Farm, 5 to 41% in Thornton, and 3 to 53% in Troy populations. Similarly, the initial date of flowering among half-sib families ranged from 61 to 93 days in Genesee and 58 to 92 days in Parker populations. Also, half-sibs of some individual families in Kambitsch, Palouse, St. John, and Thornton populations flowered for more than 1 month longer than the half-sibs of other families within these populations. Variance partitioning calculations indicated that half-sib families explained a higher proportion of variance than the population for all traits, except for anthesis and plant dry biomass (**Table 2**).

PERMANOVA on a Bray-Curtis dissimilarity matrix of 10 phenotypic traits [plant height, the total number of branches, first budding day, first flowering date, anthesis, plant life, flowering period, last day of flowering, the total number of flower heads, and plant dry biomass (g)] indicated that overall composition of traits in half-sibs among six families was dissimilar in five (Genesee, Parker Farm, Spillman, St. John, and Thornton), marginally dissimilar in one (Kambitsch), and similar in four (Palouse, Potlatch, Tensed, and Troy) populations (**Figure 1**, **Table 3**).

There was intrapopulation variation in floral scent VOCs within the four tested *A. cotula* populations. Differences among half-sib families occurred in VOC abundance (total chromatogram *m/z*) for all four populations (**Figure 2**, **Table 4**). VOC richness differed among half-sib families in the Kambitsch and Thornton populations, was marginally different in Genesee, and was not significant for the Palouse population (**Figure 2**, **Table 4**). Both Simpon's diversity and Pielou's evenness of floral VOCs differed among half-sib families within the Kambitsch population, but not within the Genesee, Palouse, or Thornton populations (**Figure 2**, **Table 4**).

TABLE 2 | Variation among half-sib families within population (i.e., variance partitioning) for each trait.

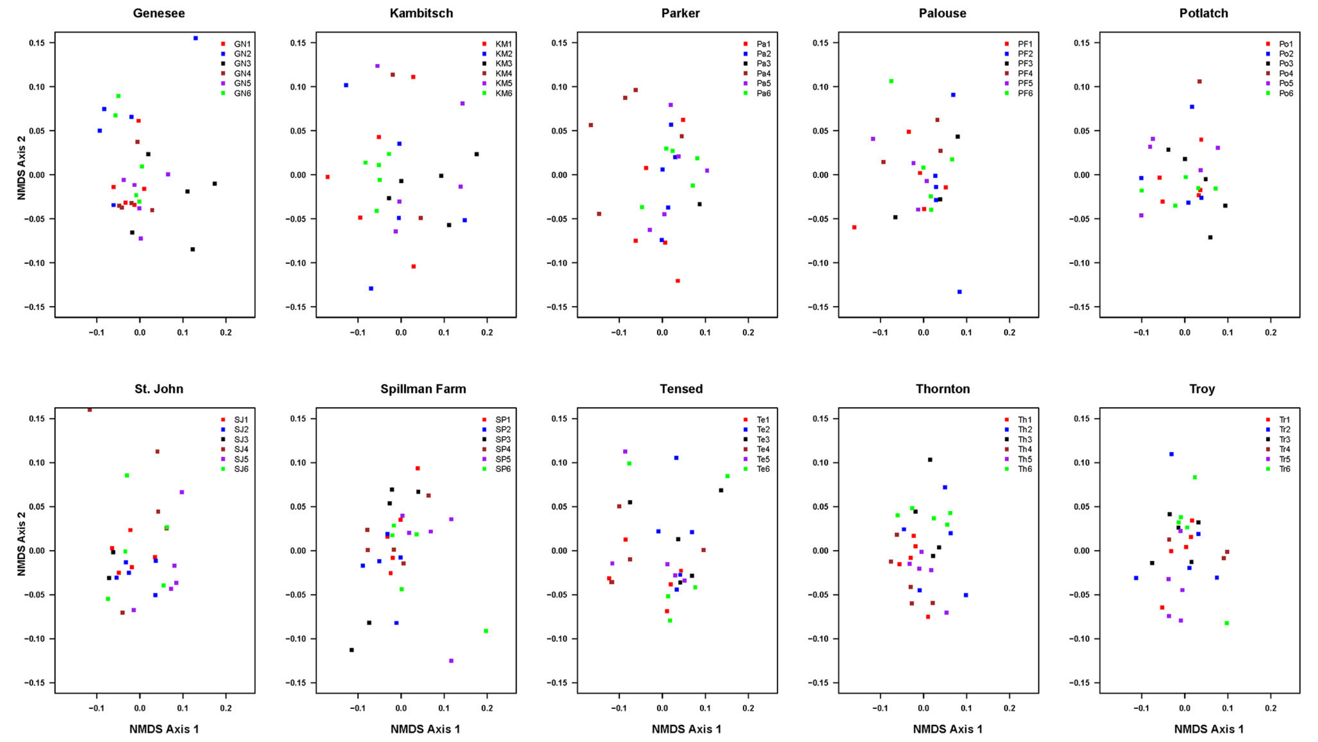
Phenotypic trait	Half-sib family	Population	Residuals	*P*-value
Plant height (cm)	0.234	0.007	0.758	0.000
Initial date of budding (d)	0.511	0.04	0.449	0.000
First flowering day (d)	0.487	0.054	0.459	0.000
Anthesis (d)	NA	NA	NA	1.000
Total number of branches	0.115	0.105	0.781	0.007
Flowering duration (d)	0.502	0.076	0.422	0.000
Total number of flower heads	0.593	0.075	0.332	0.000
Final day of flowering (d)	0.289	0.194	0.517	0.000
Plant life (d)	0.205	0.169	0.626	0.000
Plant dry biomass (g)	0.071	0.075	0.854	0.101

Heritability

Considering the individual plants as half-sibs, heritability estimates for most phenotypic traits varied among populations and were high, occasionally reaching unusually high values greater than two (**Table 5**). Heritability estimates among tested populations ranged from 0.36 to 1.61 for seedling emergence, 0 to 2.44 for plant height, 0.52 to 2.56 for the initial date of budding, 0.39 to 2.53 for the initial date of flowering, 0 to 1.19 for total branches, 0 across all populations for anthesis, 0.67 to 2.37 for the flowering duration, 0.35 to 1.81 for the final date of flowering, 0 to 2.86 for total flower heads, 0 to 1.44 for plant life, and 0 to 1.23 for dry plant biomass (**Table 5**).

DISCUSSION

Previous studies have reported phenotypic traits associated with the invasiveness of plant species (Bossdorf et al., 2005; Pyšek and Richardson, 2008; Murphy et al., 2016) but these traits have been measured at the species level, rarely among populations, and never among half-sib families within populations of invasive plants. In our common garden study, most of the individual traits and trait compositions of half-sibs differed among families across populations of *A. cotula*. For example, percent seedling emergence within 30 days of planting among half-sib families ranged from 2 to 35% in Parker Farm, 5 to 41% in Thornton, and 3 to 53% in Troy populations. Similarly, the initial date of flowering among half-sib families ranged from 61 to 93 days in Genesee and 58 to 92 days in Parker populations. Also, half-sibs of some individual families in Kambitsch, Palouse, St. John, and


Genesee

Kambitsch

Parker

Palouse

Potlatch

St. John

Spillman Farm

Tensed

Thornton

Troy

FIGURE 1 | Non-metric multidimensional scaling (NMDS) ordination of selected phenotypic traits [plant height, the total number of branches, first budding date, first flowering date, anthesis, plant life, flowering period, last day of flowering, the total number of flower heads, and plant dry biomass (g)] of half-sibs among six families across 10 *Anthemis cotula* populations (See detail statistics for each population in **Table 2**).

TABLE 3 | Permutational Multivariate Analysis of Variance (PERMANOVA) statistics of half-sibs phenotypic traits among six mother plants across 10 *Anthemis cotula* populations (see **Figure 1** for the ordination plots)[a].

Populations (Farms)	**PERMANOVA statistics**				
	Stress ($k = 2$)	**DDF**	**Pseudo- F**	**P**	**r^2**
Genesee	4.29	24	2.24	**0.01**	0.32
Kambitsch	13.88	21	1.59	0.08	0.28
Parker Farm	9.51	20	2.51	**0.01**	0.39
Palouse	11.91	19	0.94	0.54	0.20
Potlatch	11.41	19	1.25	0.26	0.25
Spillman Farm	7.41	24	1.70	**0.05**	0.26
St. John	12.19	21	2.19	**0.01**	0.34
Tensed	6.92	24	1.29	0.26	0.21
Thornton	10.39	23	2.42	**0.01**	0.35
Troy	10.70	22	1.17	0.29	0.21

[a] *Numerator degrees of freedom were five for each population ($n = 6$ half-sib families for each population), but the DDF (Denominator degrees of freedom) varied across population as some plants of certain half-sib families of certain population did not germinate. P-values ≤ 0.05 are bolded.*

Thornton populations flowered for more than one month longer time than the half-sibs of other families within these populations.

The principal potential sources that contribute to intrapopulation trait variation in *A. cotula* populations are (1) varying local selection pressures across space and time, (2) original genetic variation of the introduced populations, (3) genetic drift of initial small populations, and (4) human-mediated inadvertent introductions and reintroductions of unrelated germplasm to existing populations. Regarding the first of these sources, spatial and temporal variation in abiotic and biotic factors associated with soil and climate, and farm management practices could select for trait variation (Menalled et al., 2016; Bagavathiannan and Davis, 2018). Factors such as soil properties (Metcalfe et al., 2019; Pätzold et al., 2020), tillage, crop rotation, the movement patterns of farm equipment, herbicide regimes (Gao et al., 2018), and crop stand (Mhlanga et al., 2016; Kaur et al., 2018) can all come into play, with their spatial patterns (Blank et al., 2019) driving within-site variation in phenotypic traits [Cardina et al., 1997; Baucom and Mauricio, 2008; Vigueira et al., 2013; Hovick et al., 2018, also see Miller et al. (1994)]. Different traits respond differently to one or more of these factors (Prunier et al., 2012). The variation we detected indicates more studies are required to assess this variation to describe spatiotemporal variation in selection pressure on specific traits.

The three remaining sources of intrapopulation variation also could account for the trait variation we detected. The original variation of the introduced population or populations, genetic drift, and the number and frequency of past introduction events are unknown. The agricultural practices or variable climate that favor different traits in different years could have maintained

TABLE 4 | Results from ANOVA for floral scent VOC abundance (*m/z*), richness, diversity, and evenness among half-sibs of three families across four *Anthemis cotula* populations[a].

Population	Abundance (*m/z*)			Richness			Diversity			Evenness		
	DDF	*F*	*P*	DDF	*F*	*P*	DDF	*F*	*P*	DDF	*F*	*P*
Genesee	5	181,587	**<0.001**	5	5.59	0.060	5	1.92	0.240	5	4.42	0.080
Kambitsch	5	4,493,757	**<0.001**	5	20.56	**<0.001**	5	156.2	**<0.001**	5	17.0	**0.010**
Palouse	6	2,415,809	**<0.001**	6	3.2	0.200	6	0.67	0.550	6	0.55	0.610
Thornton	6	8,304,177	**<0.001**	6	8.96	**0.010**	6	0.91	0.450	6	0.88	0.460

[a] *Numerator degrees of freedom were two for each population across floral scent variables (n = 3 half-sib family for each population), but the DDF (Denominator degrees of freedom) varied across populations due to different number of individual plants sampled for VOCs collection. P-values ≤ 0.05 are bolded.*

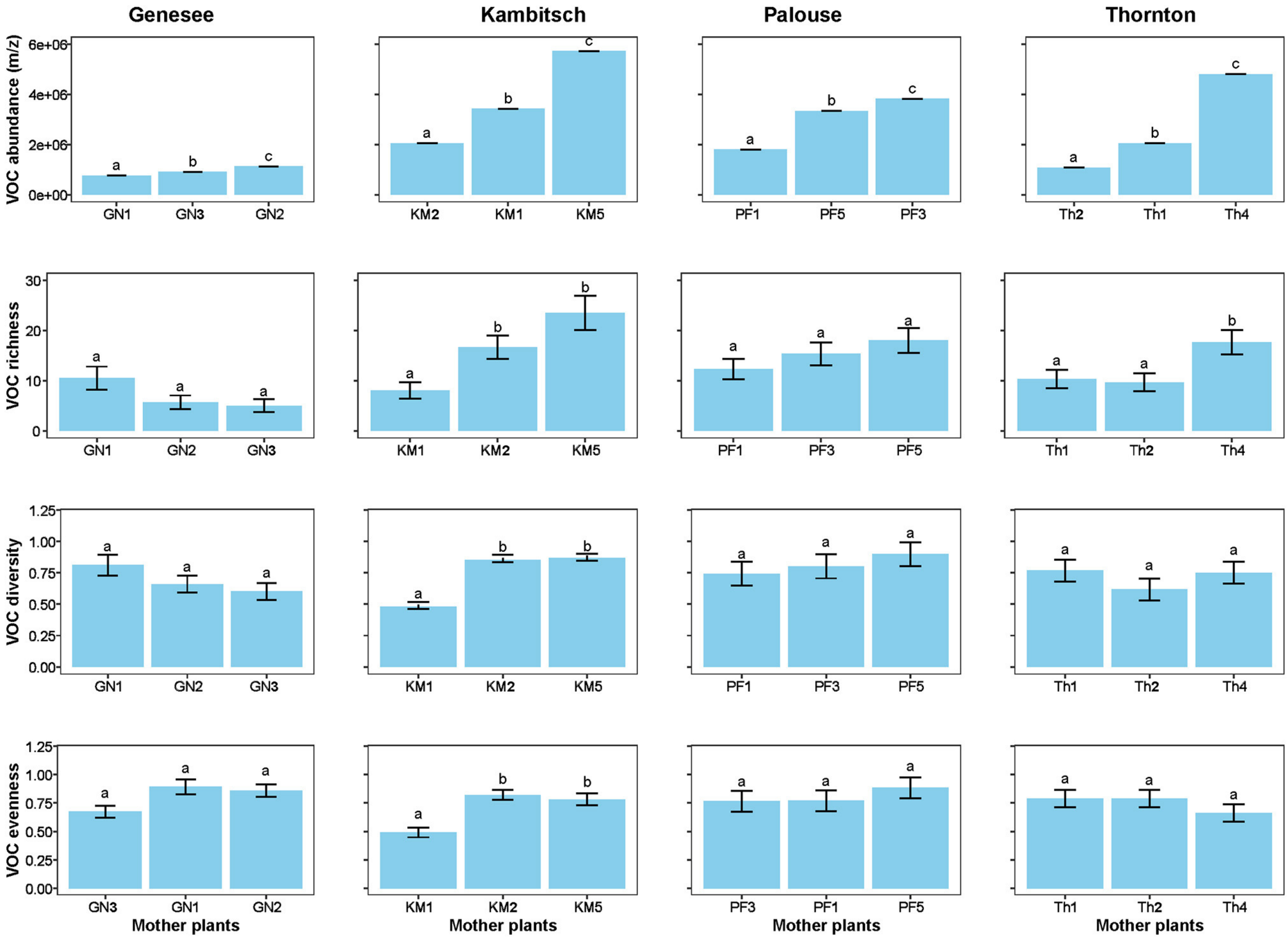


FIGURE 2 | Genetic variation of half-sib families within each population (mean ± SE) floral VOCs abundance (*m/z*), richness, diversity, and evenness across four *Anthemis cotula* populations.

or amplified the genetic diversity associated with the initial introductions. Whatever the basis for the trait variation we have detected, its presence indicates a potential for continued adaptation in response to ongoing drivers (Menalled et al., 2016; Hovick et al., 2018) contributing to weed invasiveness (Pyšek and Richardson, 2008; Murphy et al., 2016).

Floral scent profiles also differed among the half-sib families across *A. cotula* populations. Our results are consistent with previous studies (Delle-Vedove et al., 2017; Campbell et al., 2019; Friberg et al., 2019), which indicated that VOCs could differ environmentally within and between populations based on diel period and other environmental drivers, or reflect responses to selection by pollinators and natural enemies, with a genetic basis. Our common garden data indicate that the floral scent traits of *A. cotula* are heritable with the potential to continue evolving to improve fitness of local populations. For pollination of an

TABLE 5 | Heritability (h^2) estimates of 11 phenotypic traits for half-sib families from 10 *Anthemis cotula* populations.

Population	Seedling emergence in 30 days (%)	Plant height (cm)	Initial date of budding	Initial date of flowering	Total branches	Anthesis	Flowering duration (d)	Final date of flowering	Total flower heads	Plant life	Dry biomass (g)
Genesee	0.74	0.83	2.15	2.16	0.53	0	1.97	1.81	0.50	1.44	1.13
Kambitsch	0.36	0.99	1.23	1.13	0	0	1.124	1.12	0.46	1.42	0.17
Parker Farm	1.16	2.16	2.56	2.53	0	0	1.39	0.38	2.22	0.65	0
Palouse	1.61	0	0.91	1.00	0	0	1.59	0.71	0.55	0.79	1.17
Potlatch	1.49	2.17	1.00	0.94	0	0	1.29	0.35	0	0.52	1.23
St. John	1.47	2.44	1.73	1.63	1.15	0	1.88	1.51	0.81	0	0.68
Spillman Farm	0.73	0.20	2.01	1.89	0	0	0.67	0.61	2.06	0.69	0
Tensed	0.44	0.89	0.52	0.39	0	0	1.41	1.75	1.62	1.06	0
Thornton	1.61	0.82	1.96	1.88	1.19	0	2.37	0.92	2.86	0	0
Troy	1.34	0	1.00	0.56	0.30	0	1.29	0.80	1.25	0.09	0.76

outcrossing invasive species such as *A. cotula,* floral scents could ensure immediate fitness of the plants, but also attract some floral visitors away from the native plants (Burkle and Runyon, 2017; Campbell et al., 2019). Variable timing and duration of flowering, flowering for extended periods, and producing floral scent diversity among individual plants within a population could contribute to greater visitation of local pollinators and contribute to success of invaders.

Heritability estimates differed for traits within populations with higher values for seedling emergence, plant height, first budding and flowering days, flowering duration, the final date of flowering, and total flower heads than those for other traits. Previous common garden and field studies have found that the heritability of traits in outcrossing species [reviewed in Geber and Griffen (2003)] and with larger range sizes (Hoffmann and Sgró, 2011; Zeng X. et al., 2017) tend to be higher than for species with some inbreeding or smaller range size. This seems consistent with our understanding of *A. cotula* ecology in the PNW. On the other hand, heritability estimates are generally higher or over-estimated in laboratory or greenhouse conditions (Conner et al., 2007), particularly for highly plastic traits such as seedling emergence, plant height, and phenological traits (e.g., first budding and flowering days; Dicenta et al., 1993; Geber and Griffen, 2003; Franks et al., 2007; Wright et al., 2020). Hence, high heritability in *A. cotula* could have occurred because the environmental variance component is reduced, and additive variance is increased in the controlled setting in the greenhouse common garden (Geber and Griffen, 2003; Conner et al., 2007).

High heritability estimates observed in many of the traits in our study indicate that the individuals were more related than expected for half-sibs, with perhaps some inbreeding (caused by selfing, producing full sibs) or maternal effects. Maternal effects are believed to influence phenotypes and the ability to adapt to the novel environmental conditions (Leiblein-Wild and Tackenberg, 2014; Albecker and McCoy, 2019). High narrow-sense heritability estimates in our study may also suggest that many traits have the potential for adaptive evolution (Zeng X. et al., 2017) in *A. cotula*, an understudied yet globally invasive species. While *A. cotula* occurring predominantly in agricultural fields might be under selection pressure of within-field farm management practices interacting with edaphoclimatic factors, heritable traits respond to selection pressure (Christoffers, 1999). We currently lack data to support these possible explanations for the observed heritability. Future work to assess these will require a larger sample size grown for multiple generations.

Results from our *A. cotula* study have several implications for management. As *A. cotula* in the PNW mainly occurs in agricultural fields where its range is apparently expanding, genetically based phenotypic variation in the species will allow it to respond to local differences in farm management practices such as types of crop planted (Ogg et al., 1994), continuous cropping (Murphy and Lemerle, 2006), fertilizer (Lemke et al., 2015; Zeng M. et al., 2017), tillage (Ghersa and Martínez-Ghersa, 2000), mowing and herbicides (Lyon et al., 2017; Hovick et al., 2018). Herbicides impose robust directional selection on herbicide resistance traits *per se* (Powles and Yu, 2010; Neve et al., 2018) with pleiotropic effects on traits such as seed dormancy and germination (Délye et al., 2013). Adaptation in response to herbicide regimes can introduce requirements for robust weed management tactics (Menalled et al., 2016; Bagavathiannan and Davis, 2018). All these selection pressures are likely to shift as producers adopt cropping systems and management regimes in response to climate change. *A. cotula*, given its genetically based phenotypic variation, is poised to evolve in response, creating continuing difficulties for its management (Murphy and Lemerle, 2006; Vigueira et al., 2013; Hovick et al., 2018). Given this potential, integrated weed management employing "many little hammers" (Liebman and Gallandt, 1997) could minimize strong directional selection pressure.

The intrapopulation variation in traits and within a field could complicate management decisions (Sterling et al., 2004). For example, if some individuals in a field emerge and flower earlier a manager may choose to spray postemergence herbicide early. Later-emerging and flowering individuals from the same population will require additional treatment, or if not treated, lead to selection for later emergence increasing variability of that trait, exacerbating the problem. Understanding how phenotypic trait variation occurs within a field could allow targeted and more efficient herbicide treatments and reduce unnecessary applications (Cardina et al., 1997; Blank et al., 2019).

The degree of phenotypic trait variation in invading populations is thought to be determined by demographic history (Dlugosch and Parker, 2008; Hodgins and Rieseberg, 2011). The ongoing movement of *A. cotula* seeds among farms within or from outside in the PNW due to inadvertent yet common trade in crop seed, farming equipment and other inputs (Blanco-Moreno et al., 2004) should be a concern for farm managers, seed traders and others. These factors will contribute to maintaining genetic diversity of *A. cotula*, maintaining its potential to adapt to local environmental and management regimes. Hence, knowledge of anthropogenic *A. cotula* seed movement that could contribute to this diversity requires further study. Our study provides a baseline against which future assessments could be compared to assess ongoing changes in its phenotypic and genetic diversity.

CONCLUSIONS

Our study is the first of which we are aware that reports phenotypic trait variation among half-sib families in a globally invasive annual agricultural weed. In *A. cotula*, we found that half-sib families explained a higher proportion of variance than the population for most traits. Knowledge of plant functional traits among half-sibs across locally adapted plant populations can inform site-specific invasive species management and forecast their distributions in the context of global environmental changes. Farm management regime and several local abiotic (e.g., soil type, precipitation, and temperature) and biotic (e.g., natural enemies, flower visitors, symbiotic organisms, and co-occurring plant species) factors in agroecosystems could impose selection pressures affecting the response of *A. cotula* traits. As intrapopulation trait variation could favor different maternal lines under competitive local abiotic and biotic conditions, it could overall improve the invasion success of *A. cotula*. The current extensive (global) and intensive (local) distribution suggests that the climate niche of *A. cotula* is wide and its variable traits could help further spread during global environmental change, though further studies are required to confirm our hypothesis. Also, with the adoption of new crops, especially broadleaf crops and cover crops that are vulnerable to *A. cotula* because they are less competitive than traditional cereal crops or lack compatible herbicides for weed management, *A. cotula* could be more challenging to manage. To confirm whether the trait variation among half-sib families of *A. cotula* populations resulted from the adaptive responses to local selection pressure, how it is affected by maternal effects, selfing, or other factors, and how the trait variation could complicate within-farm weed management plans, requires additional study.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SA, ICB, and SDE designed the study. ICB and SDE acquired the funding and supervised the study. SA contributed to the seed collection, greenhouse experiment, data analysis, and manuscript preparation. SRR and JP contributed to data analysis. All authors contributed to the article, edited, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fagro.2021.640208/full#supplementary-material

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REVIEW
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The Impact of Polyploidization on the Evolution of Weed Species: Historical Understanding and Current Limitations

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Whole genome duplication via polyploidization is a major driver of diversification within angiosperms and it appears to confer the most benefit during times of rapid environmental change. Polyploidization offers expanded access to novel phenotypes that facilitate invasion of new environments and increased resistance to stress. These new phenotypes can arise almost immediately through the novel interactions among or between transcription factors of the duplicated genomes leading to transgressive traits, and general heterosis, or they can occur more slowly through processes like neofunctionalization, and subfunctionalization. These processes are characterized by the changes within homologs of the duplicated genomes, homoeologs. It has been proposed that redundant homoeologs are released from selective constraints and serve as an additional source of adaptive genetic variation, particularly in neo and meso-polyploids. Current practices in weed management create rapid environmental change through the use of chemicals, practices that are meant to cause the extirpation of the designated weed, and represent a strong recurrent selective event—a scenario that should favor polyploidy species. Here we ask the question, "Do polyploids make better weeds?" It is our conclusion that such a question is impossible to answer at this time due to the lack of resources and understanding in weed genomics. The growing contingent of research in weed genomics, however, driven by herbicide resistance evolution is rapidly improving our understanding of weed molecular biology and will aid in improving understanding of the impacts of ploidy levels on weed evolution and adaptation in the future.

Keywords: polyploidy, herbicide resistance, evolution, genomics, glyphosate, weeds

INTRODUCTION

All extant diploid angiosperms have been traced back to polyploid ancestors (Scarpino et al., 2014). Whole genome duplications (WGDs) are major drivers of adaptation and are responsible for the trajectory of flowering plant evolution. Phylogenetic analyses and molecular dating have traced an ancient genome-wide duplication event shared by all extant seed plants (Jiao et al., 2011). Ancient whole genome duplications (WGD), served as a major force in speciation and diversification in highly plastic angiosperm genomes. Compared to gymnosperms, angiosperms are more likely to endure the impact that polyploidy has on a genome, as <5% of gymnosperms are polyploid (Leitch and Leitch, 2008). While polyploidy is gaining traction as a viable and beneficial means of adaptation, polyploidization has previously been described and is still commonly referred to as an evolutionary "dead end," as ancient WGD were seen scarce (Arrigo and Barker, 2012; Van De Peer et al., 2017). Polyploidy studies are continuing to rise in prevalence, and more cases of ancient and neopolyploid cases are being discovered and suggests that polyploidization via whole genome duplication is more common than previously thought (Hohmann et al., 2015; Barker et al., 2016; Yang et al., 2018). In rare instances polyploids could have had an evolutionary advantage on their non-polyploid competition, especially in times of stress or environmental upheaval, providing means to survive over their counterparts (Van De Peer et al., 2017). Recent studies provided evidence that there is an increased tolerance to genomic changes in polyploids relative to diploid progenitors, including how polyploid lineages were established and the rates at which this occurs, and the mechanisms they used to spread and maintain themselves (Schoenfelder and Fox, 2015; Shimizu-Inatsugi et al., 2017). Using a literature review and a survey of reported weeds and their ploidy level, we propose to show that polyploids make better weeds. The term weed is a generally vague description designated to virtually any plant deemed undesirable in the context of where it grows. This review focuses on the undesirable plants in an agricultural perspective that have adapted to the human condition (Harlan and de Wet, 1965). Polyploidization is especially important to understand within the study of weed science in the view of climate change and the ever-increasing size of highly managed tracts of land around the world, since both of these selective forces may favor polyploids. Here we ask if polyploidy confers an advantage in the evolution of glyphosate resistance in comparison to their diploid counterparts. Glyphosate resistance is an ideal trait to test since understanding its evolution has both practical and theoretical applications. As a herbicide it was highly effective and the evolution of target site and non-target site required decades (Pratley et al., 1999; Sammons and Gaines, 2014). Understanding if polyploidy confers an advantage in the case of glyphosate will elucidate how resistance to other herbicides will evolve and if special consideration needs to be given to polyploids in application of weed control.

DEFINITIONS ABOUT POLYPLOIDY

Polyploids are organisms that contain multiple copies of their chromosomes, or simply, a species that has more copies than diploids (Glover et al., 2016). *Polyploidization* itself is defined as whole genome duplication, where it has doubled in the form of either *allopolyploidy* or *autopolyploidy,* or as a combination of both forms (**Table 1**). *Allopolyploids* are generated through the hybridization of two or more different species each contributing unique subgenomes, while *autopolyploids* arise from the duplication of a single species' genome. On a gene level, the multiple copies of genes or chromosomes in *allopolyploids* are referred to as *homoeologs*. Not to be confused with *homologs*, *homoeologs* are related genes that lie in the different subgenomes of an allopolyploid (Mason and Wendel, 2020). *Homologous genes* share a common ancestor, while *homoeologous genes* have the same parental origin (Mable, 2003). Within homologous genes, there are *orthologs* and *paralogs*: *orthologs* are genes descended from a common ancestor in different species that share the same function or formed due to a speciation event. *Paralogs* are genes derived from a single gene as the result of a duplication event (Sonnhammer and Koonin, 2002). *Homoeologs* and *orthologs* can be construed as analogous, as homoeologs are orthologous genes within a polyploid species that occur on different subgenomes. *Homoeologs* originated through speciation and were recombined in the same genome through *allopolyploidization* (Glover et al., 2016). The correct usage of "homoeolog" has been debated and the sheer amount of different terms can lead to some confusion.

Paleopolyploidy is defined as polyploidy that occurred millions of years ago (Blanc and Wolfe, 2004; Soltis et al., 2009). Genes associated with *paleopolyploidy* can also be referred to as *paleologs*. Determining whether an organism is a *paleopolyploid* or used to be a difficult task because progenitor species could not be identified through cytological tools or DNA markers (Levy and Feldman, 2002). Advances in genomics has eased the process of identification with whole genome assemblies providing the necessary data for synteny plots, gene trees constructed from gene family analyses, and Ks plots from transcriptome assembles (Husemann and Stoye, 2009; Gao et al., 2018; Leebens-Mack et al., 2019). More recent polyploids have two different categories: *mesopolyploid*, if formed within the last 17 million years, or *neopolyploids* for the species that most recently experienced polyploidization (Ramsey and Schemske, 2002; Cheng et al., 2018). *Neopolyploidy* can also be described as a species that has experienced an artificially induced chromosome duplication (Comai, 2005). *Aneuploidy* is another term associated with polyploidy, as it signifies when there is an abnormal number of chromosomes compared to the wild type, which is commonly found in triploid (and sometimes pentaploid) populations (Müntzing, 1936; Huettel et al., 2008).

HISTORY OF POLYPLOID EVOLUTION

The earliest concepts of polyploidy came about in the early 1900s. The independent rediscovery of Mendel's work by de Vries, Correns, and Tschermak was the beginning of a golden age of genetics (Corcos and Monaghan, 1990). Geneticists originally associated specific characteristics with morphological characteristics as opposed to genetic characteristics like karyotype (DeVries, 1915; Ramsey and Ramsey, 2014). Using morphological characteristics as a form identification was soon displaced by the acceptance of chromosomes as hereditary units (Roberts, 1929). While certain plants, like maize, had already been determined to be polyploid (Kuwada, 1911), the term polyploidy was coined by Winkler (1917), who created the first artificial polyploid. Winge (1917) had some of the most influential thoughts on the subject, proposing hybridization followed by the doubling of chromosomes (Harlan and De Wet, 1975; Soltis et al., 2014). Stebbins (1950) could be considered one of the most important thinkers on the importance of polyploidy, with fourteen chapters in his book *Variation and Evolution in*

TABLE 1 | Important terms relating to polyploidy and their definitions.

Term	Definition	References
Polyploidy	Condition where an organism contains more than two sets of homologous chromosomes, or more than a diploid, as a result of whole genome duplications	Glover et al., 2016
Allopolyploidy	Polyploidy generated through hybridization between two distinct species followed by genome doubling	Glover et al., 2016
Autopolyploidy	Polyploidy generated through intraspecific hybridization	Glover et al., 2016
Homolog	A gene in two species that are derived from the same ancestor	Mable, 2003
Ortholog	A homologous gene within two species that share the same function, formed as a result of a speciation event	Sonnhammer and Koonin, 2002
Paralog	A homologous gene within the same species that do not have the same function, formed as a result of a duplication event	Sonnhammer and Koonin, 2002
Homoeolog	Genes that originated due to a speciation event but were recombined due to allopolyploidization	Glover et al., 2016; Mason and Wendel, 2020
Paleopolyploidy	Ancient polyploidy, formed millions of years ago	Blanc and Wolfe, 2004; Soltis et al., 2009
Neopolyploidy	The most recent cases of polyploidy, can be used to describe artificially created polyploids	Ramsey and Schemske, 2002; Comai, 2005
Mesopolyploidy	Bridge between paleo and neopolyploidy, has occurred within the last 17 million years	Cheng et al., 2018
Aneuploidy	Situation where there is an abnormal number of chromosomes in a cell	Müntzing, 1936; Huettel et al., 2008
Subfunctionalization	Process where newly formed genes will retain some subset of the ancestral gene function	Force et al., 1999; Flagel et al., 2008
Neofunctionalization	Process where newly formed genes will obtain some new function	Force et al., 1999
Target site resistance	Herbicide resistance mechanism that is the result of a change to the genetic code	Sammons and Gaines, 2014
Non-target site resistance	Herbicide resistance mechanism that is a result of a change in the metabolism of a plant	Sammons and Gaines, 2014

Plants dedicated to the subject. Scientists were tasked with the painstaking endeavor of manually counting chromosomes under a microscope using the squash method, until the genomics era eventually brought about flow cytometry, a more accurate way to measure cellular contents, including DNA and chromosomes (Kron et al., 2007; Windham et al., 2020).

Much of what is understood about the history of polyploidization has come from studying crops (Beasley, 1940; Mcfadden and Sears, 1946). Thus far, genomic studies on *Triticum* (wheat) and *Gossypium* (cotton) have contributed the most to the current knowledge (Flagel et al., 2008; Moshe Feldman and Levy, 2009). Cultivated wheat is a good example of how studying polyploidization can be useful. Cultivated wheat is classified in three different cytogenic categories: diploid, tetraploid, and hexaploid. While the wild type progenitors for the diploid and tetraploid varieties have been determined, studies have shown that the hexaploidy varieties, like bread wheat (*T. aestivum*) have formed as a byproduct of cultivated tetraploid and wild diploid progenitors as a result of polyploidization (Feldman, 2001; Feldman and Levy, 2005). In allohexaploid bread wheat, there are three identifiable subgenomes, A, B, and D, which is seen as an AABBDD genome. These subgenomes are known to have derived from diploid progenitors *T. uratu* (AA) and *Aegilops tauschii* (DD). The progenitor of the BB subgenome is extinct, but is likely derived from a diploid closely related to *Aegilops speltoides* (Dubcovsky and Dvorak, 2007; Gornicki et al., 2014). The ability to identify these subgenomes provides a history of polyploidization in wheat, visualizing its progenitors, its center of origin (likely in southwest Asia), and estimating when the polyploidization likely occurred (Vavilov and Love, 1992; Feldman, 2001).

Polyploidization is a seemingly irreversible process, but all polyploid plants eventually undergo the process of diploidization. The process of a polyploid becoming a diploid again is a result of *genomic downsizing*, where genomes have been significantly reduced as a result of loss of DNA fragments, segmental DNA loss, and gene silencing, mainly to stabilize the genome (Wendel and Adams, 2005; Bird et al., 2019). Genomic downsizing most likely occurs immediately following a chromosomal duplication event. Drastic alterations to the genome are referred to as *genome shock*; a plant might not be prepared for such intense changes to its genome and these stabilization events could possibly occur to counteract the shock (Mcclintock, 1983). There is a case to be made that there are no true extant diploids, and should be considered to be paleopolyploids (Levy and Feldman, 2002). Combined with the fact that all diploid angiosperms are descended from polyploid ancestors, genomic downsizing over the course of millions of years could contribute to this claim (Force et al., 1999; Feldman and Levy, 2005). An example of this is present in corn (*Zea mays*); it has paleopolyploid characteristics and has origins as a segmental allopolyploid, but its genome was so drastically altered and silenced that it is a cytogenic diploid (Gaut and Doebley, 1997; Soltis and Soltis, 1999).

Duplicate genes in polyploids have many different pathways they can take: they can develop a new function (*neofunctionalization*), retain the ancestral function (*subfunctionalization*), or accumulate deleterious mutations and decay (Force et al., 1999). In the process of trying to maintain its status as a diploid, some plants will undergo the process of *instantaneous subfunctionalization*, which occurs immediately following genomic merger in order to retain all duplicate genes (Flagel et al., 2008). Different loss-of-function mutations can develop in both copies, but both copies must be retained in order to keep its ancestral function (Cheng et al., 2018). Upland cotton (*Gossypium hirsutum*) demonstrates subfunctionalization in the reciprocal silencing of its *adhA* homoeolog; the homoeolog is silenced rather than deleted, retaining all copies present (Adams et al., 2003). Larger populations are more likely to experience neofunctionalization rather than subfunctionalization because the genetic drift in large populations is going to be so slow that parental alleles are likely going to be silenced by deleterious mutations before fixation can occur (Soltis et al., 2010).

ADVANTAGES OF POLYPLOIDY IN EVOLUTION

Polyploidization allows organisms to react and survive; by their very nature, polyploids have a much higher range of genetic diversity than diploids, which certain environmental factors, such as habitat disturbance, nutritional stress, physical stress, and climate changes, can trigger new phenotypes, like increased allelopathic effect (Hegarty and Hiscock, 2007; Ramsey, 2011; Te Beest et al., 2012; Omezzine et al., 2017). New phenotypes may arise through heterosis, gene redundancy, or the formation of transgressive traits (Comai, 2005; McCarthy et al., 2016; Wei et al., 2019). The effects of heterosis was first identified by Darwin, whose experimental crosses resulted in more vigorous hybrids, i.e., heterosis (Darwin, 1876). There are two main models involved in heterosis: the dominance model and overdominance model. The dominance model hypothesizes that the slightly deleterious recessive alleles are complemented by superior dominant ones in hybrids (Hochholdinger and Baldauf, 2018). The overdominance model is used to describe polyploidization, as the progressive heterosis associated with polyploids is more complex due to the increasing vigor with increasing number of genomes (Birchler et al., 2010). While heterosis generally results in polyploids with better phenotypic performance than its parent species, plants with transgressive traits display extreme phenotypes outside of the range of its progenitors (McCarthy et al., 2016). Heterosis and transgressive traits have been shown to be potential improvements for epigenetic mechanisms in allopolyploids, like histone modification or cytosine methylation (Renny-Byfield and Wendel, 2014). Gene redundancy acts as a protective feature, shielding polyploids from the effects of deleterious mutations with the numerous copies present (Wendel, 2000). Even allelopathy (the ability to suppress growth in another plant), which is present in both diploids and polyploids, has been shown to increase in polyploids compared to diploids (Colquhoun, 2006; Omezzine et al., 2017). Hexaploid barnyardgrass (*Echinochloa crus-galli*) shows considerable allelopathic tendencies and Omezzine et al. (2017) was able to show that allelopathy increased as ploidy increased in fenugreek (*Trigonella foenum-graecum*) (Omezzine et al., 2017).

Allopolyploids provide some evidence of increased fitness over their progenitors. When diploid parents are crossed, typically their offspring have an increase in performance; polyploids produced more viable seed in extreme heat and drought conditions and differences in stomatal pore sizes that improved drought survival over their diploids counterparts (Madlung, 2013; Godfree et al., 2017). For example, cultivated wheat *(T. aestivum*) is an allohexaploid that has managed to survive over its B genome donor (Feldman and Levy, 2009). Allopolyploids also have more potential for ecological adaptation over their diploid counterparts, as shown through diploid and allopolyploid species of *Cardamine*; while different diploid species had a tendency to prefer only one environment, the allopolyploid species was able to grow and survive in all the environments tested (Shimizu-Inatsugi et al., 2017). The ability to alter phenotypes, as in functional trait divergence or generalized trait plasticity is one of the leading hypotheses regarding overall increased fitness in polyploid species (Van De Peer et al., 2017; Wei et al., 2019). Polyploid crops have huge adaptation potential and further studies are necessary to show the role of genetic variation resulting from polyploidy in this potential (Ramsey and Ramsey, 2014; Schiessl et al., 2017).

The study of neopolyploids furnishes strong insights in the evolution of polyploid species. *Spartina anglica* (common cordgrass), is an invasive neoallopolyploid weed species that arose in the last 200 years (Baumel et al., 2002). The neo-dodecaploid weed arose at the end of the nineteenth century as a result of a genome duplication between the already hybrid species *Spartina* X *townsendii*, which is a cross between hexaploids *Spartina alterniflora* and *Spartina maritima* (Ainouche et al., 2004). The duplication of the two unique subgenomes in *Spartina* X *townsendii* cements *S. anglica* as an allopolyploid as opposed to an autopolyploid. Compared to its progenitors, *S. anglica* has been shown to have increased fitness with its prolific seed production, fertility, and extensive lateral clonal growth, which was not seen in its sterile progenitor *Spartina* X *townsendii*. Baumel et al. (2002) was able to demonstrate that rapid, non-Mendelian changes involving preferential sequence elimination or modification of methylation patterns may occur in the earliest stages of polyploid stabilization. Other neopolyploids, like *Senecio* and *Tragopogon* have also been established within the last 200 years (Abbott and Lowe, 2004; Soltis et al., 2004). The development new polyploids aids in understanding gene silencing, cytosine methylation, and parental "non-additivity" play an active role in polyploidization and improving overall understanding of the process (Adams and Wendel, 2005).

WEEDS AND UNCONSCIOUS SELECTION

Aside from polyploidy, one way weeds have been able to thrive in a world that strives to exterminate them is through unconscious selection, or actively breeding plants in an environment different from their wild habitat, usually human-made (Zohary, 2004). Crops once considered weeds have been domesticated through *unconscious selection*, as they could not be differentiated from the crop they were growing alongside. The phenomenon of weeds imitating desired crops was noticed and thoroughly discussed by Nikolai Vavilov, who covered the process in "Origin and Geography of Cultivated Plants" (Vavilov, 1922). Vavilov looked into the centers of origins of crops, determining that there is more diversity in a species in an area where a species originated (McElroy, 2014). The process of an undesirable species evolving to mimic desirable ones as a means of survival has become known as *Vavilovian mimicry* (Pasteur, 1982). This phenomenon was first noticed, and well-established, between rye (*Secale cereale*) and wheat (*Triticum*) (Vavilov, 1922).

Before the time of chemical management, the only way to eliminate weeds when harvesting was by hand or hand-held implements. Since rye is remarkably visually similar to wheat, farmers often could not differentiate the two. When harvesting, rye would be selected for alongside the wheat, and when the harvested seed was replanted, unwanted rye would grow as well. Eventually, rye evolving alongside a desirable crop made it desirable as well. Rye could also perform better in colder climates than weaker wheat species did, but its increased fitness could possibly be contributed to crossing between the weed species and the crop it grew alongside (Harlan, 1965). This same principle of mimicry can be applied to modern day crop and companion weeds with cultivated rice (*Oryza*) and barnyardgrass (*Echinochloa crus-galli*, specifically ssp. *oryzicola*). In the seedling stage, barnyardgrass growing in paddy fields are virtually indistinguishable from rice, which makes manual weeding extremely difficult (Barrett, 1983). Barnyardgrass has also demonstrated allelopathetic tendencies in rice paddies, which provides even more difficulty in its management (Khanh et al., 2007; Guo et al., 2017)?

Another subset of Vavilovian mimicry is *seed mimicry*, where weeds may or may not look morphologically similar to the crop they contaminate, but the seeds produced by both crop and weed are identical in size and shape. While this might not be a problem when weeding by hand, but once mechanical winnowing came into play, the weed seeds only need to trick the machine (Harlan, 1982). An example of this is evident between balloonvine (*Cardiospermum halicacabum*) and soybean (*Glycine max*), which are morphologically dissimilar, however their seeds are indistinguishable in size and shape by a machine, which aids in the weed survival (Johnston et al., 1979). One final way weeds are unconsciously selected is through genetic mimicry. As weeds continue to grow, it is likely that they will develop herbicide resistance as an adaptation to human management practices.

As chemical herbicides became the primary weed management practice, herbicide resistance developed as the weed's survival mechanism. The more herbicides are continuously sprayed on crops, the more likely resistance to such herbicides will result in those weeds (Powles and Yu, 2010). Gene flow works in both ways; crops and weeds don't grow independently, genetic material can be shared between them, which is what leads to hybridization between the two (Harlan and De Wet, 1975; Gould, 1991). While unconscious selection plays a major role in basically how all weeds are bred, the real question is are polyploids the better weed? Do more polyploids exhibit characteristics of Vavilovian mimicry within the genetic subset? Before we answer these questions, it is important to look further into modern day weed management practices, specifically regarding herbicide and the effect it has on crops and weeds in general.

HERBICIDE RESISTANCE

In this modern era, herbicide resistance is the biggest problem currently faced with weeds. The two types of herbicide resistance typically dealt with are target site resistance (TSR) and non-target site resistance (NTSR). TSR develops directly against a mode of action, specifically as a mutation to the genetic code, as a single nucleotide polymorphism (SNP). NTSR relates to metabolism, as there are no direct changes to the genetic code (Sammons and Gaines, 2014). This can be seen as reduced absorption, translocation, or sequestration of the herbicide in the vacuole (Powles and Yu, 2010). To simplify our analysis of the effect of polyploidization on the formation of herbicide resistance traits, we have chosen to focus on well-described TSR mechanisms, specifically the glyphosate mechanism. Target site resistance provides a stronger case for increased weed survivability in polyploids, as multiple chromosome copies alone provide an environment for mutations to occur in at least one copy, and if that copy is expressed resistance should occur (Otto, 2007).

Polyploids develop glyphosate resistance at a faster rate than their diploid relatives. Glyphosate was first introduced by Monsanto in 1974 with the trade name "Roundup" and in the last decade has become the most used herbicide worldwide. It is a non-selective herbicide that targets the shikimic acid pathway and its ability produce folates and aromatic amino acids (Malik et al., 1989; Valavanidis, 2018). Target site resistance in glyphosate resistant plants results in mutations at the Pro106 location to either Thr, Leu, Ser, Ala, or a double substitution of Thr102 to Ile + Pro106 to Ser (TIPS) (Yu et al., 2015). With the introduction of Roundup Ready® (RR) crops as a staple in crop production, gene flow from RR crops has the potential to result in glyphosate resistant weeds, which presents a major problem for weed management (Mallory-Smith and Zapiola, 2008). Based on data from weedscience.org, weedy polyploid species like annual bluegrass (*Poa annua*), oat (*Avena*), junglerice (*Echinochloa colona*), and barnyardgrass (*Echinochloa crus-galli*) are just a few of the species reported resistant to glyphosate (Heap, 2019).

SHOULD POLYPLOID SPECIES SHOULD MAKE BETTER WEEDS AND BE MORE COMMON WITH HERBICIDE RESISTANCE?

Theoretically, target site resistance should be more common in polyploid weeds, since theoretically polyploids have a more flexible expression profile that allows them to silence adaptive

TABLE 2 | Weed species currently (9 June 2020) reported as resistant to glyphosate according to The International Survey of Herbicide Resistant Weeds and corresponding reported genomic data.

Family	Common name	Species	Chromosome number (2n)	Ploidy	1C (Mbp)	Glyphosate Resistant	TSR	NTSR	Genome	References
Amaranthaceae	Palmer amaranth	*Amaranthus palmeri*1	32	?	465	Yes	?	Yes	No	Gaines et al., 2011
Amaranthaceae	Spiny amaranth	*Amaranthus spinosus*1	34	2X	929	Yes	Yes	Maybe	No	Nandula et al., 2014
Amaranthaceae	Tall waterhemp	*Amaranthus tuberculatus* (syn. rudis)1	32	?	701	Yes	Yes	Yes	Yes	Nandula et al., 2013
Amaranthaceae	Smooth pigweed	*Amaranthus hybridus (syn: quitensis)*	?	?	686	Yes	Yes	Yes	No	Perotti et al., 2019
Amaranthaceae	Kochia	*Kochia scoparia*	18	2X	1095	Yes	Yes	Maybe	No	Wiersma et al., 2015
Asteraceae	Common ragweed	*Ambrosia artemisiifolia*1	36	4X	1134	Yes	?	?	No	Ganie and Jhala, 2017
Asteraceae	Giant ragweed	*Ambrosia trifida*1	24	2X	1868	Yes	?	?	No	Norsworthy et al., 2010
Asteraceae	Hairy fleabane	*Conyza bonariensis*	18	?	2043	Yes	?	Yes	No	Kleinman and Rubin, 2017
Asteraceae	Horseweed	*Conyza canadensis*	18	2X	440	Yes	Yes	?	Yes	Beres et al., 2020
Asteraceae	Sumatran fleabane	*Conyza sumatrensis*	54	?	?	Yes	?	?	No	Santos et al., 2014
Asteraceae	Hairy beggarticks	*Bidens pilosa*	72	?	1666	Yes	Yes	Yes	No	Alcántara-de la Cruz et al., 2016
Asteraceae	Greater beggarticks	*Bidens subalternans*	48	?	2915	Yes	Yes	?	No	Takano et al., 2020
Asteraceae	Plumeless thistle	*Carduus acanthoides*	22	?	?	Yes*	?	?	No	Heap, 2019
Asteraceae	Ragweed partenium	*Parthenium hysterophorus*	34	?	?	Yes	Yes	Yes	No	Bracamonte et al., 2016
Asteraceae	Common sunflower	*Helianthus annuus*	34	2X	3596	Yes	No	Yes	Yes	Singh et al., 2020
Asteraceae	Willow-leaved lettuce	*Lactuca saligna*	18	2X	2332	Yes	?	?	Yes	Amjad et al., 2018
Asteraceae	Prickly lettuce	*Lactuca serriola*	18	? (likely 2)	2606	Yes*	?	?	No	Heap, 2019
Asteraceae	Annual sowthistle	*Sonchus oleraceus*	32	4X	1568	Yes	?	?	No	Cook et al., 2014
Asteraceae	Russian thistle	*Salsola tragus*	36	?	?	Yes	?	?	Yes**	Kumar et al., 2017
Asteraceae	Coat buttons	*Tridax procumbens*	36	?	?	Yes	Yes	No	No	Li et al., 2018
Poaceae	Wild oat	*Avena fatua*	42	6X	12,646	Yes*	?	?	No	Heap, 2019
Poaceae	Sterile oat	*Avena sterilis* ssp. ludoviciana	42	6X	12,617	Yes	?	Yes	No	Fernández-Moreno et al., 2016
Poaceae	Australian fingergrass	*Chloris truncate*	40	?	?	Yes	No	Yes	No	Ngo et al., 2018b
Poaceae	Tall windmill grass	*Chloris elata*	?	?	?	Yes	No	Yes	No	Brunharo et al., 2016
Poaceae	Radiate fingergrass	*Chloris radiata*	40	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Feather fingergrass	*Chloris virgate*	20	?	?	Yes	Yes	No	Yes**	Ngo et al., 2018a
Poaceae	Sweet summer grass	*Brachiaria eruciformis*	18	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Ripgut brome	*Bromus diandrus*	56	8X	11687	Yes	No	Yes	No	Malone et al., 2016
Poaceae	Rescuegrass	*Bromus catharticus*	42	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Red brome	*Bromus rubens*	28	4X	4802	Yes?	?	?	No	Heap, 2019
Poaceae	Gramilla mansa	*Cynodon hirsutus*	?	?	?	Yes?	?	?	No	Heap, 2019
Poaceae	Sourgrass	*Digitaria insularis*	36	?	?	Yes*	?	Yes	No	Lopez Ovejero et al., 2017
Poaceae	Junglerice	*Echinochloa colona*	54	?	1320	Yes	Yes	Yes	No	Alarcón-Reverte et al., 2015
Poaceae	Barnyardgrass	*Echinochloa crus-galli*	54	?	1372	Yes*	?	?	Yes	Heap, 2019
Poaceae	Goosegrass	*Eleusine indica*	20	2X	709	Yes	Yes	No	Yes	Yu et al., 2015
Poaceae	Tropical sprangletop	*Leptochloa virgata*	40	?	?	Yes	Yes	Yes	Yes	Alcántara-de la Cruz et al., 2016

(Continued)

TABLE 2 | Continued

Family	Common name	Species	Chromosome number (2n)	Ploidy	1C (Mbp)	Glyphosate Resistant	TSR	NTSR	Genome	References
Poaceae	Annual ryegrass	*Lolium multiflorum*	14	2X	2661	Yes	Yes	No	No	Jasieniuk et al., 2008
Poaceae	Perennial ryegrass	*Lolium perenne*	14	2X	2695	Yes	Yes	Yes	Yes	Yang et al., 2018
Poaceae	Rigid ryegrass	*Lolium rigidum*	14	2X	2687	Yes	Yes	Yes	No	Pratley et al., 1999
Poaceae	Smooth barley	*Hordeum murinum* ssp. Glaucum	14	2X	5390	Yes*	?	?	No	Heap, 2019
Poaceae	Annual bluegrass	*Poa annua*	28	4X	2812	Yes	Yes	No	No	Cross et al., 2015
Poaceae	Johnsongrass	*Sorghum halapense*	40	? (sus. 4)	1614	Yes	No	Yes	No	Vila-Aiub et al., 2012
Poaceae	Liverseedgrass	*Urochloa panicoides*	44	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Arrocillo	*Paspalum paniculatum*	20	?	?	Yes*	?	?	Yes**	Heap, 2019
Plantaginaceae	Buckhorn plantain	*Plantago lanceolata*	12	2X	1174	Yes*	?	?	No	Heap, 2019
Brassicaceae	Birdsrape mustard	*Brassica rapa* syn campestris	20	2X	784	Yes*	?	?	Yes	Heap, 2019
Brassicaceae	Wild radish	*Raphanus raphanistrum*	18	?	?	Yes	?	?	Yes	Ashworth et al., 2014
Rubiaceae	Woody borreria	*Hedyotis verticillata*	?	?	?	Yes	?	?	No	Chuah et al., 2005

**Indicates that there was no paper associated with the article, just reported on weedscience.org (Heap, 2019).*
? indicates that there was no data available for that column.
***Indicates that there is only a partial genome present.*

TABLE 3 | Ploidy and glyphosate resistance status of the world's worst weeds as described by Holm and Herberger (1969), Holm et al. (1977).

Common name	Scientific name	Ploidy	Glyphosate resistant?
1969			
Purple nutsedge	*Cyperus rotundus*	?	No
Bermudagrass	*Cynodon dactylon*	6X	No
Barnyardgrass	*Echinochloa crus-galli*	6X?	Yes
Junglerice	*Echinochloa colona*	?	Yes
Goosegrass	*Eleusine indica*	2X	Yes
johnsongrass	*Sorghum halapense*	4X?	Yes
Cogongrass	*Imperata cylindrical*	2X?	No
Water hyacinth	*Eichhornia crassipes*	4X	No
Purslane	*Portulaca oleracea*	? (mixed)	No
Common lambsquarter	*Chenopodium album*	2X	No
1977			
Purple nutsedge	*Cyperus rotundus*	?	No
Bermudagrass	*Cynodon dactylon*	6X	No
Barnyardgrass	*Echinochloa crus-galli*	6X?	Yes
Junglerice	*Echinochloa colona*	?	Yes
Goosegrass	*Eleusine indica*	2X	Yes
Johnsongrass	*Sorghum halapense*	4X?	Yes
Cogongrass	*Imperata cylindrical*	2X?	No
Spiny amaranth	*Amaranthus spinosus*	2X	Yes
Sour paspalum	*Paspalum conjugatum*	2X?	No
Tropic ageratum	*Ageratum conyzoides*	? (mixed)	No

? Indicates that the data was not available.

alleles or loci with fitness costs when the allele offers no adaptive advantage (Otto and Whitton, 2000; Otto, 2007). TSR fitness costs have been identified, but the level of costs varies among different plant species (Vila-Aiub et al., 2009) and modes of action. In general, fitness costs have been associated with ALS, ACCase, and photosystem II (PSII) herbicides, which is especially evident in PSII herbicides because of the reduced photosynthetic capacity (Jansen and Pfister, 1990). Fitness costs in ACCase inhibitors should have no association with polyploidy because ACCase inhibitors only affect the plastid isoform (Murphy and Tranel, 2019). Glyphosate's role as the most widely used herbicide provides the lens for the focus of herbicide resistance in polyploids compared to other herbicides due to the possibility of both target and non-target-site resistance. Studies have shown that herbicide resistance alleles do not universally endow some type of fitness cost, but there is more of a cost in diploid species over polyploid (Vila-Aiub et al., 2009; Yanniccari et al., 2016). A reduction in fitness has been identified in glyphosate resistant goosegrass (*Eleusine indica*), rigid ryegrass (*Lolium rigidum*), and perennial ryegrass (*Lolium perenne*) (Preston et al., 2009; Yanniccari et al., 2016; Han et al., 2017). However, fitness costs in glyphosate resistant biotypes seem to be present on a case-by-case basis. The TIPS double mutation in the *E. indica* population came at a very high resistance cost, resistant *L. rigidum* populations may or may not have a fitness penalty, depending on the resistance allele present, and the fitness cost in *L. perenne* is not associated with a target-sire mutation, but rather high EPSPS activity. The Pro-106-Ser mutation, the most common target-site in glyphosate resistant biotypes, endows a low-level glyphosate resistance and is seemingly negligible in fitness costs compared to mutations endowing high level resistance, like the TIPS mutation (Vila-Aiub et al., 2019). There has been no investigation comparing the fitness cost of herbicide resistant polyploid species to the cost seen in diploid species, or even delving into the costs of herbicide resistance in any polyploid species. While there have been reviews showing the fitness costs of different herbicides, all data and conclusions are drawn from diploid species (Vila-Aiub et al., 2009). More studies should be performed in order to ascertain whether polyploidy plays a role in reduced fitness in association with herbicide resistance.

In order to examine how polyploidy affects weed survival, a survey of weeds was done on those reported as glyphosate resistant (Heap, 2019). A list of weeds reported as glyphosate resistant was assembled and the polyploidy, chromosome counts, and C-values were compared in **Table 2**. Out of 48 species selected, 12 are known to be diploid, four tetraploid, two hexaploid, one octoploid, and the remaining 29 species have a ploidy level that has not been confirmed, based on data from the Kew C-value database and the Chromosome Counts Database (Rice et al., 2015; Pellicer and Leitch, 2020). A few assumptions can be drawn about the species with unconfirmed ploidy: they could be diploid, polyploid, or have mixed ploidy, but thus far no studies have been done to confirm their ploidy. Ploidy determination is just one part of a bigger issue; according to the genome database from NCBI, out of the 48 species surveyed, only nine have fully sequenced genomes and two have RefSeq genomes. So along with the fact that there is little to no data to draw conclusions from, the majority of studies reporting glyphosate resistant are lacking in research beyond spray trials. Target site resistance should be considered a major factor for resistance and studies that just ignore the benefits of sequencing data can be detrimental. When sequencing data is in play, one can more accurately confirm TSR or NTSR, rather than just claiming NTSR.

BUT, DO POLYPLOIDS MAKE BETTER WEEDS?

Two questions need to be asked: "Are polyploids better weeds?" and "Are polyploids more likely to be resistant to herbicides?" The weeds historically referred to as the "world's worst weeds," has had relatively no changes, or at least no reported changes, to this list since first reported in 1969, and last updated in 1977 (referenced in **Table 3**) (Holm and Herberger, 1969; Holm et al., 1977). Based on data from the Plant C-Value database and the International Herbicide-Resistant Weed database, little can be determined whether ploidy or glyphosate resistance has any determining factor on what makes a better weed (Heap, 2019; Pellicer and Leitch, 2020). Barnyardgrass (*E. crus-galli*), which is known to be glyphosate resistant, a possibly hexaploid weed, would support the case for polyploidy providing better weeds; barnyardgrass has easily adapted to human activity, along with other polyploids like rye (*S. cereale*) and annual bluegrass *(Poa annua*) (Ye et al., 2014; Cross et al., 2015). A case could also be supported with the glyphosate resistant diploid species goosegrass (*Eleusine indica*), as there is a fitness cost associated with the double EPSPS gene mutation TIPS endowing glyphosate resistance (Han et al., 2017). Polyploids have adapted and survived due to polygenic selection over millennia (Stebbins, 1950). Comparatively herbicide resistance, both TSR and NTSR, is more often than not monogenic: this can be seen as a divergent single nucleotide polymorphism (SNP), a single unregulated metabolic enzyme, or even as a widely duplicated gene (Délye, 2013; Jugulam and Shyam, 2019).

Applying what is known about polyploidization in crops to weeds, one could try to assume an advantage for polyploid weeds. Factors that favor polyploid crop domestication should translate over to polyploid weed species. Heterosis, gene redundancy, and high genetic variability discussed above should act the same in weeds as they do in crops. Even in older, more established polyploid populations, you can see the benefit compared to diploids. Studies have shown that polyploids in general have the capacity to be more invasive over diploid species. Stevens et al. (2020) showed that tetraploid seeds tended to be larger than those of diploids, which contributed to tetraploid seeds being more dormant than the diploid seeds, less likely to germinate in stressful environments and therefore better adapted to said environments. Polyploid species have also been found to be more fecund and competitive than diploids, as seen in studies done with spotted knapweed (*Centaurea stoebe*) (Broz et al., 2009; Rosche et al., 2017). Studies on the three geo-cytotypes of *C. stoebe*, a native Eurasian diploid, a native Eurasian tetraploid, and an introduced North American tetraploid provided evidence that the polycarpic nature of the tetraploid biotypes allowed these biotypes to survive after the initial flowering and flower more than the monocarpic diploid biotype, and the introduced biotype even more than the native (Broz et al., 2009). Pandit et al. (2011) showed in an extensive study on rarity and invasiveness that diploid plants were more likely to be rare, while polyploids were more likely to be invasive. It has also been determined that polyploid species are less likely to experience inbreeding depression, due to the balancing effect of the presence of multiple gene copies (Rosche et al., 2017). The combination of higher seedling growth rates and diminished inbreeding depression creates an argument that polyploids are more invasive and therefore more competitive than diploids. Annual bluegrass (*P. annua*) has established itself on every continent and barnyardgrass continue to invade rice paddies, and when combined with the likelihood for developing herbicide resistance, namely glyphosate resistance, it creates some formidable weed species. And as mentioned before, there is even evidence that target site resistance in diploid plants significantly reduces fitness levels (Preston et al., 2009; Yanniccari et al., 2016; Han et al., 2017).

However, there are currently more reported diploid species resistant to glyphosate than there are polyploid. There are diploid species that are considered to be some of the most widespread and difficult weed species to manage, like smooth pigweed (*Amaranthus hybridus*) and horseweed (*Conyza canadensis*), that have high levels of glyphosate resistance with no fitness cost reported (Beres et al., 2018, 2020; Perotti et al., 2019). Purple nutsedge (*Cyperus rotundus*) and yellow nutsedge (*Cyperus esculentus*), whose ploidy levels (according to the Plant C-Value database) have not been reported, are considered some of the worst weeds on the planet because of control difficulty (Pereira et al., 1987; Arias et al., 2011; Pellicer and Leitch, 2020). And although its ploidy has, surprisingly, not yet been reported, Palmer amaranth (*Amaranthus palmeri*), is increasing one of the most difficult weeds to control (Rayburn et al., 2005; Gaines et al., 2011). Such fitness costs have not yet been reported in polyploid species and further investigation is required to determine if herbicide resistance has any negative effects in polyploids.

The sheer magnitude and complexity of polyploid genomes makes it difficult to perform large-scale genetics studies (Schiessl et al., 2017). While there have been polyploid genomes fully sequenced, the genomes sequenced have been relatively small, genome size wise, outside of the massive undertaking of sequencing the allohexaploid wheat genome (Zimin et al., 2017). Advances in genomics has made whole genome sequencing easier and cheaper as a whole, but it improving the possibility of sequencing polyploid genomes. Despite this, barnyardgrass remains the only polyploid weed genome sequenced (Kyriakidou et al., 2018). There is an obvious need for a well-established weed genomics database; while there are still challenges to this undertaking, it is a necessary step that needs to be taken in order to advance the understanding of polyploidy in weeds, and weed genomics in general (Patterson et al., 2019).

CONCLUSIONS

Based on the data that is available to us, *no conclusions can be drawn that polyploids make better weeds than non-polyploids*. At this point in time, there is no truly reliable database for genetic data on weed species, and even the available data on polyploid crops is lackluster. The Plant C-Value database is currently the most reliable, and while it offers data some data on polyploidy, including ploidy level and chromosome numbers, its purpose is to provide C-value data, not polyploid data. Even the list of the worst weeds in the world has not changed in the past 40 years, which should be highly unlikely, as the science is constantly changing. Research into weed genomics has room for improvement, and the development of weed genomics provides potential for greater understanding in how weed species evolve and the role polyploidy is playing and has played in weed evolution (Ravet et al., 2018; Patterson et al., 2019). The International Weed Genomics Consortium provides an outlet for collaborative research into weed genomics, with a growing genomics repository for weed species. The complexity of polyploids makes genomic work difficult; ploidy needs to be determined, chromosome copy number, and even then, certain genes might have more copies than are actually being tested. Next generation sequencing lends itself to providing more insight into polyploidy and its role in weed genomics. While there are more sources providing insight into weed genomics and a pathway for polyploid weeds, more extensive and in-depth research is required in order to fully comprehend the scale that polyploidy plays in understanding weeds.

AUTHOR CONTRIBUTIONS

JM and NH conceived the idea, developed the outline for the paper, and edited the paper. CR wrote the paper. JM and CR developed the tables. All authors contributed to the article and approved the submitted version.

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REVIEW
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Rapid Evolution of Invasive Weeds Under Climate Change: Present Evidence and Future Research Needs

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Although evolution has been often seen as a gradual process through a Darwinian lens, far more rapid evolutionary change has been observed in recent times. Recent examples documenting the potential speed of invasive plant evolution have included: latitudinal flowering clines, life history shifts, or abrupt changes in morphology. The timescales for such observations range from centuries down to <5 years. Invasive weeds provide good models for the rapid changes, partly because invasive weeds exhibit unique evolutionary mechanisms integral to their success. For example, purging of their genetic load may enable invasive plants to adapt more rapidly. Other genetic mechanisms include plasticity as an evolved trait, hybridization, polyploidy, epigenetics, and clonal division of labor. It is well-demonstrated that anthropogenic stressors such as habitat disturbance or herbicide use may work synergistically with climate change stressors in fostering rapid weed evolution. Changing temperatures, moisture regimes and extreme climate events operate universally, but invasive plant species are generally better equipped than native plants to adapt. Research on this potential for rapid evolution is critical to developing more proactive management approaches that anticipate new invasive plant ecotypes adapted to changing climatic conditions.

Keywords: hybridization, climate change, polyploidy, drought, plasticity, invasion biology, rapid evolution

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INTRODUCTION

Darwin's general vision for the way evolution works was via small, incremental changes, taking place over relatively long timespans (Gould and Eldredge, 1977). Although support for this Darwinian mode of evolution still pervades evolutionary theory, other models have emerged accommodating the reality that more rapid evolution than Darwin pictured frequently occurs (e.g., Alphen, 1999; Hairston et al., 2005; Pick and Heffer, 2012; Simon and Peccoud, 2018). In fact, in the past decade or two, there has been a paradigm shift where evolution occurring on a relatively short timescale is considered "ordinary" (Reznick et al., 2019).

In this review, we will look at evolutionary change in a particular group of species, invasive weeds. An invasive weed may be defined as a plant that is "either native or non-native, and may have negative effects on either natural ecosystems or agroecosystems, but must clearly be invasive in that it exhibits a tendency to rapidly colonize and spread to occupy new niches" (Clements, 2017). Some other sources define the term more narrowly, but with considerable overlap among niches among different types of plants in this general category, e.g., agricultural weeds that also invade natural areas and vice versa, we think it is useful to go with a more all-encompassing definition.

Invasive weeds provide many examples of more rapid evolutionary modes. Recent examples documenting the potential speed of invasive plant evolution have included: invasive plants establishing latitudinal flowering clines, life history shifts, or dramatic changes in root systems. The fact that many invasive plants are genetically depauperate, often due to possession of breeding systems with a high proportion of selfing (Clements et al., 2004), can work to their advantage, whereas genetic bottlenecks put endangered plants at risk of extinction (Lee et al., 2018). Even the evolutionary mechanism of purging of their genetic load may enable invasive plants adapt more rapidly (Marchini et al., 2015). The numerous other genetic mechanisms that have been attributed to rapid evolution by invasive weeds largely follow from adaptations from their roles as pioneer species for the most part, designed to respond rapidly to environmental stressors associated with disturbance.

The genetic structure of weed populations varies widely among weed species, and even varies intraspecifically among different weed populations in many cases. Outcomes of natural selection differ depending on genetic structure, so it is very important to understand the range of breeding systems among weed species. Furthermore, phenotypic plasticity is widely recognized as an extremely important trait for a large number of weed species, as first highlighted when Baker referred to weeds often possessing an "all-purpose genotype" (Baker, 1965). However, many invasive plants still rely on rapid evolutionary change to adapt to their environments, such that the "all-purpose genotype" is not a universally appropriate label for invasive weeds because many invasive weeds do have considerable genetic diversity and are capable of adapting to local conditions (Clements et al., 2004). Weed reproductive systems are diverse, and among the greatest potential influences on life-history changes during weed evolution may involve characteristics of the reproductive system itself (Barrett et al., 2008). Barrett et al. (2008) explore many possibilities for such transformations in plant reproductive systems, many of which involve clonality and asexual reproduction. For example, they cite the case of an aquatic invasive plant, *Eichhornia paniculata* (Spreng.) Solms (Brazilian water hyacinth) that went from being outcrossing in its native range to selfing in its invaded range, which was critical to establishment in its adventive range where its pollinators were absent (Barrett et al., 1989, 2008). Critically important is understanding how particular weedy traits, such as reproductive characteristics, are impacted by climate change stressors so that we can better predict what traits could adapt to higher temperatures, CO_2 levels and other climate factors (Clements and DiTommaso, 2011).

Climate change stressors such as changing temperatures, moisture regimes and extreme climate events are operating universally, but studies have repeatedly shown that invasive plant species are generally better equipped than native plants or crops to adapt. One indication of this is the observation of niche shifts. Climate niche breadths for eight weeds were on the whole, broader in China than in their native ranges (Wan et al., 2017). Plant species like *Solidago canadensis* L. (Canada goldenrod) not considered a weed in its native North American range grow much taller and larger in China making the plant more competitive, and recently becoming a serious management issue (Cheng et al., 2020). Research focusing on leading invasion edges, has demonstrated the ability of some species to adapt to rapidly changing temperatures or moisture levels that come with climate change (Lustenhouwer et al., 2018; Williams et al., 2019). Some of the clearest examples of rapid evolution of invasive plants in response to changing climate are abrupt changes in flowering timing, enabling these plants to maintain or increase their reproductive output (Barrett et al., 2008; Crimmins et al., 2009; Lustenhouwer et al., 2018; de Oliveira Xavier et al., 2019). Seed dispersal adaptations are also key to the success of many invasive plants, facilitating both population spread and population growth. Local adaption to changing climatic conditions have been studied the world over for many global colonizers. For example, adaptation to climate change by *Ambrosia artemisiifolia* L. (common ragweed) is evident on 5 continents: its home continent North America, South America, Europe, Asia and Australia (Essl et al., 2015; Gallien et al., 2016; Sun and Roderick, 2019; van Boheemen et al., 2019).

The purpose of this review is to provide an overview of what is presently known of the dynamic interaction between invasive plants and climate change, particularly focusing on the potential for invasive plants to adapt rapidly to changes in climate. This review will also reveal the numerous gaps in our knowledge of this potentially rapid weed evolution amidst climate change, and to suggest research approaches to fill these gaps. The world is changing quickly and we likewise need to respond quickly to the forecasted rapid evolution and spread of invasive plants to minimize the negative consequences.

RECENT EXAMPLES OF INCREASED INVASION UNDER CLIMATE CHANGE

There is a broad consensus that plant invasion will increase, and is already increasing due to climate change (Clements and DiTommaso, 2011; DiTommaso et al., 2014; Varanasi and Jugulam, 2016; Ramesh et al., 2017; Waryszak et al., 2018; Ziska et al., 2019). Three prominent predictions are: (1) poleward spread due to climate warming (Clements and DiTommaso, 2011), (2) range expansion due to changing precipitation regimes (Young et al., 2017), and (3) increased dispersal and establishment due to extreme climate events (Colleran and Goodall, 2015). Below we provide examples of these three predicted consequences of climate change, as well as the potential influence of rapid weed evolution as part of the response.

In terms of poleward spread of weeds due to climate warming, many documented incidences of relatively recent changes in distribution have been reported from North American, European, and Australian temperate regions, as well as in other global regions (Clements et al., 2014). Within North America, spread of numerous weed species northward, including those reaching Canada from the United States has provided abundant evidence of this prominent trend (Clements et al., 2004; Clements and DiTommaso, 2012).

One well-studied example is *Sorghum halepense* (L.) Pers. (Johnsongrass). Although originally introduced as a perennial C_4 grass from areas with Mediterranean climates in Eurasia and Africa (Warwick and Black, 1983), as it moved northward with crops, new ecotypes developed with rhizomes adapted to cold temperatures (Warwick et al., 1986). Additionally, some of the northern ecotypes may overwinter better via an annual life history. With climate change, *S. halepense* is predicted to spread further northward in North America, causing greater yield loss in *Zea mays* (corn) crops (McDonald et al., 2009). *S. halepense* exhibits many other evolutionary adaptations in addition to what we have listed here, enabling continual change of *S. halepense* populations at the northern edge of its range (Paterson et al., 2020).

Potential expansions in north-south ranges due to climate warming have been studied for a number of weeds that occur in both North America and Europe. For example, *Impatiens glandulifera* Royle. (Policeman's helmet), an invasive plant frequently infesting riparian areas has been studied in both continents (Kollmann and Bañuelos, 2004; Clements et al., 2008; Clements and DiTommaso, 2012). Presently *I. glandulifera* is distributed in relatively southerly regions within Canada, but the European research shows how life history traits tend to vary along a latitudinal gradient, thereby raising the possibility if rapid evolution occurred along the northern edge of its range, it could occupy the more latitudes in North America as seen in Europe. Furthermore, recent European research also points to *I. glandulifera* recently being able to invade forest habitats (Cuda et al., 2020; Gruntman et al., 2020) in addition to its historic spread via waterways, providing further evidence of how its adaptability might work in concert with changing climates.

As well as changes in mean temperatures in temperate regions, extensive changes in regional precipitation patterns are predicted, and have been seen trending in many areas, such as the western United States, which has seen increased frequencies of drought conditions and associated wildfires (Leung et al., 2004; Westerling et al., 2006). In the Western U.S., when modeling changes in weed distribution, precipitation variables are much more important than temperature (Bradley et al., 2009). *Centaurea solstitialis* L. (yellow starthistle) is a widespread invasive weed in many semi-arid parts of North America with Mediterranean-like climates, first having introduced as a seed contaminant in California in the mid-1800s (Bradley et al., 2009; Young et al., 2017). It has been referred to as California's worst wildland weed (Pitcairn et al., 2006). Summer and spring precipitation and winter and spring minimum temperatures currently constrain the range of *C. solstitialis* but Bradley et al. (2009) predict climate change involving more frequent droughts but higher levels of spring precipitation will lead to more widespread distribution in the western U.S. Relatively rapid genetic change seen in *C. solstitialis* via developing herbicide resistance (Sterling et al., 2001) and novel genotypes in different environments (Dlugosch et al., 2015) also predict its ability to take advantage of these changing precipitation regimes quickly (Young et al., 2017). Dukes et al. (2011) showed experimentally that *C. solstitialis* was able to increase its growth and fecundity more than other plant species with enhanced atmospheric CO_2.

There are many other invasive weed species in addition to *C. solstitialis* poised to take advantage of these changing climate regimes in western North America, with many of them already invading new areas in the wake of increased drought frequency and changing precipitation patterns. These include, but are not limited to *Bromus tectorum* L. (downy brome) (Harvey et al., 2020), *Ventenata dubia* (Leers) Coss. (ventenata) (Harvey et al., 2020), *Avena barbata* Pott ex Link (slender oat) (Nguyen et al., 2016), *Bromus madritensis* L. (foxtail brome) (Nguyen et al., 2016), and *Bassia scoparia* (L.) A. J. Scott (kochia) (Chen et al., 2020). However, it should be noted there are also invasive weed species less capable of withstanding drought conditions (Young et al., 2017). Young (2015) recorded an instance when a potential invasion by *Carduus nutans* L. (musk thistle) in Nebraska locale was halted abruptly by drought conditions that prevented the invading plants from reproducing.

Only recently have researchers turned their attention to the response of invasive weeds to extreme climate events like storms, floods and various other powerful weather events associated with climate change (Young et al., 2017). Flooding events can greatly enhance the spread of invasive weeds already adapted for spreading via seeds or vegetative fragments such as *Rosa rugosa* Thunb. (Rugosa rose) and *Reynoutria* spp. (Rouifed et al., 2011; Colleran and Goodall, 2015). A specific instance was observed in 2011, when fragments of *Reynoutria japonica* Houtt. Ronse Decr. (Japanese knotweed) were distributed widely and established new populations after Tropical Storm Irene impacted Vermont, USA in 2011 (Colleran and Goodall, 2015). Similarly, after Hurricane Sandy went through the New Jersey coast in 2012, an invasive sedge *Carex kobomugi* Ohwi (Japanese sedge) showed a much higher establishment rate in coastal dunes than the native beach grass *Ammophila breviligulata* Fernald. (American beachgrass) (Charbonneau et al., 2017). Similarly, a widespread invasive wetland grass in North America, *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), spreads much more rapidly with increased flood frequency levels, with its seed germination requiring temporary dry shoreline areas (Tougas-Tellier et al., 2015).

These examples of the potential for climate change to increase the distribution of invasive weeds reviewed here are just the tip of the iceberg of known examples, and there are no doubt many other examples of invasions and incipient plant invasions influenced by climate change that have yet to be documented and studied. In this review, we are interested in what this elevated dispersal under climate change may be accompanied by increased evolutionary potential as theorized (Clements and DiTommaso, 2011; Johnson et al., 2019), and a significant aspect of such potential evolutionary malleability are the diverse and unique genetic systems exhibited by invasive weed populations.

CLONALITY, PLASTICITY, AND EPIGENETICS AS EVOLVED TRAITS

When considering the introduction of clonal plants to novel ecosystems, one may think that such species would exhibit low diversity and therefore have low invasive success. For most plant

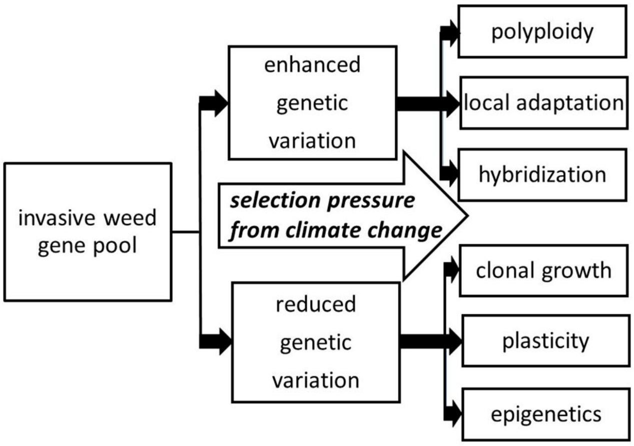

FIGURE 1 | Various directions that selection pressure from climate change can act to build on the invasive weed gene pool, including evolutionary mechanisms involving both increased and decreased genetic variation. By and large, these mechanisms are already operating for a given species prior to encountering climate change stressors, with these mechanisms providing channels for further adaptation.

populations, problems such as genetic bottlenecks and founder effects can be detrimental, leading to inbreeding depression and an overall decrease in evolutionary potential (Estoup et al., 2016). However, this idea is based on the understanding that the sole source of heritable variation comes from genes, based on the DNA sequence. In reality, there are other mechanisms of heritable phenotypic variation that are advantageous for invaders with relatively low levels of genetic variation. If the genome of an invasive weed is relatively plastic, and/or there are opportunities for adaptation through mechanisms like clonality or epigenetics, greater invasiveness can be arise under various types of selection pressure, including climate change (**Figure 1**).

In a review of 126 invasive plant species in China, researchers were able to demonstrate a significant positive relationship between clonality and invasiveness, indicating that clonality of a species greatly contributed to its invasive success (Liu et al., 2006). A unique advantage of clonal plants is the ability to share water, nutrients, and photosynthates between the individual ramets that make up the clone; this is known as physiological integration (Wang et al., 2020). The relationship between physiological integration and fitness has been studied in both heterogeneous and homogeneous environments, as well as under many environmental stresses. Physiological integration through below-ground rhizomes or stolons allows clonal plants to divide labor, with individual ramets becoming specialized to carry out a specific function within the clone. For example, a study of *Carpobrotus edulis* (L.) N. E. Br. (Hottentot fig), an aggressive clonal invader, revealed that older ramets became specialized in root production, allocating more biomass below ground than younger ramets, which became specialized in capturing above ground resources, having significantly higher chlorophyll content (Roiloa et al., 2013). Researchers also found that when compared to a clone with severed stolons, an intact clonal invader, *Fragaria chiolensis* (L.) Duchesne (beach strawberry), had higher overall biomass, greater expansion of stolons, and higher production of new ramets (Roiloa et al., 2010). This demonstrates that clonal division of labor can be advantageous for an invading species, as it directly contributes to the lateral expansion of the clone. This adaptive capability of clonal invaders can be selected for by genotypic selection, which Pan and Price (2002) describe as the selection of genotypically based traits associated with differences in the rate of ramet production. This means that ramets with more advantageous traits can be selected for in many cases. As the climate continues to change, this competitive ability will likely become even more advantageous. It has previously been documented that physiological integration can improve fitness of clones subjected to a variety of environmental stressors, such as nutrient deficiency (D'Hertefeldt et al., 2011), shading (Alpert, 1999), submergence (Luo et al., 2014) and drought (van Kleunen and Stuefer, 1999). These types of stressors, namely drought and flooding, are predicted to become more frequent and severe under climate change; the ability of clonal species to adapt and specialize ramets to overcome these stressors will allow them to continue invasion even under unfavorable conditions.

An additional advantage for clonal and non-clonal invaders alike is high phenotypic plasticity, which can be described as when a particular genotype expresses a variety of phenotypes in response to varying environmental conditions. Having high phenotypic plasticity can be advantageous for weeds if the resulting phenotypes result in an increase in fitness of the plant (van Kleunen and Fischer, 2005). The idea that this phenomenon contributed to plant invasions was proposed by Baker (1965), who posited that when a plant arrives in a novel environment with low genetic diversity, high levels of phenotypic plasticity allow the plant to adapt and eventually become established under the new conditions. As climate change progresses, it is thought that phenotypic plasticity may play a key role in helping plant populations avoid extinction. In recent years, more studies have investigated the relationship between climate change and plastic responses. In a recent review (Franks et al., 2014), 29 studies examining plastic responses of plants to climate change were analyzed, and it was found that all 29 studies demonstrated evidence of plastic responses to climate change, indicating that these types of responses can occur. However, despite adaptations to climate change occurring, the response may not be enough to keep up with the rapidly changing climate. In a review of 12 studies that investigated this, 8 found that the observed responses to changing conditions would not be sufficient to ensure survival of the population, given the predicted future climate scenarios (Franks et al., 2014).

The types of phenotypic responses to climate change are variable, including shifting flowering times, changes in biomass, stem count, or leaf size, or changes in reproduction. For example, a study of *Boechera stricta* (Graham) Al-Shehbaz (Drummond's rockcress) compared recently planted individuals to historical data of flowering time of the species in the region and found that it had shifted significantly, by 0.34 days between 1973 and 2011 (Anderson et al., 2012). Through genetic analysis, it was found that directional selection favored earlier flowering due to warming temperatures, and the researchers concluded that plasticity was an important driver of this shift (Anderson et al., 2012). In a study of the global weed *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed), which invades both terrestrial and aquatic environments, samples were taken in the species invasive ranges, USA and China, where it relies mainly on clonal reproduction and thus has lower genetic diversity, and in its native range in Argentina (Geng et al., 2007). It was therefore predicted that phenotypic plasticity in response to different water availability would be higher in the introduced ranges where genetic diversity was thought to be lower. However, researchers observed significant phenotypic plasticity responses in all three areas; in terrestrial environments, *A. philoxeroides* allocated more biomass to underground root formation, while producing smaller leaves and internodes to help balance water absorption and transpiration. In aquatic environments, *A. philoxeroides* stem pith cavities were larger, allowing them to float on the water surface in mats. Contrary to what was expected, the plasticity responses of the invasive populations fell within the plasticity response range of the native populations, meaning some of the native clones had higher plasticity than their invasive counterparts (Geng et al., 2007). However, according to a recent meta-analysis, it is thought that invasive populations of a species generally have higher plasticity than those in the native range (Davidson et al., 2011).

In addition to phenotypic plasticity, many introduced plants have the ability to respond quickly to changes in environmental conditions through epigenetic modification, which is the alteration of chromatin without changing the DNA sequence (Jones, 2012). Epigenetic modifications usually occur in the form of histone variants, histone modifications, and DNA methylation; these change the higher order chromatin structure, resulting in a change in gene expression such as altering transcription (Asensi-Fabado et al., 2017). These epigenetic modifications are often the result of changing environmental conditions, such as those in novel environments for introduced plants, or due to climate change. Epigenetic mutations have been documented in response to a variety of environmental conditions, including flooding, drought, shading, salinity, and temperature stress (Asensi-Fabado et al., 2017). For example, after several hours of drought stress, acetylation of *Arabidopsis* histones resulted in a drastic increase in transcription of drought-response genes (Kim et al., 2012). The majority of research indicates that epigenetic modifications constitute an intermediate method of rapid evolution for invasive species, as most stress-related modifications are only observed in chromatin until the stress exposure ends, then reverting back to their previous state (Pecinka and Scheid, 2012). Like DNA mutations, epigenetic mutations have the potential to be selected for if they are advantageous, so long as the stressor causing the mutation persists. This is especially advantageous for clonal invaders, which generally have lower genetic diversity, as well as for populations experiencing founder effects or bottlenecks. More recently, emerging evidence suggests that some modifications can be passed down even to non-stressed progeny through a "memory" of the stressed state (Pecinka and Scheid, 2012).

With the continued change in climate, adaptation to changing environmental conditions will likely become imperative for invasive species to thrive. Populations will begin to experience novel climates without expanding their geographic range, including more extreme temperatures as well as more frequent and severe storms. Rapid evolution through epigenetic modification, phenotypic plasticity, and clonality will continue to be used by successful invading plants of the future.

PURGING GENETIC MATERIAL DURING INVASION

In general, it can be said that inbreeding reduces the fitness of populations, as it decreases heterozygosity. Inbreeding also results in the expression of genetic load, which is the accumulation of deleterious recessive alleles which can reduce growth and expansion of a population (Keller and Waller, 2002). Small edge and founding populations are especially at risk of genetic loads, as they tend to have significantly lower genetic diversity due to drift. However, it has been observed that introduced species often become aggressive invaders despite population bottlenecks, which usually lead to inbreeding depression and genetic load expression (Estoup et al., 2016). This phenomenon has been coined the "genetic paradox" of invasion, where the anticipated negative effects of inbreeding within a limited population are not observed (Allendorf and Lundquist, 2003). Previous research of wild native plant populations revealed that at range edges, the effects of inbreeding depression were decreased, indicating that purging of the genetic load had occurred (Pujol et al., 2009; Barringer et al., 2012). Genetic purging can be described as a process where genetic load of deleterious alleles is reduced as those alleles are selected against (Barringer et al., 2012).

In order to determine whether genetic purging occurs in expanding invasive populations, a study of a recent North American invader, *Brachypodium sylvaticum* (Huds.) P. Beauv. (slender false brome) was conducted by Marchini et al. (2015). The researchers hypothesized that intermittent gene flow to a small, isolated, inbreeding population would allow for selection of high fitness alleles at loci that had previously been fixed for deleterious mutations. Limited gene flow, occurring by outcrossing once every few generations with another population, is reflective of an invasive species slowly expanding its range (Marchini et al., 2015). The study determined that genetic purging removed deleterious mutations in populations that were primarily inbreeding with periodic gene flow, as opposed to populations that were outcrossing or inbreeding only. The level of purging was variable, depending on the size of outcrossing populations, the number of deleterious loci, and the initial diversity levels throughout the metapopulation. Because the level of genetic purging is dependent on initial genetic diversity, invasive species that have higher diversity, such as those which have had multiple introductions to the invasive region, would likely exhibit higher levels of purging. In contrast, a stable metapopulation of a native species would be more likely to have populations from single origins, in turn having lower diversity and higher relatedness, which increases the likelihood of fixation of deleterious alleles. Purging levels within populations was found to be highest when outcrossed among populations every 5 generations and the number of affected loci was low; in this scenario, 90% of loci became fixed for homozygous "normal" alleles, and no loci were fixed for deleterious alleles (Marchini et al., 2015). Interestingly, the authors also found that frequency of homozygous "normal" alleles was significantly higher in an inbreeding metapopulation with gene flow, which had a frequency of over 90% after 100 generations, compared to a single large outcrossing population, where frequency was only around 65%. This confirms the hypothesis that inbreeding with periodic outbreeding can purge genetic loads, increasing fitness of populations at range edges after relatively few generations. Continued range expansion of many invasive species is anticipated under climate change; this will likely facilitate the generation of new selfing lineages due to the purging of genetic loads.

HYBRIDIZATION, POLYPLOIDY, AND RAPID EVOLUTION

The counterintuitive result of increased invasiveness of invasive weeds, even if genetic variation is relatively low, clearly operates in ecosystems subject to changing climate, as described previously. However, enhanced genetic variation is also an effective means to fuel rapid evolutionary change as natural selection generates novel, locally adapted genotypes, a process frequently accompanied by other mechanisms like hybridization and polyploidy in invasive plants (**Figure 1**).

Interspecific hybridization results in new genetic combinations that can be acted upon by natural selection and is a well-used mechanism of adaptive rapid evolution, especially in invasive plants. It provides a way for genetically impoverished species, such as clonal organisms and populations experiencing bottlenecks or founder effects, to increase their genetic diversity and overall fitness. Hybridization increases fitness through the generation of "extreme" novel phenotypes, as two genetically distinct parent species reproduce, recombining their alleles (Kagawa and Takimoto, 2018). The resultant hybrid often exhibits improved biological function compared to either parent species; this concept is known as heterosis, or hybrid vigor. Hybrids will generally be larger in size, more fecund, and more display greater growth levels when compared to the parent species. In systemic review of invasive hybrids compared to their parent taxa, Hovick et al. (2014) found that the hybrids were generally larger, more fertile, and more invasive than their parents. In plants, hybridization is often associated with invasion; many invasive plant systems support the hybridization-invasion hypothesis, which states that interspecific hybridization promotes invasiveness (Hovick et al., 2014). These systems are also often associated with polyploidy, with 63% of the hybrids reviewed reported as polyploid, and of those, nearly 50% had increased ploidy compared to their parents (Hovick et al., 2014). A systemic review of 309 invasive plants and 112 rare endemics by Dar et al. (2020) revealed that invasive species were also more likely to be polyploid than native species, and also showed that the proportion of polyploids increases with more advanced invasion. In many instances, the effects of hybridization and polyploidy in invasive plants are closely linked, and it can be difficult to tell which, or both, has the most influence on invasiveness.

Polyploidy, also known as whole genome duplication (WGD), resulting in more than two sets of chromosomes in the genome, is a common process in plants, suggesting some kind of evolutionary advantage (Chen, 2007). In plants, it is usually associated with tolerance to a broad range of ecological conditions and has also been linked to higher levels of asexual reproduction, an increased resistance to pathogens, and changes to seed germination and dormancy (Dar et al., 2020). These characteristics, along with an increase in genetic diversity, can greatly influence the fitness of polyploid invaders. Polyploid organisms can further be broken down into two categories: autopolyploids and allopolyploids. An autopolyploid is the result of doubling a diploid genome, while an allopolyploid is the result of two distinct genomes combining; allopolyploidy occurs by interspecific hybridization followed by either chromosome doubling or fusing of gametes, or by interspecific hybridization of two tetraploids (Estep et al., 2014). Allopolyploids therefore have the combined positive benefits of heterosis and polyploidy, usually exhibiting higher fertility, genetic diversity, and phenotypic plasticity (Estep et al., 2014). Knowing that polyploid species have favorable characteristics such as heterosis, gene redundancy, and high genetic variability, one may hypothesize polyploids are better weeds than diploids. In general, polyploids have a higher invasive capacity than diploids; polyploids have been shown to have larger seeds that are less likely to germinate in unfavorable conditions, have higher fecundity and competitive ability, as well as being less likely to experience inbreeding depression than diploid species (Rutland et al., 2021). However, some of the worst global invaders are diploid, not polyploid; additionally, there are many weeds whose ploidy levels remain unknown, and as a result, large scale sequencing of polyploid weeds needs to be done before conclusions their fitness can be drawn (Rutland et al., 2021).

As mentioned, the processes of hybridization and polyploidy are often linked, especially in the case of allopolyploid species, as both provide benefits to expanding invasive plant populations. One of the interesting ways that polyploidy contributes to fitness of hybrid plant populations is through "pre-adaptation" to new environmental conditions, which assists plants during early establishment (te Beest et al., 2012). For example, in the case of the tetraploid *Centaurea stoebe* L. (spotted knapweed), widespread invasion throughout the USA is attributed to pre-adaptation of the native tetraploids Europe to a wide range of climates, including extremely dry conditions, compared to diploids in the native range. Despite both the diploid and tetraploid cytotypes being introduced to the USA, invasive populations are dominated by tetraploids (Henery et al., 2010). Additionally, polyploidy and hybridization may increase fitness by "masking" genetic load, rather than purging them, in inbreeding and outcrossing populations. Non-deleterious alleles are usually dominant and can "mask" recessive deleterious alleles. In another study of *C. stoebe,* it was found that due to the multiple chromosome sets and higher number of alleles per locus, tetraploid populations could mask deleterious alleles much more effectively than diploids, resulting in significantly lower levels of inbreeding depression (Rosche et al., 2017).

Hybrid and polyploid populations are also key components of range expansion, which has been well-documented in the case of the hybrid *Reynoutria* × *bohemica* Chrtek and Chrtková (Bohemian knotweed). A shift in habitat preference has been observed in *R.* × *bohemica*, as it has been found invading environments that neither parent species usually inhabit. A study by Walls (2010) found abundant populations invading beaches, coastlines, and estuaries, a very different habitat than the ditches, roadsides, and riparian zones where the parent species are usually found. It was found that high phenotypic plasticity of the hybrid allowed the populations to exhibit high drought and salinity tolerance, which is not frequently observed in either parent species. Under continued climate change, it is likely that invasive plant populations will encounter novel environmental conditions and new ecological niches. An example of this can be observed in the genus *Spartina,* which is comprised of around 13 species, usually occupying salt marsh habitats (Ainouche et al., 2009). This genus has a complex invasion history, with multiple hybridization and polyploidization events that have contributed to its invasive success (Ainouche et al., 2009). In a study of a *Spartina* allopolyploid, *S. maritima* × *densiflora* in the Mediterranean region it was found that increased temperatures during the flowering months (June–August) was positively correlated with greater lateral expansion and increased size compared to *S. maritima, S. densiflora,* or an *S. densiflora x maritima* hybrid (Gallego-Tevar et al., 2019). The increase in mean maximum monthly temperature during the study period, which is associated with an increase in flowering time in *Spartina,* was similar to predicted temperature increases under climate change for the region (Giannakopoulos et al., 2009). Thus, we may speculate that the conditions caused by anthropogenic climate change will increase opportunities for hybridization and polyploidization events in invasive plant populations because of the expected increase in intensity of selection pressure. Given the potential for genetic change already seen in the cases we have reviewed, novel hybrids and polyploids will likely continue to rapidly adapt to evolving climate conditions, making them aggressive competitors and invaders of native habitats.

EVIDENCE OF RAPID EVOLUTION ON INVASION EDGES

Initial incursions of invasive plants are often scattered randomly across a given region. This pattern of initial invasion occurs if, as in most cases, human agency marks the beginning of the invasion. In fact, many plant invasions begin as escapes from cultivation, and may originate at a single location. However, over time an invasion front or edge becomes established, as invasive plant populations expand. For example, in North America for many invasive plant species the invasion front is on the northern edge of ranges of various species (Clements et al., 2004). If these invasive plant populations are somewhat constrained by climatic conditions, further expansion may be limited by climatic conditions at the edge of the range, and if the conditions change, invasive plant ranges predictably expand. Models may be devised to predict such range expansion utilizing data on climate change the species niches (Jiménez-Valverde et al., 2011), but if they fail to account for evolutionary processes at the edges of the range, such models may underestimate the spread of invasive plants (Clements and DiTommaso, 2011). As already described, there are particular mechanisms by which such rapid evolution at the edge of expanding ranges could occur, such as clonality, plasticity, epigenetics, hybridization, polyploidy or purging of genetic material. However, in this section of the review, we summarize case studies providing evidence for potential rapid evolution of invasive plants on invasion edges, regardless of mechanism.

It has been frequently shown that invasive species may evolve new climatic tolerance ranges in their invasive ranges by comparison to their native ranges, although this is not universally true, and in fact a recent analysis of 86 studies examining 434 invasive species concluded the invasive niches are largely conserved (Liu et al., 2020b). Still, the exceptional cases are critical species to monitor. Among the 8 weed species evaluated by Wan et al. (2017) in China, *Amaranthus retroflexus* L. (redroot pigweed) showed the broadest niche expansion by comparison to its niche in North America (**Table 1**). *A. retroflexus* is widespread weed of cropland and other environments throughout the world (Costea et al., 2004), and thus its apparent ability to evolve to new climatic conditions fairly rapidly (Wan et al., 2017) should be monitored closely. As mentioned previously, there is evidence for *Ambrosia artemisiifolia* expanding its niche breadth throughout the world (Essl et al., 2015; Gallien et al., 2016; Sun and Roderick, 2019; van Boheemen et al., 2019; Sun et al., 2020), including in China where *A. artemisiifolia* exhibited genetic differences in growth patterns compared to populations in North America where the species is native (Sun and Roderick, 2019; **Table 1**). Sun and Roderick's (2019) assessment represents evolutionary change in these Chinese populations in <100 years since the introduction of *A. artemisiifolia* in 1935 (Wan et al., 1993). Because *A. artemisiifolia* is projected to further expand its range under climate change (Qin et al., 2014), the ability to adapt quickly to different climatic conditions (Sun and Roderick, 2019) signal that this is also an important species to monitor as the climate changes, both for distributional changes and novel genotypes.

When considering the question of rapid niche expansion under climate change, as discussed previously it is important to consider unique genetic mechanisms, such as the purging of deleterious alleles seen in *Brachypodium sylvaticum* (Marchini et al., 2015) and polyploidy in *Solidago canadensis* (Cheng et al., 2020) (**Table 1**). The concept of purging of deleterious alleles during invasion is relatively new, and more research needs to be done to investigate the likelihood that other invasive species may employ the same strategy. The role of polyploidy in invasion is well-demonstrated (Estep et al., 2014), and *S. canadensis* presents a compelling case for how this might influence rapid evolutionary change in a changing climate. Cheng et al. (2020) found that diploid forms of *S. canadensis* tended to go extinct in their common garden experiment, whereas tetraploids and hexaploids competed well with native vegetation, particularly if they were

TABLE 1 | Cases demonstrating potential rapid evolution of invasive plants under climate change for species exhibiting general niche expansion in the invaded range.

Invasive plant species	Geography and climate	Potential rapid evolution	Source
Amaranthus retroflexus L. (redroot pigweed)	Novel climates experienced in China compared to North American range	Relatively high niche expansion in introduced Chinese range	Wan et al., 2017
Ambrosia artemisiifolia L. (common ragweed)	Invasive populations in China vs. native North American populations	Height, total and stem biomass greater in invasive populations than in native populations	Sun and Roderick, 2019
Brachypodium sylvaticum (Huds.) P. Beauv. (slender false brome)	Expansion of ranges along edges in Oregon (and other parts of North America)	Purging of deleterious alleles leading to lower inbreeding depression and higher fitness edge populations	Marchini et al., 2015
Solidago canadensis L. (Canada goldernrod)	Extensive spread throughout various Chinese climate zones since introduction from North America in 1935	Polyploidy enhances competitiveness in the introduced range regardless of climate	Cheng et al., 2020

from the introduced range (hexaploids from the native range eventually failed to outcompete native vegetation), suggesting that rapid evolution in the polyploid forms after introduction to China played a role in successful invasion. Field sampling by Wan et al. (2020) identified all populations of *S. canadensis* in China they sampled between 2013 and 2016 as hexaploid, in contrast to North American samples which displayed a range of ploidies. In terms of climate change, latitudinal clines in China indicate *S. canadensis* is adapting to particular climates, and therefore capable of adapting to future climate changes (Li et al., 2016).

As described previously, there is considerable evidence for potential future poleward spread of invasive plants, in addition to observations of latitudinal spread over the previous century due to warming occurring in temperate regions, and furthermore there is evidence for a role of rapid evolution in accelerating this movement (**Table 2**). Similar to trends seen for many Angiosperm species, native or non-native, *Dittrichia graveolens* (L.) Greuter (stinkwort) has exhibited recent genetic changes in flowering phenology across a north-south European gradient (Lustenhouwer et al., 2018). The same pattern and ability to adapt flowering phenology was seen in *I. glandulifera* in Europe (Kollmann and Bañuelos, 2004). Because *I. glandulifera* also invades over a similarly broad latitudinal range in North America (Clements et al., 2008), it likely forms a similar genetic gradient on the North American continent. Genetic variation in *I. glandulifera* populations is derived from outcrossing, whereas other species like *S. halepense* although mostly selfing derives some of its genetic diversity through introgression with the crop sorghum [*Sorghum bicolor* (L.) Moench] (Warwick et al., 1984; Clements and DiTommaso, 2012). Indeed, the evolutionary novelty allowing *S. halepense* to colonize more northerly environments in North America has been attributed to this genetic diversity. Its rhizomes have evolved cold tolerance, even though when it was introduced in the early 1800s it was a C_4 grass adapted only to the warmer climates consistent with its origin in western Asia (McWhorter, 1971; Paterson et al., 2020). Furthermore, northern populations may exhibit an annual life history, allowing *S. halepense* to overwinter more readily along the northern edge of its range (Warwick et al., 1986). The adaptation of *S. halepense* to both warm and cooler climates illustrates its striking ability to adapt to a range of climates, and thus the species is poised to benefit from climatic changes across its six continent distribution.

The potential for adaptation by *Spartina maritima* × *densiflora* to novel environments, including warmer climates, stem from greater genetic variability achieved through hybridization (Gallego-Tevar et al., 2019; **Table 2**). As detailed previously, *S. maritima* × *densiflora* is part of a complex of *Spartina* species which hybridize extensively, providing a much greater range of genetic material than in the gene pool of a single species. Ironically, the parental species *Spartina maritima* (M. A. Curtis) Fernald is relatively uncommon and with increased warming in Europe, *S. maritima* × *densiflora* threatens to competitively supplant its parent (Gallego-Tevar et al., 2019).

Taraxacum officinale F. H. Wigg (common dandelion) is well-known for its adaptability the world over, invading urban and agricultural environments. A Chilean study found considerable variation in *T. officinale* over a north-south latitudinal gradient, with more southern populations featuring thinner seed coats (Molina-Montenegro et al., 2018; **Table 2**). Despite the dominant mode of asexual reproduction by *T. officinale* via apomixis, the Chilean study found that there was enough sexual reproduction occurring to create diverse genotypes forming the latitudinal gradient (Molina-Montenegro et al., 2018). As well as the impact of north-south temperature gradient, Molina-Montenegro et al. (2018) attributed the genetic differences in seed coat thickness to moisture patterns, in that in drier conditions, seeds with thicker coats will be tend to germinate only when rainfall is sufficient for growth and development. They pointed out that this adaptive feature may allow *T. officinale* to adapt to changes in moisture regimes predicted under climate change, as has been shown for many other invasive plant species (**Table 3**).

One particular region that represents changing moisture regimes subject to more frequent droughts under climate change is western USA, including California where a 5-year grassland study showed that two invasive grasses were able to evolve more drought-resistant traits with just 5 years of selection pressure (Nguyen et al., 2016; **Table 3**). The affected traits were slightly

TABLE 2 | Cases demonstrating potential rapid evolution of invasive plants under climate change for species evolving along latitudinal gradients.

Invasive plant species	Geography and climate	Potential rapid evolution	Source
Dittrichia graveolens (L.) Greuter (stinkwort)	Invading northward in Europe from the Mediterranean region	Within 50 years, northern populations evolved to flower as much as 4 weeks earlier than southern populations	Lustenhouwer et al., 2018
Impatiens glandulifera Royle. (policeman's helmet)	Invasive populations occur along a latitudinal gradient including most central and north-eastern European countries	Northern ecotypes flowered earlier but had lower above-ground biomass, height and basal diameter	Kollmann and Bañuelos, 2004
Sorghum halepense (L.) Pers. (Johnsongrass)	Recent spread across 6 continents, poised to extend range 200–600 km northward in 21st century	Seed size, lutein, and rhizome growth and survival fueled by introgression with domestic sorghum	Paterson et al., 2020
Spartina maritime × *densiflora*	Increased ability to invade during high temperature events in the Mediterranean region	Earlier flowering times, greater lateral expansion, increased size	Gallego-Tevar et al., 2019
Taraxacum officinale F. H. Wigg (common dandelion)	Populations occur over a latitudinal gradient in Chile, expanding southward	Southern populations have a thinner seed coat than northern populations	Molina-Montenegro et al., 2018

different for *Avena barbata* by comparison to the other grass species, *Bromus madritensis* (**Table 3**), but in both cases the plants subject to more frequent droughts exhibited markedly changed genotypes, illustrating that this kind of evolutionary change can occur over just a few generations (Nguyen et al., 2016).

An important consideration in the rapid evolution of invasive plants to climate change, is the interaction of anthropogenic stressors, i.e., synergism between human-caused climate change and other human habitat modifications favoring invasive species. Potential and observed changes in *Bassia scoparia* provide clear examples, such as the potential for this widespread invasive plant in western North America to form herbicide resistant genotypes and become more drought-resistant (Chen et al., 2020; **Table 3**). Similarly, various species of *Centaurea* introduced from Eurasia are exhibiting evolutionary change in their invaded range in western North America, where they have already been taking advantage of anthropogenic disturbances, such as overgrazing of rangeland by livestock, and now threaten to become even more abundance and widespread as drought frequency increases (Henery et al., 2010; Dlugosch et al., 2015; Turner et al., 2017; **Table 3**).

The annual forb *Erodium cicutarium* (L.) L'Hér. ex Aitonv (redstem filaree) is a global invader, having invaded all continents from its native Europe, and reaching both California and Chile some 300 years ago (Mensing and Byrne, 1998; Fiz-Palacios et al., 2010). Latimer et al. (2019) were able to observe a similar pattern of evolutionary adaptation among genotypes in both regions, with traits arising specifically adapted to local moisture conditions. This finding demonstrates the ability of global invasive plants like *E. cicutarium* to adapt to moisture gradients wherever they are introduced, in a relatively short period of time, presumably mirroring environmental changes expected as the climate continues to change.

An important consideration in understanding probable distribution changes of invasive plants under climate change is the ability to both adapt to novel climatic conditions and also effectively modify their dispersal and establishment abilities. *Reynoutria* × *bohemica* exemplifies this important consideration in many different ways (Walls, 2010; Gillies et al., 2016; **Table 3**). Walls (2010) found *R.* × *bohemica* was able to develop traits allowing it to better invade coastal areas in eastern North America. In the next session we focus on rapid evolution within this particular taxa, and implications for management.

CASE STUDY OF RAPID WEED EVOLUTION IN *REYNOUTRIA* SPP. (KNOTWEEDS)

The hybridization event that has repeatedly created *Reynoutria* × *bohemica* (Bohemian knotweed) in different continents, including Europe, North America, Australia and New Zealand (Bailey and Wisskirchen, 2004), has produced a plant with a much more potential for long-distance dispersal than its largely sterile male parent, *Reynoutria japonica* (Japanese knotweed) (Gillies et al., 2016). Similarly, the fertile female parent, *R. sachalinensis* (F. Schmidt) Ronse-Decraene (giant knotweed) tends to be less problematic for management, including being less likely to spread vegetatively via rhizomes (Parepa et al., 2014). The importance of this hybridization between *Reynoutria* species for the invasiveness of knotweed is still unclear because the hybrids have only recently spread and been discovered (Bailey and Wisskirchen, 2004; Gaskin et al., 2014; Parepa et al., 2014; Gillies et al., 2016). It seems clear that the genetically diverse hybrid swarm constituting the *R.* × *bohemica* hybrid should enable this invasive weed to adapt more rapidly to climate change than either parent. There are concerns that the increased diversity could facilitate adaptations such as herbicide resistance (Strelau et al., 2018). The hybrid has frequently been observed forming incursions into crop fields from field edges, and thus

TABLE 3 | Cases demonstrating potential rapid evolution of invasive plants under climate change for species adapting to new moisture regimes in the invaded range.

Invasive plant species	Geography and climate	Potential rapid evolution	Source
Avena barbata Pott ex Link. (slender oat)	Southern California grasslands subject to droughts	Leaf chlorophyll, seed biomass and flowering time values changed after 5 years simulated drought treatment	Nguyen et al., 2016
Bassia scoparia (L.) A. J. Scott (kochia)	Range expansion in parts of North America with increased droughts	Large genetic variability including adaptations for germination, seedling emergence and herbicide resistance	Chen et al., 2020
Bromus madritensis L. (foxtail brome)	Southern California grasslands subject to droughts	Water use efficiency and flowering times changed after 5 years simulated drought treatments	Nguyen et al., 2016
Centaurea diffusa L. (diffuse knapweed)	Invasion of drought prone areas of North North America from Eurasia	Invasive genotypes with higher expression of genes related to energy production enabling greater drought resistance	Turner et al., 2017
Centaurea stoebe L. (spotted knapweed)	USA tetraploid population invades range of climates readily including drought prone regions	Pre-adaptation to extreme climates due to polyploidy in life history	Henery et al., 2010
Centaurea solstitialis L. (yellow starthistle)	Invasion of California grasslands and continued invasion of disturbed habitat subject to drought	Evolution of ability to utilize scarce water resources more rapidly than native competitors	Dlugosch et al., 2015
Erodium cicutarium (L.) L'Hér. ex Aitonv (redstem filaree)	Invasive populations occupy similar wetter and drier zones within both Chile and California	In both regions, genetic differences in growth, flowering time and leaf functional traits evolved in response to moisture level	Latimer et al., 2019
Reynoutria × *bohemica* Chrtek and Chrtková (Bohemian knotweed)	Enhanced ability to invade areas of coastal North America	Compared to parent plants, hybrid showed differences in growth, lamina, specific leaf area and biomass allocation	Walls, 2010

could potentially become a serious crop pest in addition to being an invasive weed degrading natural and urban habitats. Extensive dispersal via agricultural drainage ditches is on the increase in coastal British Columbia, Canada (Clements and Jones, pers. Comm.). Parepa et al. (2014) argued that because the hybrid species was clearly the most variable among various European populations sampled from the three species, it was more competitive than its parents and similar trends have been seen in North America (Gaskin et al., 2014; Clements et al., 2016; Gillies et al., 2016). Epigenetic mechanisms are also involved in the specialized adaptations of *Reynoutria* spp., even the sterile *R. japonica*, and Parepa et al. (2014) predicted that such epigenetic mechanisms will be even more effective in facilitating local adaptations in genetically diverse *R.* × *bohemica* populations.

In their combined invasive and native ranges, *Reynoutria* spp. encounter a vast range of climates. Generally, *Reynoutria* spp. prefer a temperate or continental climate, and thrive in areas with >500 mm of annual precipitation. Beerling (1993) identified an annual threshold of 2,505 degree days and minimum temperature of −30.2°C for knotweed establishment. Young shoots are susceptible to frost in the late spring and early fall, which can cause dieback followed by new growth from the rhizome when conditions are favorable, as the rhizomes can survive temperatures well below freezing (Sołtysiak, 2020). As the global climate continues to warm, an expansion in the range of all three knotweed species is anticipated. Bourchier and Van Hezewijk (2010) modeled suitable habitat for *R. japonica* in British Columbia, Canada and found that 12.3% of the province was suitable based on precipitation, minimum temperature and degree day thresholds. At that time, only about half of the suitable area was inhabited with knotweed. The modeling was repeated in Ontario, Canada and found that 35% of the province was suitable habitat for *R. japonica*; however, when the climate thresholds were changed from normal values between 1971 and 2000 to data from 2000 to 2008, the suitable habitat increased to 53%. This indicates that northward expansion will likely occur as the climate continues to gradually warm. In fact, *Reynoutria* spp. populations at the northern edge of their ranges in Quebec, Canada have already been observed to exhibit increased flowering and seed germination associated with climate change (Groeneveld et al., 2014). Even the less invasive *R. sachalinensis* was predicted to invade the relatively cool Canadian province of Alberta under future climatic conditions (Chai et al., 2016). As previously mentioned, clonal plants like *Reynoutria* spp. often have high phenotypic plasticity, which will likely allow the plant to adapt over time to the temperature increases brought by climate change. The high-fitness progeny of *R.* × *bohemica* will also likely aid in producing knotweed genotypes that are well-suited to novel climates.

In their study, Groeneveld et al. (2014) examined the potential for *Reynoutria* spp. to extend their range northward in Quebec, Canada, through looking at genetic structure and seed production in Quebec. The ability of *R.* × *bohemica* to produce seeds 500 km north of the formerly reported limit was taken as a harbinger of northward movement, especially because in their study the more genetically diverse *R.* × *bohemica* tended to produce adventive new patches in adventive locations than *R. japonica*. Note *R. japonica* did produce viable seeds in their region, but with less genetic variability. Furthermore, the fact that *R.* × *bohemica* was rare in the region until recently was another indication that evolutionary change was pushing the boundaries for *Reynoutria* spp. in Eastern Canada, just as average temperatures were reaching historic highs.

Climate change involves more than simply changes in precipitation and temperature, and the increase in storm frequency and severity has already been demonstrated as a potential means to further spread the rhizomes of *R. japonica* (Colleran and Goodall, 2015) and by extension, the hybrid *R.* × *bohemica*. Increased weather severity will no doubt increase dispersal of the seeds of *R.* × *bohemica* as well, as the seeds are capable of surviving many days floating in water, and germinate at higher rates following periods of immersion (Rouifed et al., 2011). Given the ability of seeds to float for days and therefore be transported many kilometers down river, dispersal of seeds by hydrochory may provide powerful selection pressure for *R.* × *bohemica* to changing hydrological regimes involving more flooding, especially considering that the seeds and/or vegetative fragments must both be carried down river and deposited on shore at some point. A Quebec study of *Reynoutria* spp. populations distributed along the 185 km Chaudière River found widespread populations but with limited genetic variation (only one genotype each for *R. japonica* and for *R.* × *bohemica*) indicating that most of the spread in this case was by rhizome and stem fragments (Duquette et al., 2016). Nonetheless the massive invasion along the river with few riparian species able to outcompete the invasive weed.

Given the expected changes in climate involving increases in the growing season in temperate zones, annual temperatures, annual precipitation, and extreme climate events such as flooding it is expected that *Reynoutria* spp. will only continue to pose problems and extend its range in North America, Europe, Australia and Asia. Looking at the six major mechanisms promoting rapid evolution in invasive weeds (**Figure 1**), *Reynoutria* spp. exhibit all six: polyploidy, local adaptation, hybridization, clonal growth, plasticity, and epigenetics. As some of the studies reviewed here indicate, *Reynoutria* spp. deploy these mechanisms in different ways under different environmental circumstances often resulting in better adaptation than any neighboring native vegetation (Parepa et al., 2014; Duquette et al., 2016; Gillies et al., 2016). As the climate changes, more habitat and more pathways (e.g., by flooding and other extreme events) will become available for *Reynoutria* spp. to establish. Proactive management measures should include monitoring disturbed areas for knotweed plant parts, including landscapes subsequent to extreme climate events (Colleran and Goodall, 2015), and managing incipient infestations as quickly as possible, given the tremendous dispersal and persistence capabilities of this plant taxon.

FUTURE RESEARCH NEEDS

Research on this potential for rapid evolution is critical to developing more proactive management approaches that anticipate new invasive plant ecotypes adapted to changing climatic conditions. Clearly, research on weed evolution in response to climate change has advanced considerably over the last several decades, but there are still many questions to be explored more fully if we are to approach the goal of devising more proactive management strategies.

Because invasive weed life histories are so extremely diverse, along with the associated reproductive characteristics and genetics (Barrett et al., 2008), there are numerous questions regarding the implications of this diverse array of life histories under climate change. Even within individual weed species, there can be multiple life history strategies at play, such as for *R.* × *bohemica* (Gillies et al., 2016) or *Sorghum halepense* (Paterson et al., 2020). New methods of genetic analysis, including even whole-genome characterizations offer promising possibilities for understanding weed life histories better (e.g., see Liu et al., 2020a). Yet classic evolutionary ecology approaches, as seen in many of the studies reviewed here, still offer important ways of unveiling impacts of climate change on weed life history and adaptation, such as common garden experiments, reciprocal transplants or artificial selection (Colautti and Lau, 2015).

In the face of the numerous factors at play, frameworks have been developed to help cut through the complexity. Young et al. (2017) presented a framework for studying invasive plant dynamics aimed at establishing research priorities, revealing gaps in theoretical understandings, and identifying components of invasion processes that could be used to improve management, i.e., get to the point of a more proactive approach in the case of managing invasive plants in the face of climate change. Their framework revolves around three key components: climate dynamics, invader fitness, and ecosystem resistance.

The first element of the framework, *climate dynamics*, potentially influences weed invasions in a variety of ways, because climate change itself has multiple aspects. Initially most studies of climate change and invasive weeds were focused on temperature changes and resultant poleward extension of invasive weed distributions (Clements et al., 2004), and there is still a need to investigate these dynamics as the mean global temperature inexorably increases. However, it is evident from the frequent focus on the response of invasive weeds to changes in drought frequency and extent (**Table 3**) that the impact of anticipated changes in moisture regimes under climate change on rapid weed evolution is an important research area. Furthermore, climate dynamics under climate change also include more frequent floods, fires, storms and other extreme events (Tamarin-Brodsky and Kaspi, 2017; Patricola and Wehner, 2018) and there is an urgent need for more research on such extreme events, which potentially create even greater selection pressures than more gradual changes in climate.

A challenging area of research on climate dynamics in relations to invasive weeds, is to research the problem on a global level; climate change itself is a global phenomenon and many invasive plants have likewise "gone global." Thus, there is a need for more collaboration among invasive plant specialists from different world regions. For example, more studies like the study we reviewed on *E. cicutarium* which compared its invasion of both California and Chile (Latimer et al., 2019). A series on the biology of invasive plants was recently initiated in the journal *Invasive Plant Science and Management* which encourages the formation of multi-national author teams from far-flung world regions, in order to adequately review the biology of invasive plants in a global context (Kriticos et al., 2020). Organizations which bring together invasive plant specialists from across the globe, such as EMAPi likewise have a vital role to play in understanding whether the dynamics of invasion by the same species differ in different world regions (Pyšek et al., 2019).

The second element of the invasive plant research framework (Young et al., 2017), *invader fitness*, similarly involves many important research questions that have only emerged recently, especially when considering the many novel mechanisms that have recently been explored for invasive weeds such as polyploidy, local adaptation, hybridization, clonal growth, plasticity, epigenetics, and hybridization (**Figure 1**). Barrett et al. (2008) pointed out that little research had been conducted on potential changes in plant reproductive systems such as these during invasion. More detailed research on these mechanisms is imperative to grasping the way future invasions under climate change might look, including which conditions would favor reduced or increased genetic diversity, and whether purging genetic diversity (*cf.* Marchini et al., 2015) is a common element in plant invasions. Rutland et al. (2021) provide a comprehensive overview of what is known of the evolution of polyploidy in weeds, but make it clear that more research is needed. They maintain that it is impossible to definitively answer the question, "Do polyploids make better weeds?" at this juncture because of our lack of understanding of weed genomics. The evolution of clonality, including the ongoing evolution at present may be critical to understanding dispersal dynamics of species like *Reynoutria* × *bohemica* which spreads by both seed dispersal and clonal growth (Gillies et al., 2016). Williams et al. (2019) suggest ways of researching the eco-evolutionary dynamics of range expansion by systematically looking at the factors that work to generate genetic variance, to determine more clearly how processes effect the degree to which weeds evolve at the edge of their ranges. At the core of invader fitness are the particular traits that may evolve, of which there are many, but the goal should be to demonstrate the actual mechanisms involved utilizing the unique features of invasive species (Hodgins et al., 2018). To this end, van Kleunen et al. (2018) offer some useful ways forward, including synergism between molecular and phenotypic research.

The new molecular techniques referred to by van Kleunen et al. (2018) offer exciting avenues for researching the important questions we have reviewed, such as the relationship between polyploidy and hybridization, epigenetic response dynamics, and the evolution of phenotypic plasticity. In most cases we have clues from certain well-studied invasive species like *Alternanthera philoxeroides*, *Solidago canadensis*, *Sorghum halepense*, *Reynoutria* spp., and *Ambrosia artemisiifolia* but as indicated by these species, every invasive weed is different, and differences in life history have implications for adaptation to climate change (Clements and DiTommaso, 2012). One particular examples that illustrates the gap is that of *Tragopogon* hybrids in North America; although hybridization leading to the formation of new hybrid species is well-studied in Washington State (Clements et al., 1999), no research has been done in Canada on hybridization and its implications under climate change. In sum, there is much more that we do not know about *invader fitness* under climate change than we do know; as we speculated earlier, the conditions caused by anthropogenic climate change may increase opportunities for hybridization and polyploidization events in invasive plant populations, but this is only speculation without supporting research.

Ecosystem resistance, the third element of the invasive plant research framework (Young et al., 2017), is subject to wide variation in the face of climate change, such as the vulnerability of drought prone areas in the western USA to invasion and concomitant evolution of plant invaders taking advantage of low levels of ecosystem resistance (**Table 3**). Research on particular species like *Sorghum halepense* (Paterson et al., 2020) and *Impatiens glandulfera* (Cuda et al., 2020; Gruntman et al., 2020) indicates that invasive plants may invade new habitats under climate change, raising the alarm that other invasive plants may adapt to new habitats as climate changes. This presents a clear challenge to developing proactive management systems; as well as the need to understand and monitor the formation of novel invasive weed ecotypes, there is the need to manage ecosystems for greater resistance to invasion. Climate modeling approaches for invasive plants to this point have largely relied on large-scale geographic inputs (e.g., regional, national or international scales), but ecosystem resistance tends to act at local levels, and thus there is a need to research the potential for finer-scale modeling (Bradley, 2016; De Kort et al., 2020). Weed researchers conducting a horizon scan of weed research priorities identified the underlying challenges largely related to combining agroecological, socio-economic and technological approaches (Neve et al., 2018). Climate change, weed evolution and weed invasiveness were seen as important themes to pursue.

Certainly the ever clearer link between climate change and weed evolution and invasiveness calls for creative research approaches leading to creative solutions to this problem that is both on the horizon, and already upon us. As our focus on the case of *Reynoutria* spp. indicates, more diligent monitoring and characterization of the genetic characteristics of invasive weed populations is needed, and along with that, more attention paid to mechanisms for producing novel genotypes (**Figure 1**), especially at the edges of species ranges where expansion due to changes in climate are likely to occur, and are already occurring for many species in many regions.

AUTHOR CONTRIBUTIONS

All authors contributed substantially to the literature review, analysis and writing, and approved the final version.

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Seed Biology of Witchgrass (*Panicum capillare* L.) Ensures Its Success Under Different Environmental Conditions

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Witchgrass (*Panicum capillare* L.) is a summer growing grass weed species and is increasing its prevalence in southern Australia. A better understanding of the seed biology is needed to effectively manage this weed. A series of field and laboratory studies were conducted to determine seed germination factors, field emergence patterns, and soil seedbank longevity. Witchgrass germination was stimulated by light and it germinated better at temperature over 20°C, with 93–100% germination at the two constant temperatures of 20 and 30°C, and the two alternating day/night temperatures of 30/25 and 35/25°C. It is highly tolerant to moisture stress at germination, with 2–7% germination even at −0.48 Mpa. Witchgrass seed lost 47–68% viability after 12 months of burial in the soil, however the seed persisted for more than 4 years if buried at 10 cm in the soil. Witchgrass emergence in southern New South Wales (NSW) commenced in mid spring (early October), with peak emergence of 63–83% in November and then significantly reduced to 16–37% emergence in December. Little emergence (<1%) occurred in the summer months from January to February. These results provide useful information for designing effective management strategies and the optimum timing of control. Climate change could favor the phenological development and the further spread of this weed, which present new challenges for its effective management. Further study is needed to investigate the impact of climate change on the biology, spread, and management of witchgrass.

Keywords: germination biology, seed viability, temperature, seedbank, seed burial, field emergence, persistence

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INTRODUCTION

The genus *Panicum* is one of the largest genera in the Poaceae, with more than 500 species worldwide, mostly occurring in the tropics (Crins, 1991; Aliscioni et al., 2003; Byng, 2014). *Panicum* species are also widespread in Australia, with 24 indigenous and nine introduced species (CHAH (Council of Heads of Australasian Herbaria), 2021). These *Panicum* species are among the key summer weeds in Australia (Llewellyn et al., 2016). Due to the taxonomic confusions in the genus *Panicum* (Darbyshire and Cayouette, 1995; Dirkse and Holverda, 2016), DNA barcoding techniques have been employed to assist the species identification and the subsequent control (Chen et al., 2018).

Witchgrass (*Panicum capillare* L.) is an annual grass belongs to the genus *Panicum* and it is indigenous to North America (Baskin and Baskin, 1986). It is a summer active growing C_4 grass weed species and has invaded many non-native ranges throughout the world, from subtropical to temperate areas. These include Asia, South America (Argentina and Chile), New Zealand, Australia, Morocco, Russia, and many European countries (Clements et al., 2004). In Australia, the earliest herbarium record of witchgrass was collected in South Australia in 1911, followed by the second earliest report in Sydney in 1927 (AVH, 2021). Witchgrass has increased in abundance in southern Australia in recent years. Currently, it has widely distributed in the south western states of Australia. A recent summer weed survey from Western Plains through the Riverina districts of New South Wales (NSW) showed that witchgrass was the second most prevalent annual weed in the region (Weston et al., 2016). The weed is commonly found in the cropping fields soon after harvest, in fallows and pastures, waste land, along fence lines and on roadsides. In Australia, it can be easily confused with a native perennial grass, Hairy Panic (*Panicum effusum* R.Br.) (Phillips, 2010).

Witchgrass is more problematic in no-till farming systems than conventional tillage systems (Frick et al., 1990). It can cause yield loss in crops, toxicity in animals and is a host to several pests and diseases. It often infests summer crops in the northern hemisphere such as corn, soybeans, sorghum, and in winter wheat (Clements et al., 2004). If left uncontrolled, it can cause 4–5% yield loss in corn and soybean at a weed density of 5 plants/m^2 (Ontario Weed Committee, 2021). In southern NSW, witchgrass thrives in bare areas of winter crops and grows rapidly to a thick mat soon after crop harvest due to the removal of crop competition. It is also a competitive weed in degraded pastures under drought conditions (Phillips, 2010). The vigorous growth in the summer consumes valuable stored soil moisture and nutrients which could otherwise be used by crops sown in autumn.

Witchgrass can pose significant animal health issues. It has been found to accumulate nitrate which could be toxic to livestock under certain conditions (Kingsbury, 1964). Additionally, hepatogenous photosensitization was reported in Merino sheep grazing on witchgrass in Australia (Quinn et al., 2014). Furthermore, witchgrass is an alternative host to a range of pests and diseases, including cereal aphids such as *Rhopalosiphum padi* L. and *R. maidis* Fiotch (Kieckhefer and Lunden, 1983), western corn rootworm (Coleoptera: Chrysomelidae) (Chege et al., 2005), and wheat streak mosaic virus (Christian and Willis, 1993; Coutts et al., 2008).

The prevalence of witchgrass is associated with its high seed production, unique spreading mechanism, and persistent seedbank (Clements et al., 2004). Witchgrass is a prolific seed producer, producing upto 56,400 seeds per plant in the absence of competition (Stevens, 1932). It has an unusual tumbleweed-like seed dispersal mechanism. The mature spherical inflorescence is brittle, easily breaking off and is spread long distances by wind. Large piles of grass inflorescence often engulf country roads and streets, fenceline, yards, garages, sheds, and houses in wet summers in southern Australia.

The seed of witchgrass has a hard seed coat and possesses strong innate dormancy. Brecke (1974) found that witchgrass seeds collected in autumn in Central New York State had broken all dormancy after dry storage for 5 months in the dark at room temperature. In the field, dormancy releases during late autumn and winter and the seeds subsequently germinate in spring and summer, while hot summer tends also to induce secondary dormancy (Baskin and Baskin, 1986). The seed germinates better under light and alternating temperatures (Cross, 1931; Brecke, 1974; Baskin and Baskin, 1986). Witchgrass germination is low at temperatures below 20°C and is greatest above 25°C (Rivera and Peters, 1971; Vengris and Damon, 1976; Baskin and Baskin, 1986).

Witchgrass is a poor competitor and does not grow well in shaded environments (Vengris and Damon, 1976; Clements et al., 2004). Shading delayed both the vegetative and reproductive growth of witchgrass and reduced the number of tillers and panicles (Vengris and Damon, 1976). Brecke (1974) found that witchgrass mostly emerged from near or on the soil surface (0–2.5 cm), with limited emergence occurring below 5 cm of burial.

Despite the increasing prevalence of witchgrass in pastures and arable land, little is known of the seed germination biology, persistence and emergence of this weed in Australia. Improved understanding of the biology and ecology of witchgrass has become increasingly important, particularly in relation to the changing climate. The altered temperature and rainfall patterns associated with global climate change will have direct effects on seed dormancy, germination, emergence, persistence, and reproduction (Walck et al., 2011). These characteristics will subsequently affect the distribution, species shift, population dynamics, life cycle, phenology, competitive potential, and herbicide control efficacy (Peters et al., 2014; Varanasi et al., 2016; Ramesh et al., 2017). Therefore, this study was conducted to determine: (1) the factors that affect the seed germination of witchgrass; (2) the emergence patterns and the longevity of the seed in the soil seedbank. This information will help in determining the population dynamics of this problematic species and in identifying the suitable timing for its early control.

MATERIALS AND METHODS

Seed Collection and Preparation

Mature seeds of witchgrass were collected from a summer fallow paddock (147.337207E, 35.029273S) in February 2007 (Source A) and in March 2009 (Source B) in Wagga Wagga, New South Wales (NSW), Australia. Both seed sources were highly dormant at the time of collection. The freshly collected seed was stored at room temperature for 1 year to break the dormancy. The germination was 95 and 60% for the seed Sources A and B prior to the following experiments, respectively. The seed Source A was used in all the experiments except the light and moisture stress experiments when the seed Source B was used.

Temperature on Germination

One hundred seeds of witchgrass (seed Source A) were placed on a piece of filter paper (Whatman No.2) moistened with 5 ml of deionised water in a 9 cm petri dish. Petri dishes were sealed with parafilm and incubated at three constant temperatures of 10, 20, and 30°C, and four fluctuating nigh day/night temperatures of 20/15, 25/15, 30/25, 35/25°C with a 12-h photoperiod. These fluctuating temperature regimes were a good representation of the wide emergence window of this weed from spring to summer in southern NSW. The germinated seeds were recorded after 7 d of incubation based on our preliminary studies.

Light on Germination

The influence of light on the germination of witchgrass was tested at four sets of fluctuating temperatures (20/15, 25/15, 30/25, and 35/25°C) in April 2010 by using the seed Source B as the viability of seed Source A was low 3 years after collection. Two layers of aluminum foil were used to wrap petri dishes to achieve complete darkness during incubation. Germination recorded at 7 days after incubation in a 12-h photoperiod at the respective temperature regimes was compared.

Moisture Stress on Germination

The effect of drought stress was studied using the seed Source B at three fluctuating day/night temperatures of 25/15, 30/25, and 35/25°C with a 12-h photoperiod. Solutions with osmotic pressures of 0, −0.03, −0.06, −0.12, −0.24, −0.48, and −0.96 MPa were prepared by dissolving polyethylene glycol (PEG) 8000 in 80 ml of distilled water using appropriate quantities for each temperature as determined from Michel (1983). The PEG 8000 quantities were determined from the average for the two fluctuating temperatures.

Seed Persistence in the Field

Seed burial experiments were commenced on 15 April 2008 on the Research Farm (147.334958E, 35.029780S) of Wagga Wagga Agricultural Institute, NSW. One hundred witchgrass seeds (seed Source A) were placed in a 4 × 6 cm mesh packet together with a small quantity of sieved soil to improve soil and seed contact. The packets were then placed at three soil depths (0, 5, and 10 cm) in a minimum-tilled field free of vegetation under natural conditions. The soil type was a duplex Red Kandosol. The packets were recovered at six intervals [3, 6, 12, 24, 36, and 48 months (mo)] in a randomized complete block design with three replicates.

Recovered seeds were counted and placed on moistened Whatman No.2 filter paper in a 9-cm petri dish, which was then sealed with parafilm and incubated for 7 d under the fluctuating temperatures of 30/25°C with a 12-h photoperiod. The number of germinated seeds was recorded and viability of ungerminated seeds determined by tetrazolium staining. Briefly, seeds were cut in half and incubated in darkness at 30°C for 5 h in a 0.5% 2,3,5-triphenyltetrazolium chloride solution. Seeds were deemed to be viable but dormant if the radical had stained red. Total viability of the exhumed seeds included the germinated seeds and the viable but dormant seeds.

Seed Emergence in the Field

Three trials were conducted to determine the emergence of witchgrass under field conditions in the summer of 2008/2009 and 2012/2013 in southern NSW. In the 1st trial (Site A), four permanent quadrats (1 × 1 m^2) were randomly placed in a cropping paddock (147.353080E, 35.049480S) on 17 April 2008. The site was heavily infested with witchgrass in the summer of 2007. Two hundred additional seeds (seed Source A) were evenly spread onto the surface in each quadrat and lightly harrowed to increase the seedbank size for subsequent emergence monitoring. No further tillage or harrowing was imposed.

Two additional trials (Sites B and C) were conducted in the summer of 2012/2013. Four permanent quadrats (1 × 1 m^2) were randomly placed in August in two fields (147.360067E, 35.032868S, Site B and 147.353080E, 35.049480S, Site C) with a known history of witchgrass. No additional seeds were required due to the heavy infestation in the previous season.

The trials were maintained under natural conditions without additional irrigation. Emerged seedlings in each quadrat in the three trials were assessed from September to February until no further emergence. Seedlings were counted and removed by spraying with glyphosate on fortnightly or monthly intervals, dependent upon rainfall events.

Statistical Analysis

A randomized complete block design with three replications was used in all experiments. The experiments of temperature and light conditions on germination were repeated twice. Data from repeated experiments were combined as there were no significant differences over time. Homogeneity of variance was not improved by transformation, therefore analysis was performed on raw percentage germination. Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. Data were analyzed using analysis of variance and *post-hoc* Fishers tests used to determine statistically different means.

Results

Temperature

Temperatures significantly affected the germination of witchgrass (**Figure 1**). It germinated poorly at the lower temperature treatments, with no germination at 10°C and only 10–20% germination at the fluctuating temperatures of 20/15 and 25/15°C. Germination did not significantly differ between constant temperatures of 20 and 30°C, and the alternating temperatures of 30/25 and 35/25°C. The highest germination was achieved at temperatures over 20°C, with 93–100% germination at the two constant temperatures of 20 and 30°C, and the two alternating temperatures of 30/25 and 35/25°C in a 12-h light/dark cycle.

Light

The germination of witchgrass was significantly encouraged by light (**Figure 2**). The germination was 56% under the photoperiod of 12 h at 30/25 and 35/25°C, while it was only 1–8% in complete darkness under the same temperature conditions. Light stimulation of the germination was also evidenced at the lower day/night temperature regime 25/15°C.

Moisture Stress

Osmotic potential significantly influenced the germination of witchgrass (**Figure 3**). Without the osmotic stress, the

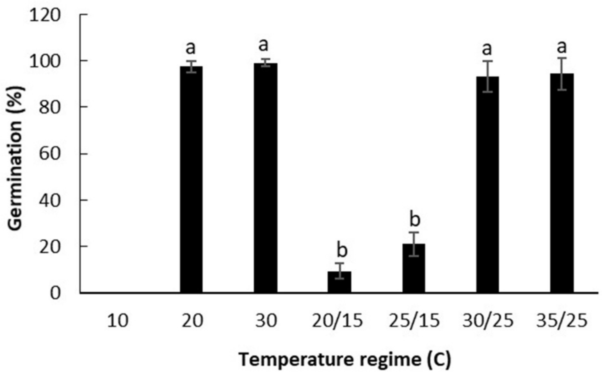

FIGURE 1 | Impact of constant and alternating temperatures on the germination of *P. capillare*. Vertical bars represent the standard error of the mean.

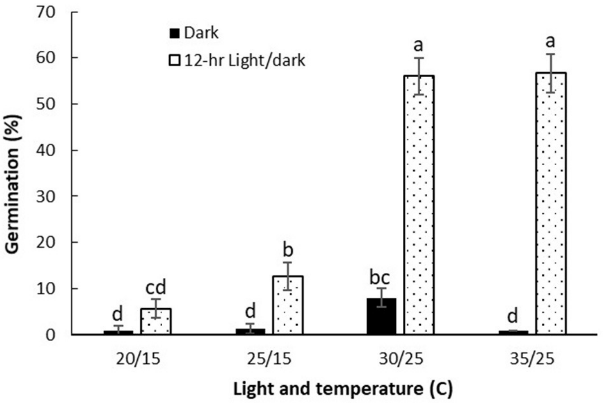

FIGURE 2 | Impact of light on the germination of *P. capillare*. Vertical bars represent the standard error of the mean.

germination of witchgrass was 12.7, 48.0, and 56.7% at the temperatures of 25/15, 30/25, and 35/25°C, respectively. Increasing osmotic stress levels reduced germination under all temperature regimes. At the fluctuating temperatures of 35/25°C, seed germination decreased from 56.7 to 2% as osmotic potentials decreased from 0 to −0.48 MPa, and no germination was observed at −0.96 MPa. Similarly, the germination at −0.48 MPa was very low (4–7%) at 25/15and 30/25°C. Even at −0.96 MPa, limited germination (0.7%) occurred at the temperatures of 30/25°C.

Seed Persistence

Both duration and depth of burial significantly reduced *($P < 0.01$)* germination and viability of witchgrass seed (**Figure 4**). There was no interaction between duration and depth of burial. The initial germination at the time of burial (0-mo) was 95% and declined slightly after 3 months of burial at 0- and 5-cm depths, which was then followed by a sharp decrease after 6 months of burial at both depths (**Figure 4A**). However, at the burial depth of 10 cm, the germination at 6-mo remained high at 88%, then decreased rapidly to 53% at 12-mo. After 12 months of burial, the germination at the three burial depths followed similar declining trend, with 29–46, 0–10, and 0–5% germination after 2, 3, and 4 years of burial, respectively.

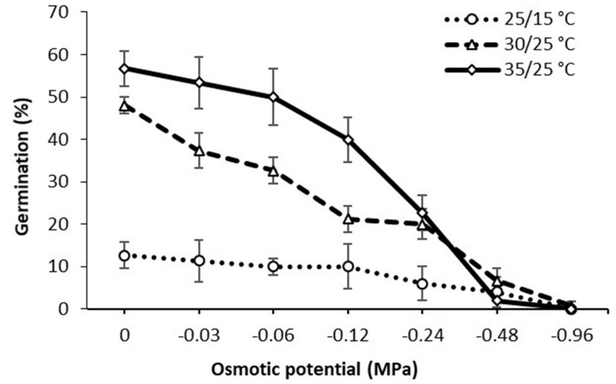

FIGURE 3 | Effect of osmotic potential on germination of *P. capillare* seeds incubated at alternating temperature regimes with a 12-h photoperiod. Vertical bars represent the standard error of the mean.

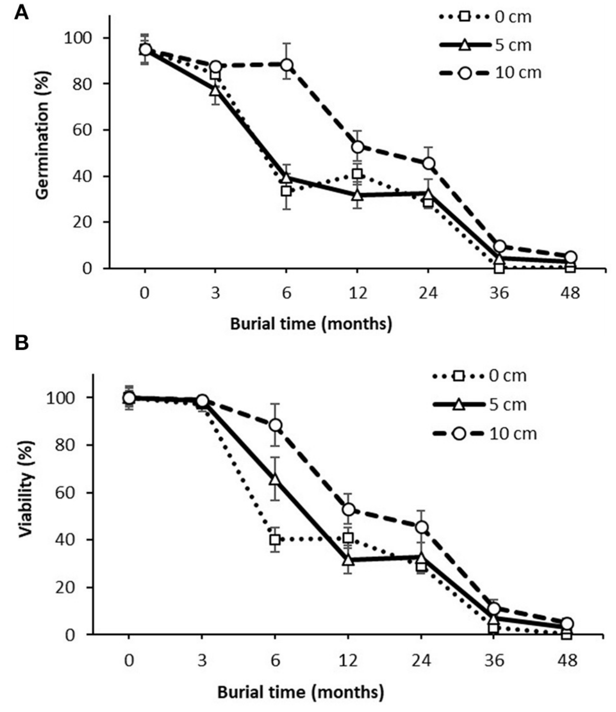

FIGURE 4 | Effect of burial duration and depth on *P. capillare* seed **(A)** germination (total germinated seeds from the recovered seeds divided by the buried seeds, %) and **(B)** viability (total viable seeds from the recovered seeds divided by the buried seeds, %). Vertical bars represent the standard error of the mean.

The viability of buried seeds remained little changed during the first 3 months of burial, which was then followed by a steady decline, irrespective to the burial depth (**Figure 4B**). Most of

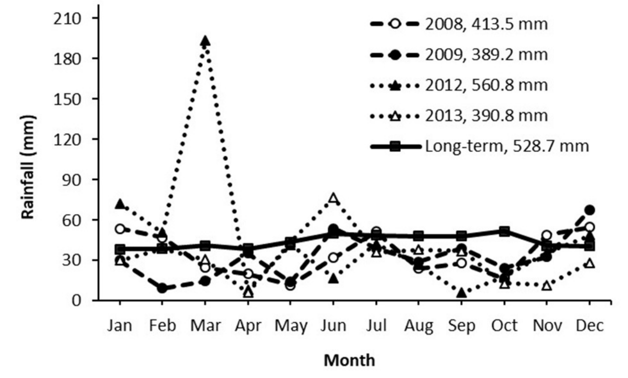

FIGURE 5 | Annual rainfall in years 2008, 2009, 2003, and 2013 as compared with the long-term average (115 years).

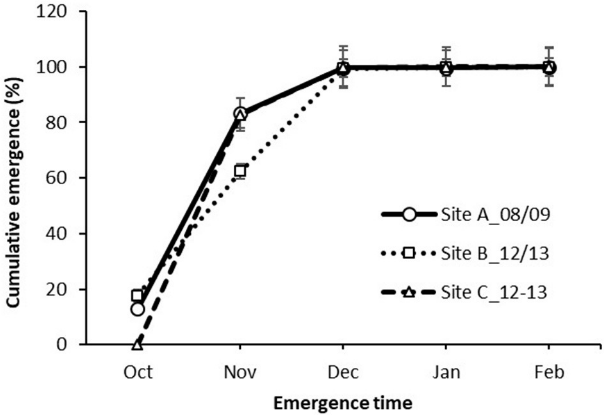

FIGURE 6 | Emergence of *P. capillare* over time in the field. Emerged seedlings were counted and removed by spraying glyphosate. Vertical bars represent the standard error of the mean. Cumulative emergence (%) was calculated from the cumulative number of emerged seedlings at the respective month divided by the total number of emerged seedlings during the entire experimental period.

the viability loss occurred within the first year after burial. The viability was reduced from the initial 100% before burial (0-mo) to 32–53% after burial for 12 months. The viability continued to decline to 3–11 and 0–5% after 3 and 4 years of burial, respectively, with seeds exhumed from deeper in the soil profile having higher viability than the shallower depths. No viable seed remained on the soil surface (0 cm) after 4 year, compared to 3–5% at the 5- and 10-cm burial depth during the same period.

Emergence in the Field

The average rainfall was 413.5, 389.2, 560.8, and 390.8 mm for the respective year 2008, 2009, 2012, and 2013, compared to the long-term average of 528.7 mm (115 years) (**Figure 5**). The rainfall received during the active weed growth period from September to February was 187.7 mm in 2008/2009 and 176.9 mm in 2012/2013, which was only about 68–73% of the long-term average. Spring rainfall is critical to trigger the emergence events as temperature is not a limiting factor during this period. However, the total rainfall in September and October in both 2008 and 2012 was only 24–45% of the long-term average, which could restrict the emergence of witchgrass.

Despite of the significantly lower than long-term average rainfall in spring, witchgrass still managed to emerge, with total emerged seedlings of 428 plants/m^2 at Site A in the summer of 2008/2009, and 203 and 1,557 plants/m^2 at Sites B and C in 2012/2013, respectively (**Figure 6**). The emergence patterns followed similar trends between the sites and years. Witchgrass emergence initiated in late September, with 0–18% seedlings counted in early October, followed by a major emergence of 63–83% in November and 16–37% emergence in December. Little emergence (<1%) was recorded from January to February across the three sites.

DISCUSSION

Witchgrass is a warm season C$_4$ grass and prefers higher temperatures (over 20°C) to improve germination, which is consistent with previous studies (Cross, 1931; Brecke, 1974; Baskin and Baskin, 1986). Higher constant temperatures of 20 and 30°C achieved a high level of germination (97–100%), which is not different to 93–94% germination achieved under the alternating temperatures of 30/25 and 35/25°C. However, better germination under alternating temperatures have been reported previously in witchgrass (Cross, 1931; Brecke, 1974).

The high sensitivity of witchgrass germination to light reported in this study agrees with Baskin and Baskin (1986). They found that high germination of witchgrass (76–100%) was achieved in light at a wide range of alternating temperatures, while the germination was only 1–24% under complete darkness. These results indicate that inversion tillage and stubble cover could be effective control options in suppressing the germination and emergence in the field. However, shallow soil disturbance could encourage the emergence as it will bring buried seed to the surface where light becomes unlimiting (Baskin and Baskin, 1986). We propose that response to light might be an adaptation tactic to ensure the germination of this small-seeded species, particularly when they are near or at the soil surface.

Studies related to water stress tolerance in witchgrass are scant. This study found that decreases in osmotic potential resulted in reduced germination in witchgrass. Limited germination can even occur at the water potential of −0.96 MPa under optimum alternating temperatures of 30/25°C, indicating that witchgrass is drought tolerant at germination. It is incongruent with many other annual grasses that require adequate soil moisture for germination, with complete germination suppression at osmotic potentials between −0.6 and −1.3 MPa (Masin et al., 2005; Seepaul et al., 2012; Fernando et al., 2016). Seepaul et al. (2012) reported that germination of switchgrass (*Panicum virgatum* L.) was significantly suppressed at −0.8 MPa, with no germination at the osmotic potential between −1.2 MPa. Wild proso millet (*Panicum miliaceum* L.) also had low germination (2%) at −1.0 and −1.4 MPa (Stump, 1984). These results indicate that witchgrass germination is tolerant to moisture stress, which is supported by the high seedling numbers up to 1,560 plants/m^2 emerged in the field during late spring and early summer of 2008/2009 and 2012/2013 even when the spring rainfall between September and October (a critical period for emergence) was only 24–45% of the long-term average. The success of witchgrass under drought conditions could also be due to its unique seedling root structure. Gross et al. (1992) reported that the root growth of witchgrass exhibited a herringbone topology (i.e., magnitude = altitude), which favors plants growing in water-limited habitats.

Viability of seeds in the soil decreases with the duration of burial and increases with the depth of burial. The seed of witchgrass persists well in the soil, possibly due to the presence of a hard seed coat. Although majority of seed viability (47–68%) was lost after 12 months of burial, seed can survive after 4 years of burial at the deeper burial depths of 5 and 10 cm. The rapid loss of viability within 12 months of burial and the long persistence after several years of burial have also been documented in other *Panicum* species (Alex, 1980; Burnside et al., 1981; Stump, 1984). After 21 months of burial, the seed viability of *P. miliaceum* was only 23% at the burial depth of 5 cm, but it was 77 and 93% at 10 and 30 cm, respectively. Alex (1980) reported that loss of viability of *Panicum dichotomiflorum* was influenced by soil type, depth and duration of burial. Seeds in gravelly loam lost viability faster than those in silt loam soil, and seeds at 1 and 2 cm lost viability faster than those at deeper depths. After 54 mo of burial, seeds buried at depths between 5 and 20 cm in silt loam remained 5–14% viability. These results indicate that witchgrass seed could persist well in the field and deeper burial would result in longer persistence with a low but tenacious tail of more than 4 years. Failure to stop seedset would mean the on-going battle of this weed. Consistent control efforts over several years are required to overcome the persistent nature of the seed and to effectively manage this weed.

Better understanding the emergence patterns is important to the effective management as better control timing can be tailored to individual circumstances. Witchgrass has a staggered emergence pattern in southern NSW. It started to emerge in mid spring, with major emergences in late spring and early summer. This emergence pattern is similar to a study in Tennessee (Baskin and Baskin, 1986) who reported that witchgrass emerges over an extended period during spring and summer. Earlier emergence cohorts have taller plant height, tillers, more panicles per plant as compared to later emergence cohorts (Vengris and Damon, 1976). Therefore, management efforts should be directed to control the early and major emergence cohorts in late spring and early summer before setting seeds. Controlling early cohorts can stop seedset and reduce further infestation.

Witchgrass is predominantly a surface germinator. Most emergence is likely to come from the seeds on or near the soil surface due to the light requirements for germination. Seeds buried in the soil are unlikely to emerge in summer (Baskin and Baskin, 1986). Brecke (1974) reported 52–95% emergence occurred at depths between 0 and 2.5 cm and no emergence at depths over 5 cm. Also, optimum emergence at shallow burial depths was documented in *P. dichotomiflorum* (Fausey and Renner, 1997). However, another *Panicum* species, *P. miliaceum,* was able to emerge from deeper depths, with a maximum depth of emergence at 14 cm (Stump, 1984). Strategic tillage could be an effective option to bury witchgrass seed into deeper soil layers to suppress the emergence. However, prolonged persistence of witchgrass seeds in the deeper soil means that care should be taken not to re-introduce the buried but viable seeds back to the soil surface through tillage operations.

Successful seed emergence is the most important phase of plant establishment for weed to survive, thrive and proliferate, which is strongly influenced by temperature and moisture. However, these two important environmental clues are being influenced by climate change.

Rising CO$_2$, temperature and altered precipitation patterns are three key indicators of climate change. Under the current rates of CO$_2$ emissions, the concentration of CO$_2$ is predicted to reach ~1000 ppm by the end of the twenty-first century, resulting in an increase of 2–4°C in the Earth's annual surface temperature (IPCC, 2007). However, the predictions for long-term rainfall patterns are far less certain (Giannini et al., 2008; Varanasi et al., 2016). In Australia, it is generally agreed that summer rainfall had increased in eastern Australia over the past century, while winter rainfall had decreased in the southwest, with large decadal-scale variations and distinct changes in different regions (Liu et al., 2020). They further reported an increasing trend in long-term rainfall in Northern and Central Australia, and a decreasing trend across Southern Australia.

The anticipated changes in temperature and moisture projected under changing climates will directly affect seed longevity, dormancy release, germination, and emergence (Walck et al., 2011; Ooi et al., 2014; Jaganathan and Liu, 2015). Indirectly, climate change will also affect seed predators and soil microbial activities, which in turn could affect the fate of seeds in the soil seedbank (Wu, 2015). The seed aging process is accelerated under high temperature and moisture conditions (Walck et al., 2011; Fenollosa et al., 2020). However, little research is available in this emerging field in regard to climate change.

Temperature is the key driver for the onset of emergence, flowering and other phenological traits (Menzel et al., 2006a,b; Otto et al., 2007). The increasing temperature would accelerate the accumulation of growing degree days required for the growth and development of plants, which would result in the changes in dormancy release, emergence timing and phenological development. Therefore, weeds are likely to grow and develop quicker, with earlier emergence and flowering and maturity (Lee, 2011; Singh et al., 2011; Pagare et al., 2017). Vengris and Damon (1976) claimed that witchgrass normally completes its life cycle between 80 and 105 days. However, later emerged plants only require 35 days from seeding to maturity under warm conditions.

Witchgrass exhibits substantial phenotypic variations and it is well-suited to a broad range of soil types and climatic conditions (Darbyshire and Cayouette, 1995), enabling witchgrass to adapt well in the changing climate. Witchgrass is a C$_4$ grass (Hattersley, 1984). The lower water requirement of plants with the C$_4$ photosynthetic pathway, along with higher optimal temperatures makes it more adaptable to changing climate as compared to C$_3$ plants (Tubiello et al., 2007; Pagare et al., 2017; Ramesh et al., 2017). Increasing numbers of fall panicum

(*P. dichotomiflorum*) have been observed in more northern areas of Europe (Peters et al., 2014). Shahidul et al. (2014) also reported that some tropical and subtropical C_4 species could shift northwards to temperate zones. The impact of climate change on the distribution range of witchgrass deserves further investigation.

Understanding weed biology and the timing of phenological development is critical for determining the most effective control timing. Future research on the impact of climate change on weed phenology, morphology, physiology, and reproduction through altered temperature and rainfall patterns will assist in monitoring and adaptive management of the weeds.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

HW planned and designed the research. AS and MA performed the experiments and conducted fieldwork. MA and XM analyzed the data. HW and XM wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Distribution and Biology of the Invasive Weed *Parthenium hysterophorus* L. in Israel

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Parthenium weed (*Parthenium hysterophorus* L.) (Asteraceae; Heliantheae) is an invasive allergenic species that has invaded many countries worldwide, probably through an imported pasture, grain seeds, and livestock feed. In recent years, there has been increasing concern about the spread of the invasive *P. hysterophorus* in agricultural and non-agricultural habitats across Israel. In addition, as *P. hysterophorus* is a quarantine plant; any contaminated produce exported will be rejected by the European market. The current study aims to document the current distribution and invasiveness status of *P. hysterophorus* in Israel. Moreover, we aimed to study the life cycle and biology of *P. hysterophorus*. In this research, we detected invasion reports to new areas and habitats in the Jezreel valley, the Jordan valley, and the Mediterranean coastal plain. Studying the biology of the weed, we found that optimal temperatures for seed germination are between 15 and 25°C. We observed that *P. hysterophorus* seeds are able to emerge from a depth of 0–3 cm only. *P. hysterophorus* thrives under high light intensities. Our results show that under induced shading of 60 and 90%, a significant reduction in biomass, height, and a number of flowers per plant were observed. Studying the biology and phenology of *P. hysterophorus* is a crucial step in the path to develop an integrated management program aimed to reduce the further spread and negative impacts by *P. hysterophorus*.

Keywords: emergence, seed bank, seed germination, weed mapping, radiation levels

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INTRODUCTION

Invasive species present major economic and ecological threats to agricultural and natural areas. In recent years, we have been experiencing a rise in reports of invasive weed species due to a significant man-made global change. Among the leading causes for this trend are import–export trade (Levine et al., 2003; Shimono et al., 2010) and climate change (Peters et al., 2014; Hulme, 2016). In the United States alone, annual losses caused only by crop-related invasive weeds are estimated at more than $27 billion (Pimentel et al., 2005). The damage of invasive weeds is not restricted to yield losses; they may increase the spread of fire fuel (Mound, 2002; Setterfield et al., 2013; Büyüktahtakin et al., 2014), and health hazards-mainly allergies (Wopfner et al., 2005; Kaur et al., 2014; Hamaoui-Laguel et al., 2015). In Israel, several invasive species, such as *Parthenium hysterophorus* L., *Verbesina encelioides* (Cav.), *Ambrosia confertiflora* DC., and *Amaranthus tuberculatus* (Moq.) Sauer, apparently entered the country along with seed shipments imported for animal feed

(Rubin and Matzrafi, 2015). *P. hysterophorus* was introduced into Israel in a wide range of ecosystems, the first one documented in 1980 at a fish farm in northern Israel (Yaacoby, 2013). In recent years, there has been a growing concern due to the spread of *P. hysterophorus* into the central part of the country and its increasing establishments in agricultural lands, such as orchards, as well as vegetable and field crops.

P. hysterophorus is an invasive weed species in more than 50 countries. It is considered as one of the worst weeds in the world due to its high fecundity (∼20,000 seeds/plant), rapid germination, fast growth rate, and allelopathic nature (Adkins and Shabbir, 2014). *P. hysterophorus* seeds can germinate in a wide temperature range, and germination is mainly limited by soil moisture content (Navie et al., 1998a; Tamado et al., 2002b; Bajwa et al., 2018). This species is generally unpalatable, but, in the absence of other food sources, livestock will feed on it. Allergic effects of *P. hysterophorus* for both animals and humans include severe dermatitis, hay fever, and other symptoms (Kaur et al., 2014). *P. hysterophorus* thrives under high light intensities (Navie et al., 1998a) and elevated nitrogen levels (Singh, 2014). *P. hysterophorus* can cause 40–97% yield reductions in agricultural crops and acts as a secondary host for many crop plant diseases (Adkins and Shabbir, 2014). Effective *P. hysterophorus* management can be achieved *via* chemical (Reddy et al., 2007) and biological control (Navie et al., 1998b; Javaid and Adrees, 2009). In addition, the growth of highly competitive crops has been found to be very effective in suppressing both the emergence and initial growth of *P. hysterophorus* (Khan et al., 2013; Shabbir et al., 2013).

Hence, the objectives of the present study were the following: (1) to document the current distribution of *P. hysterophorus* throughout Israel and (2) to study the life cycle of *P. hysterophorus* by examining biological and phenological parameters, such as seed germination, emergence from soil depth, and the effect of shading on height, biomass production, and flowering of *P. hysterophorus*.

MATERIALS AND METHODS

Distribution of *P. hysterophorus*

In order to better understand the distribution and invasiveness of *P. hysterophorus* throughout Israel, a detailed mapping of the infested sites and estimation of the level of infestation at each location was performed in 2018.

The mapping was done using ArcGIS (ArcGIS 9 Desktop. version 9.3.1, ESRI, Redlands, CA), with the application "Collector for ArcGis." The main mapping of *P. hysterophorus* was focused on the northern part of Israel, as the majority of the reports came from this region. The mapping was performed using two methods: first, scouting for *P. hysterophorus* from a vehicle on the main roads, from the southern border of its known distribution in "Hefer Valley," all the way to its northern border of distribution in the "Golan Heights." Second, brochures and social media directed to local communities, farmers, agronomists, park rangers, and others who have sighted *P. hysterophorus* were distributed. These individuals were asked to access a link and update *P. hysterophorus* location in a designated map. After a reasonable number of sites were reported by human resources, we visited each location, confirmed the identification, analyzed the level of distribution for each site as well as the distribution of *P. hysterophorus* in a one-kilometer radius around each site. If a *P. hysterophorus* plant was sighted, an additional kilometer would be surveyed and so on, until no *P. hysterophorus* plants were detected. For each site, the adjacent farms and villages were surveyed in what we concluded to be "prime locations," such as livestock farms, tool shades, and their surrounding perimeter. Data analysis and layer mapping were conducted using QGIS Desktop 2.8.1 (QGIS Delopment Team, 2018).

Plant Material

Seeds of *P. hysterophorus* were collected at the Newe Ya'ar Research Center (32.7115458716′′N, 35.1777440341′′E) in November 2015. To ensure appropriate representation of field population, mature inflorescence from 30 to 40 randomly selected plants were collected and pooled. Collected seeds were air dried and stored in the dark and at 4°C until used.

Effect of Temperature on Seed Germination

Seed germination was tested under constant and alternating temperatures. For this purpose, seeds were placed in a 9 cm Petri dish on a thin layer of Newe-Ya'ar soil collected at the same site as the seeds (57% clay, 28.2% silt, 8.1% sand, and 1.63% organic matter). Petri dishes were randomly placed in an incubator (Conviron®, plant growth chamber A1000, Winnipeg, Canada). To determine the effect of temperature on seed germination, 20 seeds were incubated in Petri dishes under eight different constant temperatures (5, 10, 15, 20, 25, 30, 35, and 40°C), 12 h photoperiod and watered as needed. Seed germination was recorded every day for 60 days. Experiments were replicated four times and arranged in a randomized complete block design.

Models for Predicting *P. hysterophorus* Development Dynamics

Linear Model

In order to develop thermal-time-based germination and development prediction models for *P. hysterophorus*, a calculation of accumulated growing degree days (GDDs) was used. Temperatures were converted to GDD units using Equation (1):

$$GDD = \sum \left[\frac{T_{\max} + T_{\min}}{2} - T_{base} \right] \tag{1}$$

Accumulated GDDs are calculated using T_{max} as the maximum daily temperature, T_{min} as the minimum daily temperature, and T_{base} as the minimum temperature for plant development (Mcmaster and Wilhelm, 1997).

Beta-Function Model

A four-parameter beta-function model was used to calculate the effect of temperature on *P. hysterophorus* germination dynamics using Equation (2):

$$\beta = \left(\left(\frac{T - T_b}{T_0 - T_b} \right) * \left(\frac{T_m - T}{T_m - T_0} \right)^{\frac{T_m - T_0}{T_0 - T_b}} \right)^a \quad (2)$$

where β is the calculated partial development rate, T is the hourly measured temperature, T_b is the minimal temperature for development, T_0 is the optimal temperature for development, T_m is the maximal temperature for development, and a denotes the shape of the slope.

The β-value was multiplied by the measured soil temperature and summed to estimate the effect of temperature on *P. hysterophorus* dynamics, where Ri is the accumulated GDDs using Equation (3):

$$Ri = \sum\nolimits_{n=1}^{i} \beta * T \quad (3)$$

At this point, the β-value may be used to validate the GDD calculation using Equation (4) (Cochavi et al., 2016):

$$\mathrm{GDD}\beta = \beta * \mathrm{T} * \mathrm{days} \quad (4)$$

Effect of Burial Depth on Seed Emergence

Following seed germination, emergence from different burial depths was tested. This experiment was conducted in a net-house during a natural season for *P. hysterophorus* emergence, using the same soil used for seed germination studies. Seeds were sown at different burial depths (0, 1, 2, 3, 4, and 5 cm below soil surface) in 250 ml pots; experiments were arranged in a randomized complete block design with five seeds sown in each pot with five replicates for each treatment. Emergence was recorded for 30 days; A data logger (HOBO® data logger, Onset, USA) was used to collect temperature data during the course of the experiment. Emergence was recorded for each pot every day, and the emergence rate was calculated as a percentage of the total for each treatment.

The Effect of Shading on Vegetative and Reproductive Growth

To assess the effect of different shading levels (radiation intensities) on plant productivity, plant vegetative and reproductive parameters were tested under different shading levels; 0 (full natural light, 1,000–1,100 μmol m^{-2} s^{-1}), 30, 60, and 90% shading. Experiments were performed in a net house during the natural growing season for *P. hysterophorus* in Israel (May–July). Pre-germinated seedlings at the stage of 2–3 true leaves were sown in 2.5 L pots filled with the soil of Newe-Ya'ar. Different shading levels were achieved using a black-shading net. For each treatment, 50 plants were used. Plant height, number of flowers, and aboveground biomass were recorded each week using five plants. Plants were irrigated and fertilized (Ecogan®, NPK 20:20:20, Israel) as needed. A data logger (HOBO®) was used for temperature recording during the course of the experiment.

Statistical Analyses

Data were analyzed and visualized using SigmaPlot (ver. 12) software (Systat Software Inc., San Jose, CA, USA). Parameters were optimized using the Solver function (Excel software, Microsoft Office Professional Plus 2016). The dynamics of seed germination were described using both the sigmoidal three parameters model as described in Equation (5):

$$f(x) = \frac{a}{1 + e^{\frac{x - x_0}{b}}} \quad (5)$$

and log-logistic three parameters model as described in Equation (6):

$$f(x) = \frac{a}{1 + \left(\frac{x}{x_0} \right)^b} \quad (6)$$

For both equations, X_0 is the inflection point, b is the slope in the inflection point, and a is the upper asymptote.

Curve fitting was estimated according to the root mean square error values (RMSE), where an RMSE-value represents the error between the observed and expected value, as described in Equation (7):

$$RMSE = \sqrt{\frac{1}{n \sum_i^n (x_i - y_i)^2}} \quad (7)$$

Lower RMSE-values indicate a better-fitted model (Lati et al., 2011a).

RESULTS

Distribution of *P. hysterophorus*

P. hysterophorus distribution across the northern region of Israel is shown in **Figure 1**. Populations were clustered in three main hot spot areas (**Figure 1A**). The first reported invasion sites were in the Beit Shean Valley, and two more major areas of infestation were reported in the Jordan valley and the Jezreel valley. In addition, several scattered populations were recorded in the Mediterranean coastal plain and in the upper Galili region in the Hula valley. It is important to state that no reports of *P. hysterophorus* populations were found south of the reported area.

As previously described, Beit Shean Valley is assumed to be the first introduction area for *P. hysterophorus* in Israel (Yaacoby, 2011). In our survey, plants from this region were detected in both cultivated and non-arable habitats, including roadsides, lawns, private gardens, field margins, and orchards (**Figure 1B**). For the Jordan valley hot spot, plants were detected alongside route 90 and were found to be scattered mainly in agricultural areas along the road (**Figure 1C**). However, in several communities such as Kibbutz Degania Bet and Kvutzat Kinneret, a high infestation level was recorded in close proximity to neighborhoods and public gardens. The distribution of *P. hysterophorus* in the Jezreel valley has several moderated infestation spots (**Figure 1D**). These spots are present in both cultivated fields and private gardens. Interestingly, one of the major hot spots of *P. hysterophorus* plants found in this area was

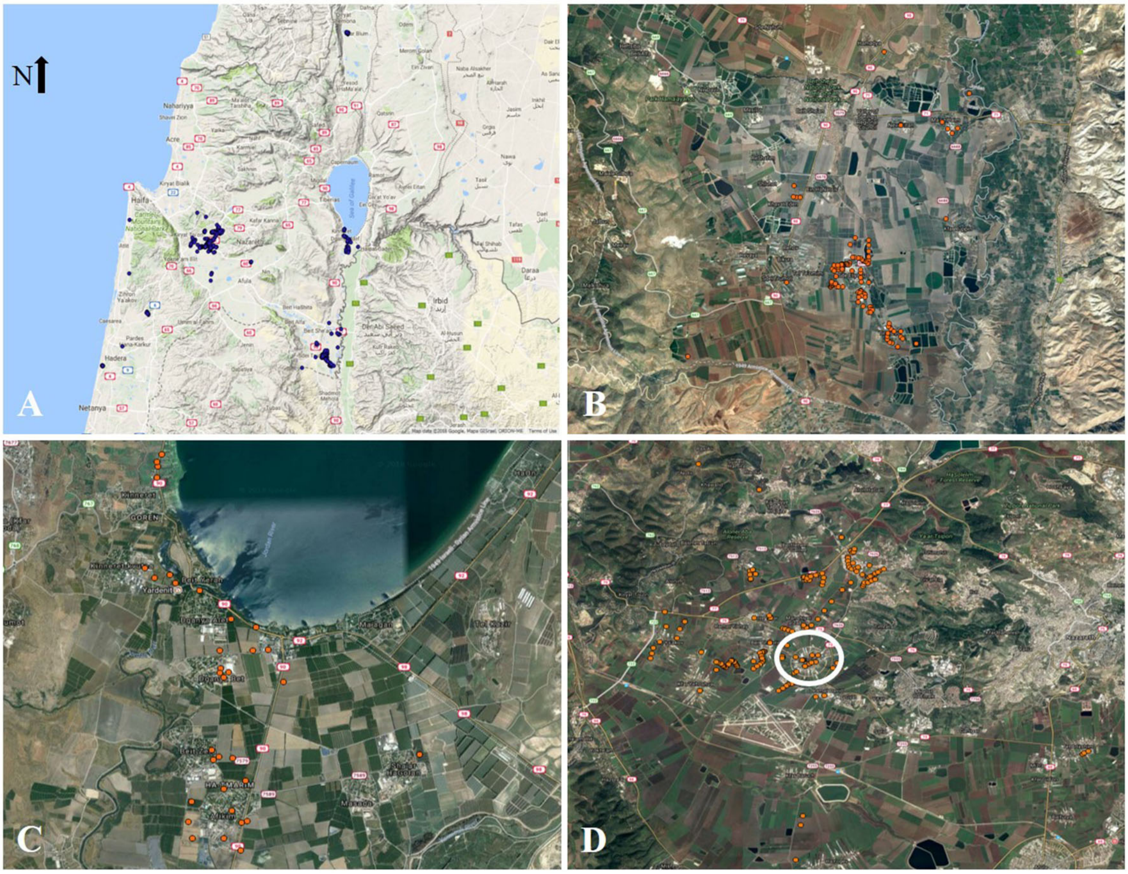

FIGURE 1 | Distribution of *Parthenium hysterophorus* across Israel. **(A)** Overview of the current *P. hysterophorus* distribution region. **(B)** Specific distribution in the Beit Shean Valley, **(C)** the Jordan Valley, and **(D)** the Jezreel Valley.

detected near a livestock feed distribution industry located near Nahalal (circled in white in **Figure 1D**).

Seed Germination

P. hysterophorus germination was tested under eight constant temperatures for 60 days. Our findings suggest a high association between germination and incubation temperature (**Table 1**). For the lowest temperature of 5°C, maximum germination was only 8%, recorded after a long incubation period of 54 days (**Figure 2A**). The highest temperature for *P. hysterophorus* seed germination was 35°C. The time required for maximum germination at this temperature was 21 days; however, the final germination rate was still lower than 10% (**Figure 2G**). The optimal temperatures for seed germination of *P. hysterophorus* were 20–25°C. For both temperatures, high germination rates of 92 and 99% were achieved after 10 and 14 days, respectively (**Figures 2D,E**). The time required to achieve 50% germination at these two constant temperatures was the lowest compared with all other incubation temperatures (**Table 1**). For seeds incubated at 15°C, the germination rate reached a total of 78% after 21 days (**Figure 2C**). No germination was recorded when seeds were incubated at a temperature of 40°C (**Figure 2H**).

P. hysterophorus Germination Dynamics

Data collected in germination tests under constant temperature regimes were used for the development of a beta-function model to better fit *P. hysterophorus* seed germination dynamics to temperature (**Figure 3A**). This model is in agreement with previous studies related to seed germination (Xinyou and Kropff, 1996; Cochavi et al., 2016; Goldwasser et al., 2016). According to the model, the *P. hysterophorus* seed germination rate increases as the temperature rises from a minimal value (5°C) to the optimal value (25°C). At supraoptimal temperature, the germination rate decreases until the ceased temperature are reached (40°C) (**Figure 3A**).

Accumulated seed germination is estimated by GDD. Based on the beta-function equation and parameters that were developed in the previous stage, a GDD accumulation of the seed germination model was developed (**Figure 3B**). *P. hysterophorus* seed germination started after 130 GDD, and 50% germination was achieved after 175 GDD. Maximum germination was recorded at 350 GDD. Reviewing both models, an equation predicting seed germination was developed Equation (8):

$$Seed\ germination\ (\%) = \frac{100}{1 + \left(\frac{GDD}{175.3}\right)^{-5.69}} \tag{8}$$

TABLE 1 | The coefficient of three parameters log-logistic equation fitted to describe the germination of *Parthenium hysterophorus* seeds under constant temperatures.

Temp	Coefficient parameter						Regression	
°C	*a*	*P*(*a*)	*b*	*P*(*b*)	X_0	$P(X_0)$	*P*	RMSE
5	7.7202	0.0001	11.694–	0.0001	41.2875	0.0001	0.0001	0.38
10	51.9089	0.0001	−3.5177	0.0001	37.0257	0.0001	0.0001	1.7106
15	78.0143	0.0001	−5.1716	0.0001	12.7006	0.0001	0.0001	2.8404
20	95.3907	0.0001	−4.6154	0.0001	6.5620	0.0001	0.0001	5.1866
25	99.999	0.0001	−5.7202	0.0001	6.4975	0.0001	0.0001	3.4748
30	30.6784	0.0001	−3.8417	0.0001	11.6728	0.0001	0.0001	1.5721
35	7.2162	0.0001	−2.5421	0.0001	20.7193	0.0001	0.0001	0.6865
40	–	–	–	–	–	–	–	–

a, maximal asymptote.
P(a), probability of maximal asymptote.
b, slope at the inflection point.
P(b), probability of the slope at the inflection point.
X_0, inflection point, 50% of maximal germination.
$P(X_0)$, probability of inflection point.
P, probability for the regression equation.
RMSE, root mean square error, as calculated by the RMSE equation (Lati et al., 2011a).

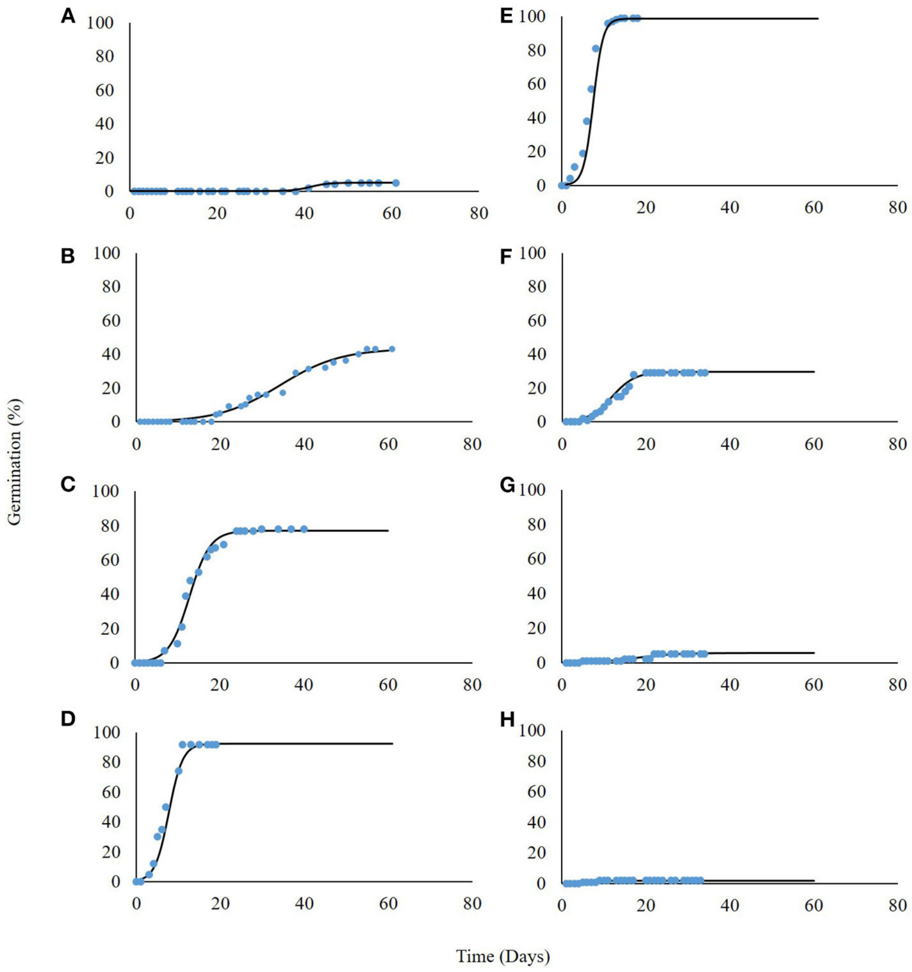

FIGURE 2 | Germination of *P. hysterophorus* seeds under constant temperatures: 5, 10, 15, 20, 25, 30, 35, and 40°C (**A–H**, respectively). The coefficient for non-linear regressions are given in **Table 1**.

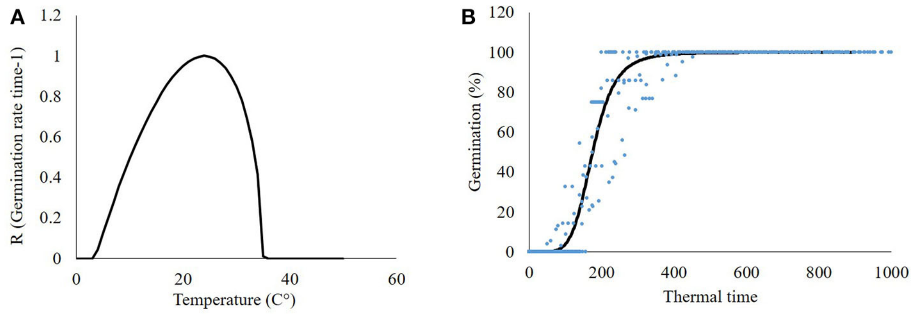

FIGURE 3 | Mathematical models describing the germination dynamics of *Parthenium hysterophorus* seeds. **(A)** Beta-function model describing the rate and maximum temperature-dependent germination and **(B)** seed germination dynamics according to a log-logistic model.

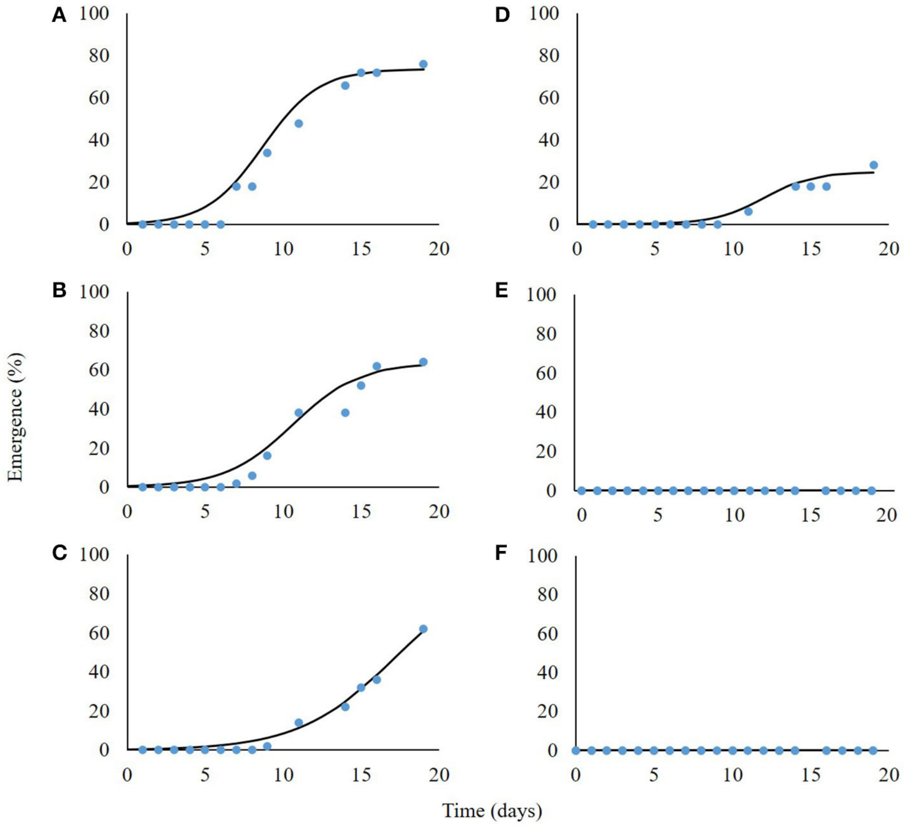

FIGURE 4 | Seedlings emergence of *Parthenium hysterophorus* seeds sown in different soil depths: 0, 1, 2, 3, 4, and 5 cm (**A–F**, respectively). Coefficient data are given in **Table 2**.

Seed Emergence

Seedling emergence was assessed from soil depths of one to five cm. Both the emergence rate and total emergence percentage were in negative correlation with the planting depth, i.e., *P. hysterophorus* emergence decreased dramatically with increasing planting depth (**Figure 4**). Seeds that were placed on the soil surface (0 cm) showed 76% emergence; the rate of emergence as described by parameter *b* (Equation 6) was the highest as compared with seeds emergence from other tested planting depths (**Table 2**). Seeds sown at both 1- and 2-cm-soil depths showed emergence of 64 and 62% and an emergence rate of 2.1 and 2.5%, respectively (**Figures 4B,C**; **Table 2**). Only 28% emergence was recorded for seeds sown at 3 cm soil depth, whereas seeds sown at 4- and 5 cm depth did not emerge at all (**Table 2**).

The Effect of Shading on Vegetative and Reproductive Growth

Plant Biomass

The shading level had a negative effect on plant biomass, reduced light intensity resulted in shoot biomass reduction, and significant differences were found among shading levels

TABLE 2 | The coefficient of three parameters log-logistic equation fitted to describe the emergence dynamics of *Parthenium hysterophorus* seeds sown in different soil depths.

Depth	**Coefficient parameter**						**Regression**	
Cm	***a***	***P*(*a*)**	***b***	***P*(*b*)**	**X_0**	**$P(X_0)$**	***P***	**RMSE**
0	74.174	0.0001	1.639	0.0001	8.769	0.0001	0.0001	3.545
1	64.018	0.0001	2.124	0.0001	10.686	0.0001	0.0001	4.773
2	66.325	0.0001	2.453	0.0001	14.619	0.0001	0.0001	3.131
3	27.469	0.0001	2.032	0.0001	12.798	0.0001	0.0001	1.948
4	–	–	–	–	–	–	–	–
5	–	–	–	–	–	–	–	–

a, maximal asymptote.
P(a), probability of maximal asymptote.
b, slope at the inflection point.
P(b), probability of the slope at the inflection point.
X_0, inflection point, 50% of maximal emergence.
$P(X_0)$, probability of inflection point.
P, probability for the regression equation.
RMSE, root mean square error, as calculated by the RMSE equation (Lati et al., 2011a).

TABLE 3 | The coefficient of three parameters log-logistic equation fitted to describe the effect of shade levels on *Parthenium hysterophorus* final shoot biomass.

Shading level	**Coefficient parameter**						**Regression**	
%	***a***	***P*(*a*)**	***b***	***P*(*b*)**	**X_0**	**$P(X_0)$**	***P***	**RMSE**
0	27.9996	0.0001	300.765	0.0001	1299.6	0.0001	0.0001	1.1191
30	24.1975	0.0001	260.741	0.0001	1181.7	0.0001	0.0001	0.4637
60	16.0926	0.0001	259.636	0.0001	853.65	0.0001	0.0001	0.7478
90	2.3228	0.0001	32.2981	0.1671	234.04	0.0001	0.0461	0.863

a, maximal asymptote.
P(a), probability of maximal asymptote.
b, slope at the inflection point.
P(b), probability of the slope at the inflection point.
X_0, inflection point, 50% of maximal final shoot biomass.
$P(X_0)$, probability of inflection point.
P, probability for the regression equation.
RMSE, root mean square error, as calculated by the RMSE equation (Lati et al., 2011a).

(**Table 3**). For the non-shading control treatment (0% shading), the maximal asymptote that represents maximal accumulation of shoot weight was 28 g (**Figure 5A**). At the 30% shading level, maximal biomass accumulation was 24.2 g (**Figure 5B**). A higher reduction in biomass was recorded at the 60% shading level when the maximal accumulated plant weight reached only 16.1 g (**Figure 5C**). The highest effect of the radiation level on plant biomass accumulation was recorded for the 90% shading level. Accumulated shoot biomass was only 2.3 g. Moreover, for the 90% shading level, biomass accumulation peaked at 350 GDD, and no significant increase in plant biomass was shown for the rest of the experiment (**Figure 5D**).

Plant Height

As in the case of plant biomass, plant height was also in a negative correlation with shading levels (**Figure 6**; **Table 4**). At 0% shading, the accumulated maximal plant height was 128.9 cm. Shading levels of 30 and 60% resulted in maximal plant heights of 88.8 and 77.2 cm accumulated, respectively. At the 90% shading level treatment, plants were not able to complete their life cycle and transition from the rosette stage to the bolting stage. Plant height at the 90% shading level ranged from 2.6 to 6 cm accumulated over 1,000 GDD with no further change until the end of the experiment (**Figure 6D**). For all other treatments (0, 30, and 60% shading levels), the transition from rosette to the bolting stage occurred at approximately 1,000 GDD.

Inflorescence Development

High-radiation levels accelerated the development of plant inflorescence (**Figure 7**). For both 0 and 30% shading, the maximal amount of flowers per plant was 71.1 and 81.5, respectively (**Table 5**). Total flowering was higher by 13% for the 30% shading in comparison with the 0% shading level as presented by the *a* parameter (maximum flowering) in **Table 5**. At the 60% shading level, the maximal number of flowers per plant was 42.1, and, for the 90% shading level, flower initiation

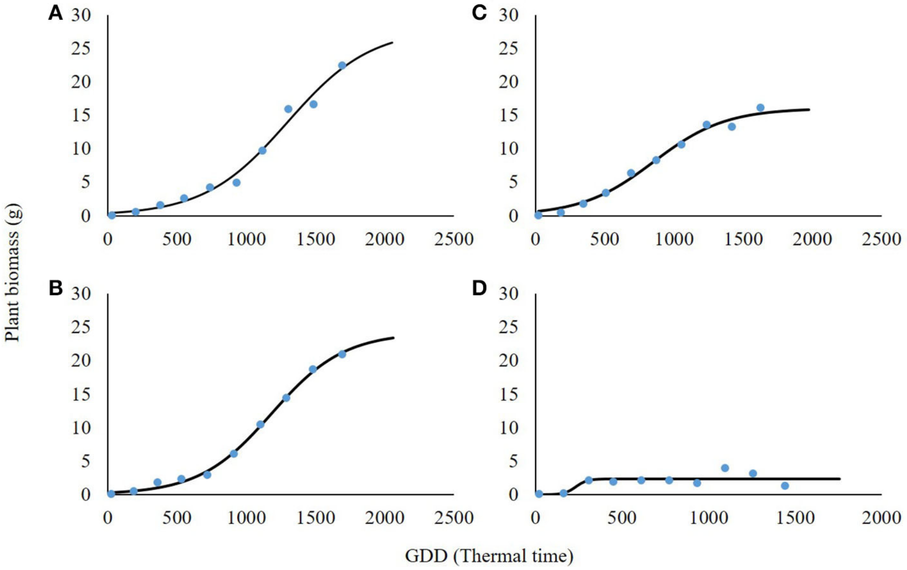

FIGURE 5 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on final shoot biomass of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 3**.

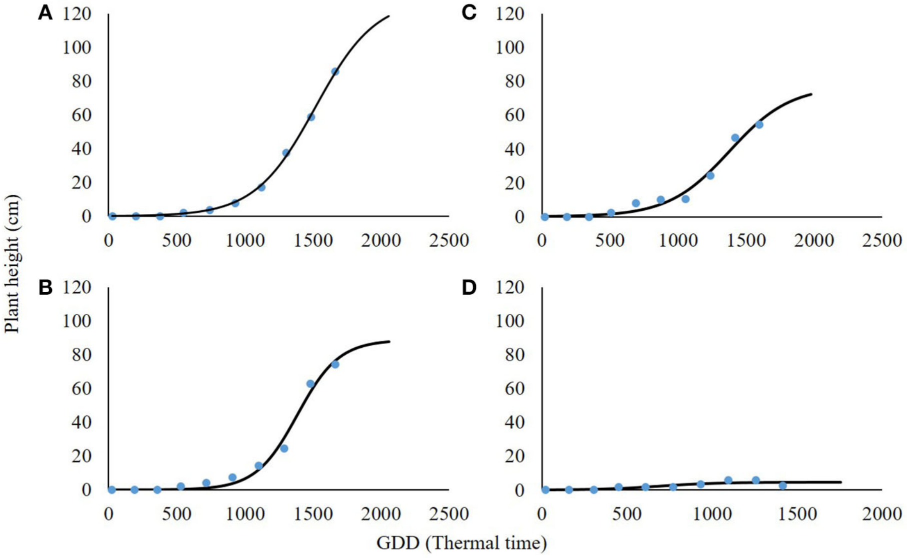

FIGURE 6 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on final plant height of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 4**.

did not occur. The transition from the vegetative to reproductive stage occurred under all shading treatments, except for the 90% shading level at approximately 1,000 GDD and corresponding to the changeover from rosette to the bolting stage described above.

DISCUSSION

Colonization of invasive species can be characterized in two main stages: the lag phase between initial introduction and subsequent rapid population growth, and the exponential phase when explosive range expansion occurs (Radosevich et al., 2007). In Israel, these two main stages can be detected. *P. hysterophorus* populations found at Beit Shean Valley, Jezreel Valley, and Jordan Valley are showing vast distribution, aggressive expansion, and high competitiveness as compared with the local vegetation. In addition, the proximity of hot spots to human-populated areas indicates significant anthropogenic influence on the spread of the weed. In populations found at specific habitats such as the one found along the coastline of the Mediterranean coastal plain and in the Hula Valley, plants are located in

TABLE 4 | The coefficient of three parameters log-logistic equation fitted to describe the effect of shade levels of *Parthenium hysterophorus* on final plant height.

Shading level	Coefficient parameter						Regression	
%	*a*	*P*(*a*)	*b*	*P*(*b*)	X_0	*P*(X_0)	*P*	RMSE
0	128.91	0.0001	221.7	0.0001	1517.5	0.0001	0.0001	1.1214
30	88.811	0.0001	152.5	0.0001	1386.1	0.0001	0.0001	3.8203
60	77.179	0.0001	222.7	0.0001	1375.8	0.0001	0.0001	3.3410
90	4.7196	0.0036	172.3	0.0105	693.49	0.0001	0.0093	1.2780

a, maximal asymptote.
P(a), probability of maximal asymptote.
b, slope at the inflection point.
P(b), probability of the slope at the inflection point.
X_0, inflection point, 50% of maximal final plant height.
P(X_0), probability of inflection point.
P, probability for the regression equation.
RMSE, root mean square error, as calculated by the RMSE equation (Lati et al., 2011a).

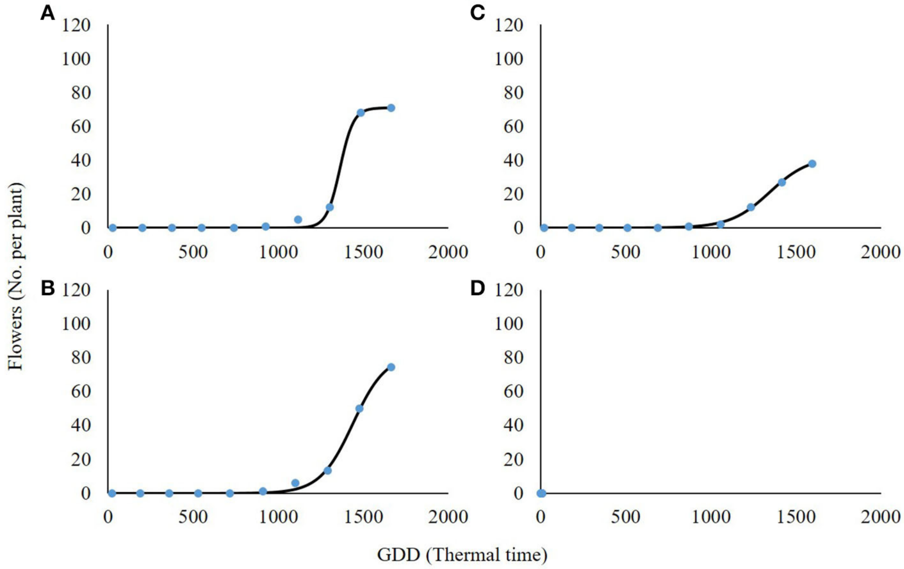

FIGURE 7 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on the final number of flowers per plant of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 5**.

dense clusters with minimal expansion. The distribution pattern of an invasive weed in a specific area is a key factor in the control efforts. Limited distribution across a specific site may increase the success of chemical and non-chemical weed management methods.

Previous studies have hypothesized that the invasion of weeds such as *P. hysterophorus* into the Israeli flora is facilitated by grain shipments imported for animal feed (Rubin and Matzrafi, 2015). This is in agreement with previous studies, describing *P. hysterophorus* invasion pathways (Vertak, 1968; Haseler, 1976; Tamado et al., 2002a). Our results show a high correlation between the presence of *P. hysterophorus* and close proximity to dairy barns, animal farms, and agricultural tool sheds. These patterns have mostly been found in new introduction areas such as the Mediterranean coastal plain (**Figure 1A**). However, further and more thorough work should be done to better understand these pathways of spread.

P. hysterophorus seed germination was found to be correlated with temperature increase (**Figure 2**). Overall, temperature increase resulted in higher seed germination; however, over the optimal temperature of 24°C, the germination rate declined. Previous work exploring the effect of temperature on *P. hysterophorus* seed germination has shown that different biotypes may germinate over a wide range of constant temperatures (8–32°C) under dark conditions (Bajwa et al., 2018). Tamado et al. (2002b) showed that germination occurred at a minimum of 10°C and a maximum of 25°C. Williams and Groves (1980) concluded that only temperatures higher than 35°C or lower than 5°C limit the germination of *P. hysterophorus*. In agreement with other studies, the optimal range for *P. hysterophorus*

TABLE 5 | The coefficient of three parameters log-logistic equation fitted to describe the effect of shade levels on *Parthenium hysterophorus* final number of flowers per plant.

Shading level	**Coefficient parameter**						**Regression**	
%	***a***	***P*(*a*)**	***b***	***P*(*b*)**	**X_0**	**$P(X_0)$**	***P***	**RMSE**
0	71.045	0.0001	39.56	0.0013	1364.8	0.0001	0.0001	1.8792
30	81.472	0.0001	97.06	0.0001	1438.5	0.0001	0.0001	1.4154
60	42.096	0.0001	115.8	0.0001	1347.9	0.0001	0.0001	0.4729
90	–	–	–	–	–	–	–	–

a, maximal asymptote.
P(a), probability of maximal asymptote.
b, slope at the inflection point.
P(b), probability of the slope at the inflection point.
X_0, inflection point, 50% of maximal final number of flowers per plant.
$P(X_0)$, probability of inflection point.
P, probability for the regression equation.
RMSE, root mean square error, as calculated by the RMSE equation (Lati et al., 2011a).

germination found in our study is 20–25°C. The GDD model based on beta-function was found to be very precise in describing *P. hysterophorus* seed germination dynamics (**Figure 3**). Good understanding of the germination dynamics may be harnessed to the process of developing new integrated weed control approaches suitable for *P. hysterophorus* biology as proposed for other weed species (Lati et al., 2011b; Eizenberg et al., 2012; Cochavi et al., 2015, 2016).

Examining the effect of burial depth on seed emergence showed a negative relation between burial depth and the emergence rate (**Figure 3**). Tamado et al. (2002b) showed that shallowly buried (0–1 cm) seeds had a high emergence rate (∼60%) compared with seeds buried at 2–3 cm (10–20%). This negative correlation was also found for several other weed species such as *Amaranthus palmeri* (Sosnoskie et al., 2013), *Rumex obtusifolius* (Benvenuti et al., 2001), and *Datura stramonium* (Benvenuti and Macchia, 1995). Germination inhibition caused by burial depth might be due to secondary dormancy linked to interactions between seed metabolism and the soil gas environment, or depletion of seed energy reserves (Benvenuti and Macchia, 1995, 1997). From a practical point of view, the deep burial of seeds using mechanical cultivation methods may reduce the emergence rate and thus increase the depletion of a viable seed bank as a weed-control approach.

Studying the effect of different shading levels on plant development, three different parameters were examined: shoot biomass, plant height, and flowering time. Our results show that high-light intensity conditions resulted in increased shoot biomass and taller plants as compared with plants grown under low-light intensities (**Figures 5**, **6**). The same trend was found in *A. tuberculatus* var. *rudis* when plant biomass and seed production were found to be lower as radiation levels decreased to 60, 32, and 1% light intensity (Steckel et al., 2003). For *Echinochloa crus-galli*, the shading level of 75% resulted in a 22% reduction in plant height; however, this was not the case for two other *Echinochloa* species (*E. colona* and *E. glabrescens*) (Chauhan, 2013). The same study showed that seed production for all *Echinochloa* species declined under reduced radiation levels. In *Abutilon theophrasti*, no differences were observed for plant height, leaves, or branches per plant when plants were grown under a shading level of 30%; however, for the 76% shading, reduced height, leaf number, stem branches, and plant biomass were observed (Bello et al., 1995). The effect of shading can be translated to weed/crop competition. As *P. hysterophorus* thrives under high-light intensities (Navie et al., 1998a), using strong competitive crops such as corn, cotton, and others may impair the growth of the weed, thus reducing its overall competitive ability. Studying the biology, phenology, and weed-crop competition aspects of *P. hysterophorus* is crucial in order to identify key traits that can improve its management.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

HR, BR, TY, and HE conceived the study and advised on the methodology. HR and MM conducted the experiments and statistical analyses. MM, HR, and HE wrote the manuscript, with contributions from BR and TY. All authors contributed to the article and approved the submitted version.

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REVIEW
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Effects of Climate Change on Weeds and Invasive Alien Plants in Sri Lankan Agro-Ecosystems: Policy and Management Implications

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Changes in the climate have worsen the problems caused by weeds and invasive alien plants (IAPs) in agro-ecosystems at global scale resulting from their changes in the range and population densities. Over the past six decades, Sri Lanka has experienced a slow but steady increase in annual environmental temperature by 0.01–0.03°C. Increasing extreme events of rainfall, wetter wet seasons, and drier dry seasons are some of the characteristic features of the changes in the climate observed in Sri Lanka over the years. The Ministry of Environment (MOE) in Sri Lanka has established a National Invasive Species Specialist Group (NISSG) in 2012 and adopted the National Policy on Invasive Alien Species (IAS) in Sri Lanka, Strategies and Action Plan in 2016. Further, the MOE has developed and adopted protocols to assess the risk of IAS at pre- and post-entry level to the country while incorporating climate change concerns. Periodic risk assessments have being carried out to prioritize actions against IAS in Sri Lanka. The Ministry of Agriculture as adopted a National Weed Strategy (NWS) and has identified the Weeds of National Significance (WONS) under different priority crops. A study done in 2014 has clearly shown that weed control costs in agricultural lands in several district of Sri Lanka were nearly doubled during the years that experienced *El Niño* Southern Oscillation (ENSO). Further, studies have clearly indicated that IAPs also survive, expand and impact the continuously disturbed environments in agro-ecosystems. *Panicum trichocladum*, a species listed as a potential invasive based on the risk assessment done in 2016, has shown an increase in its population density and distribution in Sri Lanka during the last 2–3 years. However, weeds and IAPs in agro-ecosystems have drawn less attention of policy makers, scientists, and practitioners in relation to impact of climate change in island ecosystems. This paper focuses on the scientific evidence reported in agro-ecosystems in Sri Lanka on climate-related impacts on agriculturally important weeds and IAPs, and the efforts made to manage their introduction and spread across the country.

Keywords: agro-ecosystems, weeds, invasive alien plants, climate change, Sri Lanka

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INTRODUCTION

Sri Lanka (7.8731° N, 80.7718° E), occupying a land area of 62,707 km² and water bodies of 2,905 km² (Department of Census and Statistics, 2020) is an island nation with a physically diverse geography and tropical climate. Four geographical and topographical features considerably influence the climate of Sri Lanka, namely being (1) a relatively small island in the Indian Ocean coupled with warm and humid air–resulting in a slower cooling in the nights in areas closer to the coastal belt, (2) located about 645 km north to the equator–resulting in hot environments owing to the fall of greater solar energy per unit area (3) existence of central highlands perpendicular to two monsoon wind streams—resulting in eastern and western slopes having contrasting climates at a given season (e.g., when western slopes of the central highlands are wet, the eastern slope experience a dry climate, and *vice versa*), and (4) the proximity to the Indian subcontinent with a vast landmass in the immediate north and northwest of the country–resulting in rapid cooling effect in the nights of the northern peninsular of Sri Lanka due to the buffering effect created from the release of long-range radiation with heat from the Indian sub-continent. The monsoonal winds originated from the surrounding oceans mainly determines climate patterns observed in Sri Lanka. Based on the annual rainfall, Sri Lanka is divided into Wet zone (>2,500 mm); Intermediate zone (1,750–2,500 mm); and the Dry zone (<1,750 mm). The country is further divided into seven agro-climatic zones and 46 agro-ecological regions (Punyawardena, 2007). The rainfall and cultivating seasons in Sri Lanka are shown in **Table 1** together with the vital atmospheric parameters.

The Intergovernmental Panel on Climate Change (IPCC, 2014) confirms that South Asia will experiences a significant change in its climate during the 21st century. According to Abeysekera et al. (2015, 2021) the frequency of occurrence of extreme rainfall events in Sri Lanka would increase in the future, resulting in excess soil moisture stress in the rainfed uplands, flood damages in lowland paddy fields and rapid drying out in cascade of tanks in the long-run, thus imposing a significant negative impact on Sri Lanka's agricultural productivity. Several reports have indicated an increase in the minimum and maximum ambient temperature in most districts of Sri Lanka and a decrease of rainy days resulting in prolonged dry spells and droughts (Premalal and Punyawardena, 2013; MMDE, 2016a; Naveendrakumar et al., 2018). Being a party to the United Nations Framework Convention on Climate Change (UNFCCC−1992) and to Paris Agreement (2016), Sri Lanka recognizes the need to accelerate addressing climate-related issues.

Weeds, including invasive alien plants (IAPs), are the major biological constraint in agro-ecosystems (Ghersa, 2013; Paini et al., 2016; Kariyawasam et al., 2017; Chauhan, 2020). Peters et al. (2014) reported that over the years, many weed species have increased their population densities, and expanded in their range of distribution, thus making them a major biotic component in agro-ecosystems. The impact of weeds and IAPs on productivity of food crops have been increasingly experienced worldwide (Vilà et al., 2004; Paini et al., 2016), under variable and changing climate (Peters et al., 2014; Ramesh et al., 2017; Beaury et al., 2020). Recent reports identified IAPs as a serious threat to agricultural production and food security in Sri Lanka (Paini et al., 2016; Kariyawasam et al., 2017). Changes observed in the global environment could increase the risks of biological invasions worldwide (Ricciardi et al., 2017). Increasing concentrations of atmospheric CO_2, and other changes observed in the temperature and rainfall are considered as major issues related to managing weed populations in agro-ecosystems (Varanasi et al., 2016). Considering this future impact, and a country that rely heavily on agriculture sector for rural livelihood development (Central Bank, 2019), this review is focused on the climate change impacts on weeds and IAPs in agro-ecosystems in Sri Lanka. The objectives were to elucidate the climate impacts on the distribution and persistence of weeds and IAPs in agriculture, especially focusing on food crop production, and to identify a way forward in managing these troublesome species in a changing and variable climate, in Sri Lanka. In this effort, we carried out a thorough literature survey using the Google® search engine to scan the published information pertaining to the topic. A keywords search, which included "invasive alien plants," "weeds," "agro-ecosystems," "agriculture," "climate change," "climate impacts," "climate-weed interactions," "climate-invasive alien plant interactions," "policies," and "Sri Lanka," was done to increase the precision of the survey. The climate impact on weeds and IAPs in Sri Lanka was mainly focused on the 25 year period from 1996 to 2020. The following sections of this paper summarizes the climate change experienced in Sri Lanka and its impacts, major weeds and IAPs of the agro-ecosystems, implications of weeds, IAPs and climate interactions, and conclusion.

Climate Change and Overall Climate Impacts in Sri Lanka

The climate risk to South Asia could result in significant damage to the economies, social development, and environmental aspects (Ahmed and Suphachalasai, 2014), and Sri Lanka is not an exception. The INFORM Risk Index (EU, 2019), considering the climate-related natural disaster, has categorized Sri Lanka under "moderate disaster risk" by ranking the country in the 97th position in terms of overall risk, out of 191 countries. Further, the World Bank and the Asian Development Bank (WB and ADB, 2020) reported that Sri Lanka is positioned at 56th in terms of for exposure to flooding, 45th in the exposure to tropical cyclones and their associated hazards, and 76th for drought exposure. The WB and ADB (2020) have reported the projected changes in the Sri Lankan climate (**Table 2**). With an annual increment of ambient temperature at 0.01–0.03°C since 1960 (Marambe et al., 2015a), the daily minimum temperature (night time) has shown a rapid increases than that of daily maximum temperature (day time), which could facilitate establishment of more perennial weeds (Ziska, 2004) as explained in detailed later in this review. Analyzing the rainfall using data collected from 400 rain gauging station, Nissanka et al. (2011) reported that the seasonal annual rainfall in Sri Lanka does not show a discernible significant

TABLE 1 | Rainfall and cultivating seasons and vital atmospheric parameters of Sri Lanka (source: Punyawardena, 2007).

Cultivating seasons	Rainfall	Months
Yala season (minor cultivating season)	First Inter Monsoon (FIM)	March–April
	South East Monsoon (SEM)	May–September
Maha season (major cultivating season)	Second Inter Monsoon (SIM)	October–November
	North East Monsoon (NEM)	December–February
	Atmospheric parameters	
Average annual temperature	26.5–28.5°C–at altitudes <1500 m	
	15°C–at altitudes >1500 m	
Average annual precipitation	5,500 mm–in the south-western slopes of Central Highlands	
	900 mm–southeastern part of the Dry zone of country (Hambantota)	
Monthly relative humidity	55–90%	
Pan evaporation	3–8 mm–*Yala* season	
	205 mm–*Maha* season	

TABLE 2 | Projected changes in climate of Sri Lanka (source: WB and ADB, 2020).

Parameter	Projected change
Temperature	• Under RCP8.5 scenario, increase by 2.9–3.5°C by the year 2090s (compared to 1986–2005 baseline) • Under RCP2.6, increase by 0.8–1.2°C by the year 2090 (compared to 1986–2005 baseline) • Rise of minimum temperatures faster than rises in average temperatures.
Heat	• Under RCP8.5, more than 100 days of a year surpassing 35°C (baseline of 20 days) by the 2090s. • Extreme heat events threatening human health and living standards, especially in urban areas without adequate cooling systems
Rainfall	• Frequency and intensity of extreme precipitation events would increase posing a huge risk on human and animal lives, livelihoods, and infrastructure, due to riverine flooding, flash floods, and landslides.

trend, except in few locations. However, the extreme rainfall events, as reported by Premalal and Punyawardena (2013) and WB and ADB (2020) would affect the floristic composition in ecosystems (Jewitt et al., 2014), including weeds and IAPs, which is discussed later in this review. All these results indicate the need for prioritization of climate actions in Sri Lanka focusing on the exposure to the climate risk factors.

MAJOR WEEDS OF THE AGRO-ECOSYSTEMS OF SRI LANKA

Weeds are an important biotic constraint to achieve increased productivity (Chauhan, 2020) having direct and/or indirect interferences with the crop production. Analysis done by Bambaradeniya et al. (2001), Rajapakse et al. (2012) and Rao et al. (2017) clearly indicate that weeds have caused about 50% of crop yield losses, in addition to reducing the quality of the crop harvest and threatening the native biodiversity of Sri Lanka. For example, paddy yield in Sri Lanka is reduced by about 20–40% (Herath Banda et al., 1998) or even by 80–90% (Marambe, 2009; Chauhan et al., 2013) due to weed competition. Availability of water plays an important role in determining the level of the weed interference where Amarasinghe and Marambe (1998) reported that paddy cultivated in rainfed lowlands are more susceptible to weed competition compared to that in irrigated lowlands. Furthermore, the climatic zone will also determine the competitive pressure exerted by weeds on crops as reported by Weerakoon et al. (2000), where the weed pressure higher in moisture-stressed Dry zone than that in the Wet zone. Abeysekera et al. (2006) showed that the floristic composition of weeds have changed in paddy fields due to the method of crop establishment, where wet-seeding has resulted in a shift of weed flora from annuals to perennials. The perennial weeds such as *Isachne globosa* are more difficult to control in paddy fields due to their multiple propagation techniques, by using sexual (seeds) and vegetative (stolons) propagules.

Apart from the specific weeds identified under different cropping systems, Sri Lanka has periodically identified the Weeds of National Significance—WONS (SLCARP, 2011, 2017; **Table 3**) to support prioritization of weed management in different agro-ecosystems in the country in terms of allocation of finances for research and practical application of weed control strategies. The WONS of Sri Lanka have been identified for different crops including more than 30 troublesome weeds in paddy, which is the major staple crop of Sri Lankans.

INVASIVE ALIEN PLANTS IN AGRO-ECOSYSTEMS

Alien plants have become invasive in their introduced habitats due to the absence of natural enemies, and outcompete the native species in the ecosystem (Hornoy et al., 2011), showed rapid reproduction rates (Richardson et al., 2000), higher adaptability to new and changing environments (Pyšek et al., 2012), and

TABLE 3 | Weeds of National Significance in Sri Lanka (source: SLCARP, 2017).

Weed	Habitat	Crop	Weed	Habitat	Crop
Aeschynomene indica L.	Semi-aquatic	Paddy	*Eclipta alba* (L.) Hassk.	Semi-aquatic	Paddy
Anredera cordifolia (Ten.) Steenis	Upland	Tea	*Eichhornia crassipes* (Mart.) Solms.	Aquatic	Paddy
Brachiaria brizantha (SM.) Griseb.	Upland	Rubber	*Eleusine indica* (L.) Gaertn.	Semi-aquatic	Paddy
Cyperus difformis L.	Semi-aquatic	Paddy	*Fimbristylis dichotoma* (L.) Vahl.	Semi-aquatic	Paddy
C. iria L.	Semi-aquatic	Paddy	*F. mileacea* (L.) Vahl.	Semi-aquatic	Paddy
C. rotundus L.	Upland	Paddy, Horticultural crops, Tea, Sugarcane	*Hedyotis auricularia* (L.) Bremek.	Upland	Rubber
Caladium spp. Vent.	Upland	Tea	*Hyptis suaveolens* (L.) Poit.	Upland	Coconut
Chromolaena odorata (L.) R.M.King and H.Rob	Upland	Coconut, Rubber	*Imperata cylindrica* (L.) Raeus.	Upland	Horticultural crops, Rubber, Sugarcane
Commelina benghalensis L.	Semi-aquatic	Paddy	*Ipomoea obscura* (L.) Ker Gowl.	Semi-aquatic	Paddy
C. diffusa Burm.f.	Semi-aquatic, upland	Paddy, Tea	*M. pudica* L.	Upland	Floricultural crops
Conyza sumatrensis (Retz.) E.Walker	Upland	Tea	*Murdannia nudiflora* (L.) Bren.	Semi-aquatic	Paddy
Crassocephalum crepidioides	Upland	Tea	*Oryza sativa* sp. Spontanea (L.)	Semi-aquatic	Paddy
E. crus-galli (L.) P.Beavuv.	Semi-aquatic	Paddy	*I. violacea* L.	Upland	Coconut, Flower crops
E. glabrescens (Munro) ex. Hook.f.	Semi-aquatic	Paddy	*Ipomoea* spp. L.	Upland	Sugarcane
Isachne globosa (Thunb. Kuntze.	Semi-aquatic	Paddy	*Panicum maximum* (Jacq.)	Upland	Coconut, Sugarcane, Spice crops, Floricultural crops, Fallowed agricultural land
Ischaemum rugosum (Salisb.)	Semi-aquatic	Paddy	*P. repens* L.	Upland	Paddy, Tea, Sugarcane
Ischnocarpus frutescens (L.) W.T. Aiton	Upland	Sugarcane	*Panicum trichocladum* Hack. ex Engl.	Upland	Tea
Lantana camara L.	Upland	Coconut, Floricultural crops, Fallowed agricultural land	*Parthenium hysterophorus* L.	Upland	Upland food crops, Fallowed agricultural land
Leptochloa chinensis (L.) Nees	Semi-aquatic	Paddy	*Paspalum distichum* L.	Semi-aquatic	Paddy
Limnocharis flava (L.) Buch.	Semi-aquatic	Paddy	*Pennisetum polystahion* L.	Upland	Spice crops
Ludwigia octovalvis (Jacq.) Raven.	Semi-aquatic	Paddy	*Salvinia molesta* D.Mitch	Aquatic	Paddy
L. perennis L.	Semi-aquatic	Paddy	*Scirpus supinus* L.	Semi-aquatic	Paddy
Mikania cordata (Vahl.) Willd	Upland	Rubber	*Spermacoce* spp. L.	Upland	Tea
M. micrantha Kunth.	Upland	Rubber, Spice crops	*Sphaeranthus indicus* Linn.	Semi-aquatic	Paddy
Marsilea aquadrifolia L.	Semi-aquatic	Paddy	*Sphagneticola trilobata* (L.) Pruski	Semi-aquatic, Upland	Paddy, Fallow agricultural land
Mimosa pigra	Semi-aquatic, upland	Paddy, Fallowed agricultural land	*Sphenoclea zeylanica* Gaertn.	Semi-aquatic	Paddy
Monochoria vaginalis	Semi-aquatic	Paddy	*Syngonium* spp. L.	Upland	Tea
			Vernonia zeylanica (L.) Less.	Upland	Coconut

aggressive growth and spread with early maturity. The IAPs have continued to affect the biodiversity of the natural ecosystems (Pyšek et al., 2012) and food security (Paini et al., 2016). The socio-economic impacts of IAPs have been extensively reviewed by Raj and Singh (2020). Wijesundara (2015) reported that invasive plants have caused a loss of ∼US$ 23 billion in USA due to their impacts on agriculture, industry, recreation and the environment. Shackleton et al. (2017) reported an economic loss of US$ 500–1,000 per household per annum due to *Opuntia stricta* invasion in the African continent. The losses due to *E. crassipes*, a WONS in Sri Lanka (**Table 3**), in South Africa was estimated to be US$ 58,195 per year (Wise et al., 2007). All studies on record clearly indicate that biotic invaders are a significant component of the anthropogenic environmental change. It is important to note that the mechanisms of such invasions could depend on many factors other than climate such as the resilience of the ecosystem and biotic interactions, and natural dispersal mechanisms, man-made pathways and vectors of IAPs, etc.

Invasive Alien Plants Reported in Sri Lanka

Internal trade, aid, and travel and transportation have helped movement of IAPs into natural and man-made ecosystems in Sri Lanka (Marambe et al., 2015b), which could have been facilitated by the liberalized economic policies adopted in Sri Lanka since 1978. The first official publication of the IAPs was released in Sri Lanka in 1999 (MEFR, 1999), with a list of such species in Sri Lanka. However, such listing were based mainly on the limited available literature, and perceptions of scientists/environmentalists without a scientifically valid risk assessment process. Sri Lanka conducted its first nation-wide risk assessment in 2009–2010 using a post-entry risk assessment (PERA) protocol developed, where 28 IAPs have been identified (Ranwala et al., 2012). The second effort to assess the impact of IAPs was carried out in 2015, by the NISSG of the MOE, using an updated PERA protocol, where 20 species were identified (**Table 4**) as nationally important priority IAPs. Further to those, 15 potential IAPs have also been recognized (Wijesundara, 2015).

The IAPs are a significant and growing threat to the natural and agro-ecosystems, and economy of Sri Lanka (Marambe et al., 2015b; Marambe and Silva, 2016; Kariyawasam et al., 2021). For example, Marambe et al. (2002a) reported of yield losses of 72% in tomato (*Solanum lycopersicum*) and 29% in chili (*Capsicum annuum*) due to the parasitic weed *Cuscuta* spp. Jayasinghe et al. (2004) reported that *Cuscuta* spp. lives on 161 host plants of which 27 are crops and 22 are other weeds, highlighting the threat of this holo-parasitic IAP in agro-ecosystems. Munasinghe et al. (2008), in their studies carried out in selected man-made reservoirs in the Anuradhapura district of the north central province of Sri Lanka, suggested that *S. molesta* and *E. crassipes* covered the water surfaces by 35 and 45%, respectively. This would negatively affect the aquatic life and increase water losses, including irrigation water, due to high rates of evapotranspiration.

About US$ 1.61 million has been spent by the Department of Irrigation of Sri Lanka since 2008 to clean reservoirs, irrigation canals and other waterways invaded by IAPs (Dharmasena, 2018). In mid 1980s, *S. molesta* invasion has cost the rice production in Sri Lanka by about US$ 163,000–375,000 per annum (Doeleman, 1989).

INTERNATIONAL CONVENTIONS AND NATIONAL POLICIES

The Ministry of Foreign Affairs of Sri Lanka, through its Ocean Affairs, Environment and Climate Change Division, promotes and coordinates projects and activities in relation to international conventions treaties entered into agreement by the country. It further ensures consistency and coherence in the engagement of Sri Lanka at international level in ocean affairs, environment and climate change, and provide relevant guidance to line ministries and agencies of the government of Sri Lanka.

The Biodiversity Secretariat (BDS) and the Climate Change Secretariat (CCS) of the MOE is the Sri Lankan focal point for the Convention on Biological Diversity (CBD; https://www.cbd.int/countries/nfp/?country=lk), and the UNFCCC including Paris Agreement (https://unfccc.int/process/parties-non-party-stakeholders/parties/national-focal-point), while the Department of Agriculture (DOA) of the Ministry of Agriculture (MOA) is the focal point for the International Plant Protection Convention (IPPC; https://www.ippc.int/en/countries/all/contactpoints/). All three conventions are of prime importance in the subjects concerned in this review paper. Sri Lanka has also enacted the Plant Protection Act No. 35 of 1999 to regulate the entry of weeds including IAPs, while the National Invasive Species Act is currently in the making, providing more authority to regulatory officers to deal with the entry to, and spread of IAPs in Sri Lanka (Source: Ms. Pathma Abeykoon, BDS, MOE).

The National Climate Change Policy (NCCP) of 2012 (MMDU, 2012), National Adaptation Plan for Climate Change Impacts in Sri Lanka (NAP-CC) in 2016 (MMDE, 2016a) and Nationally Determined Contributions (NDCs) in 2016 (MMDE, 2016b) have been adopted in Sri Lanka to tackle the climate change. The NAP-CC identifies the need to assess the impacts of enhanced levels of atmospheric CO_2 on biomass production of natural vegetation and spread of IAPs as priority actions under the theme food security (MMDE, 2016a). The Sri Lanka Council for Agriculture Research Policy (SLCARP, 2017) of the MOA has also published a National Weed Strategy (NWS) to deal with the WONS in agro-ecosystems. The NWS also focuses on the weed control under main food and export crops in relation to climate change (Rajapakse et al., 2012). The Ministry of Environment (MMDE, 2016c) has adopted the National Policy on Invasive Alien Species (IAS) in Sri Lanka, Strategies and Action Plan as the guiding document to control IAPs, in Sri Lanka. The National Agriculture Policy (NAP) of 2007 (MOA, 2007) and the National Agricultural Research Policy and Strategies 2018–2027 (SLCARP, 2018) of the MOA make provisions to management of weeds and IAPs and related research in Sri Lanka, respectively. A weed list, identifying list of weeds that are prohibited to be imported to Sri Lanka in addition to the WONS is expected to be adopted toward late 2021 under the Plant Protection Act No. 35 of 1999 (Source: Dr. W.A.R.T. Wickremarachchi, National Plant Quarantine Service, DOA).

TABLE 4 | Invasive alien flora in agro-ecosystems of Sri Lanka (source: updated from Wijesundara, 2010).

Plant species	Family	Country/Region/from which the species was introduced to Sri Lanka	Ecosystems affected	Reason of introduction	Year of introduction
Salvinia molesta	Salviniaceae	India	Island wide; Tanks, ponds, marshes, streams, paddy fields	Educational/Scientific study	1939
Panicum maximum	Poaceae	Africa	Islandwide; Disturbed forests and scrubland, roadsides, agricultural land	Fodder	1801
Cuscuta campestris Yunck	Convolvulaceae		Islandwide, except in upper montane zone; wastelands, agricultural land in low country	Accidental: Contaminant of grains	Unknown
Clidemia hirta	Melastomataceae	Tropical America	Sub-montane Wet zone; open areas in lowland, rainforest edges, tea fields	Ornamental	1894
Parthenium hysterophorus	Asteraceae	India	Dry and Intermediate zones; wastelands, irrigation canals, agricultural land	Accidental: Contaminant in imported chili and onion seeds	1980s
Mimosa pigra	Fabaceae		Dry and Intermediate zones; wastelands, agricultural lands, river banks	Protecting river banks	1980s
Sphagneticola trilobata	Asteraceae		Wet and intermediate zone; wastelands, roadsides, abandoned paddy fields		

Other national policies and action plans that have made provisions for the management of weeds and IAPs in Sri Lanka are the National Environment Policy and Strategies of 2003 by the Ministry of Environment (MENR, 2003), National Wildlife Policy for Sri Lanka 2007 of the Department of Wildlife Conservation (DWLC, 2007), and National Biodiversity Conservation Action Plan (NBSAP) of the Ministry of Environment (MMDE, 2016d). From among its actions, the NBSAP has identified priority interventions targeting to prevent the entry and the spread of IAPs as a key activities to safeguard the environment of the country.

WEEDS, INVASIVE ALIEN PLANTS, AND CLIMATE IMPACTS - IMPLICATIONS

Global climate change would significantly influence the population dynamics of IAPs in the future (Fandohan et al., 2015). The conceptual framework (**Figure 1**) illustrates the climate impact on ecosystems services and the survival and population explosion of weeds and IAPs in agro-ecosystems. The efforts to identify biological invasions and predicting their impacts on ecosystems under changing climate have yielded inconsistent results (Hulme, 2016). Some studies have reported that the current distribution of IAPs may not be in equilibrium with the current climate, nor that their potential establishment and/or spread be determined primarily by climate. For example, Sathischandra et al. (2014) used rainfall and temperature data for a period of 40 years from 1982 to 2012 in Sri Lanka, while using cost of weed control as the proxy to assess pest incidences. They reported the absence of a linear correlation between the occurrence of weeds and insect pests with climate variables. However, Sathischandra et al. (2014) further reported that the occurrence of weeds and insect pests can be relatively higher with extreme climate events that occur during *El Niño* and *La Niña* (ENSO) years. With such complexities, Kariyawasam et al. (2019a) highlighted the need for accurately predicting dynamics of IAPs under future climate change/global warming scenarios for more informed decision making to manage the IAP populations.

In a changing climate, the C_3 crops are expected to be benefitted by elevated CO_2 levels in the atmosphere, especially during their vegetative stages, compared to that of C4 crops (Patterson, 1995). The C_3 food crops are expected to become less competitive compared to C_4 weeds in a changing climate (Korres et al., 2016) as the C_4 photosynthesis pathway is more effective and efficient at higher temperatures compared to that of plants withC_3 photosynthesis (Carter and Peterson, 1983; Ziska and Bunce, 1997). However, Ziska (2000) also reported that yield losses in C_4 crops such as *Zea mays*, *Saccharum officinarum* and *Sorghum bicolor* are affected by weeds having C_3 photosynthetic mechanism, indicating that such impacts would enhance with increasing levels of CO_2 in the environment. Weeds and IAPs are also known to have a greater physiological plasticity (Treharne, 1989), while perennial weeds may become more noxious under elevated CO_2 levels (Ramesh et al., 2017). Ziska and Runion (2006) reported that growth of weeds is benefitted from elevated CO_2 thus outcompeting crops even when the photosynthetic pathway of both crop and weeds are the same. As depicted in **Figure 1**, Ziska and George (2004) also reported that weeds with

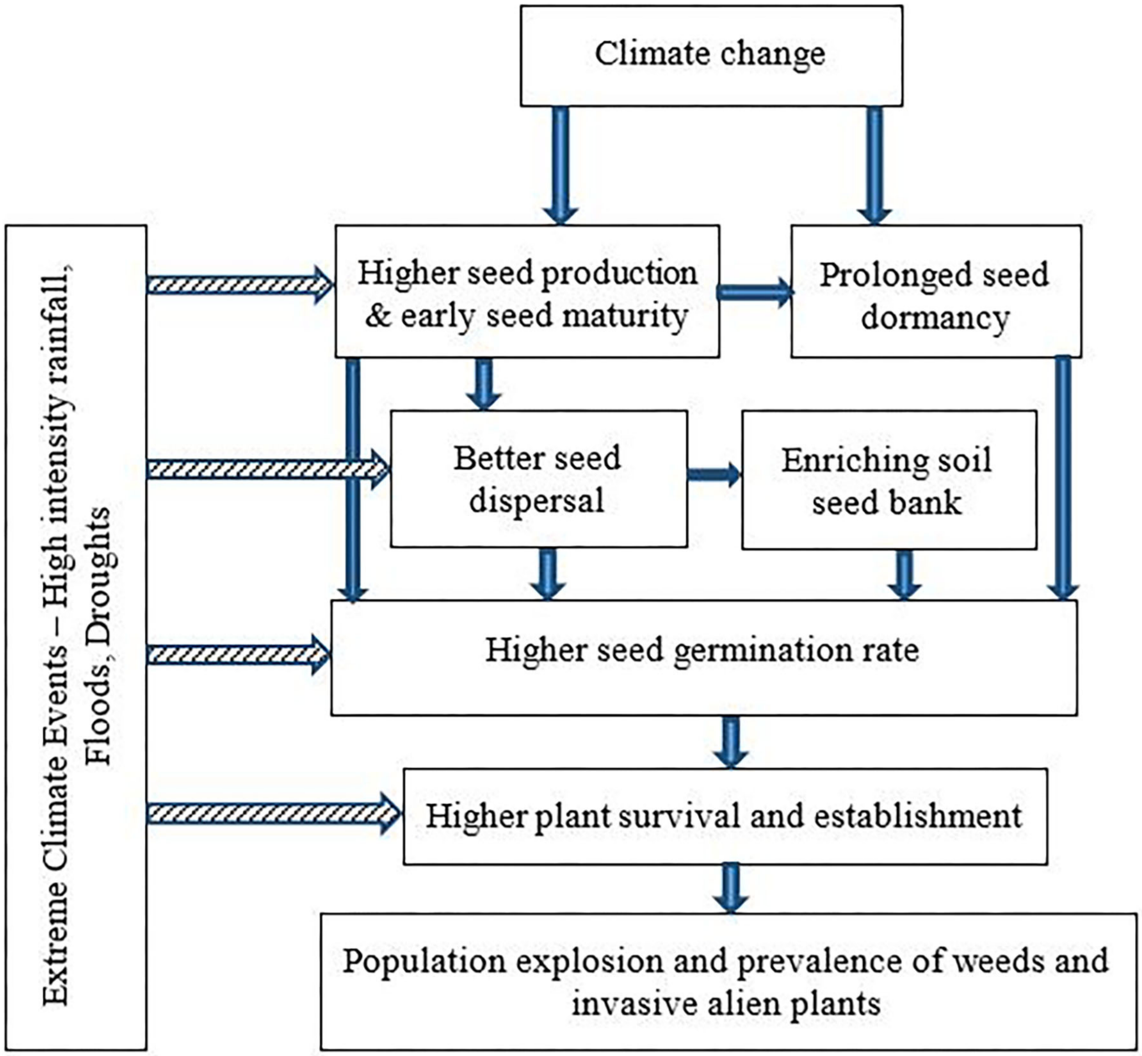

FIGURE 1 | A simplified model depicting only the direct general impacts and specific impacts of climate change on survival of weeds and invasive alien plants ➡ Direct general impacts Lower the arrow to align with the center of the text line, ⇨ Specific impacts of extreme events.

invasive behavior and reproduce vegetatively have shown a more positive response to increasing CO_2 levels than crops. These findings highlight the greater level of complexity in predicting weed-crop interaction in a climate change scenario rendering it more difficult to design and adopt management strategies to overcome such problems in agro-ecosystems.

The IAPs have been reported to adapt to climate change showing plasticity in their growth patterns. For example, Patterson (1995) reported that *Bromus tectorum* has shortened its life span under drought conditions and extended its root system to deeper soil layers thus, demonstrating better adaptation of IAPs compared to most of the native plant species. In India, evidence for a rapid population expansion of IAPs was evident under higher environmental temperatures with a synchronized mass scale seed germination of *Trianthema portulacastrum* (Masters and Norgrove, 2010), a noxious weed that is also reported in Sri Lanka (Kaur and Aggarwal, 2017). Several reports have also shown differential performance by weeds in a changing environment especially in terms of seed germination. Studies carried out by Huxman et al. (1998) reported of delayed germination and slower growth rate of seeds of an IAP (*Bromus* spp.) grown under elevated CO_2 levels compared to those obtained from plants that have grown under ambient environment.

Increasing flooding depth is known to affect the germination and seedling growth of many weeds. For example, a study done in the Philippines (Chamara et al., 2018) has shown a decrease in seedling emergence of *Echinochloa crus-galli* and *Ludwigia hyssopifolia* from 53% to 95% thus, reducing the competitive pressure on paddy plants. However, they also reported that the seedling emergence of *Cyperus difformis* is increased by 49–68% with increase in flowing depth from 2 to 5 cm, thus, indicating the differential performance of weeds and a potential shift in weed flora in paddy fields for changing climates, especially under extreme climate events. Both *E. crus-galli* and *C. difformis* are listed under WONS (**Table 3**) while *L. hyssopifolia* is also reported as troublesome weed in rice-growing environments (Perera and Dahanayake, 2015) in Sri Lanka. Experimental data of Chamara et al. (2018) also suggest that *C. difformis* would dominate paddy fields with increasing rainfall intensity in a changing climate.

Movement of propagules of IAPs to different locations and the loss of capacity of the native plants to tolerate IAPs has been identified as the primary processes that biological invasion could take place due to climate change (Diez et al., 2012). Marambe et al. (2002b) reported that river water flow helps dispersal of *Mimosa pigra* seeds, suggesting that flooding due to extreme weather events could help spread of this IAP further. We also have observed a marked increase in population sizes of *Clidemia hirta*, an identified IAP of Sri Lanka (**Table 4**), during the past several decades in tea plantations in the country. However, there has been no quantitative ecological studies to compare its population sizes at different time intervals. Peters et al. (2014) reported of the difficulty in quantifying the niche shifts of arable weeds. Recently, a climate suitability study carried out by Kariyawasam et al. (2019b) considering 14 IAPs under RCP 4.5 and 8.5 scenarios concluded that species-specific patterns of spread of IAPs depend on their existing growing environments in Sri Lanka. They also predicted that the southern and western parts of Sri Lanka are climatologically more suitable for IAPs. Potential impacts of climate change on the spread of IAPs, including that of agriculturally important weeds (**Table 5**).

Ramesh et al. (2017) reported that an increase in rainfall would increase the cost of production of crops owing to increased weed pressure. For example, increase in rainfall frequency and intensity would adversely affect the efficacy of soil-applied herbicides (Rodenburg et al., 2011). Further, Patterson (1995) reported that drought conditions would increase the cuticle thickness and leaf pubescence of weeds and reduce the entry of herbicides through leaves. These scenarios will increase cost of weed management and thus the total cost of crop production. Growth, reproduction and invasiveness of *Parthenium hysterophorus*, a WONS (**Table 3**) and an IAP (**Table 4**) in Sri Lanka, has been favored by changing climate (Bajwa et al., 2016), especially under changing rainfall patterns, and increasing temperatures and atmospheric carbon dioxide (CO_2) levels. Moreover, Javaid et al. (2010) reported of prolonged seed dormancy in *P. hysterophorus* with increasing temperature. Lopez et al. (2015) reported that the germination process of plant species is generally synchronized within the optimum temperature range. These results indicate that IAPs such *P. hysterophorus* could enhance its persistence in the environment and opportunity for developing into new invasions by temporal variations in seed germination due to non-synchronized breaking of seed dormancy.

The IAPs readily germinate with better seedling growth at high temperature compared to the native plant species (Xu et al., 2019). For example, Hou et al. (2014) reported that IAPs are more tolerant in terms of seed germination and seedling growth. These results suggest the risk of seed bank enrichment by weeds and IAPs, and potentially high biological invasions with global warming.

Furthermore, non-existence or weak implementation of the IAP management plans, none to poor financial commitments for IAP control, absence of an information management system resulting in non-availability of reliable data, and poor institutional coordinating mechanism are the other key challenges affecting successful IAP management. Bambaradeniya et al. (2006) reported that, apart from climate change, the natural disasters such as Tsunami in 2004 has led to a rapid expansion of IAPs such as Siam weed (*Chromolaena odorata*) in the southern coastal belt of Sri Lanka bordering agricultural lands.

The IAPs are often equipped with mechanisms to disperse their seeds and other propagules through wind or animals over long distances (Pyšek and Richardson, 2007). Invasive flora has been reported for their rapid colonization ability after an extreme climate event, after maintaining low profile under strong inter-specific competition (Groves, 1999; Grice and Ainsworth, 2003). Finch et al. (2021) reported that extreme climate events could assist the movement of IAP propagules from one location to another, facilitating their establishment and spread within a region. This suggest that climate extremes would help rapid expansion in the geographic distribution of IAPs, and their establishment at higher population densities in new and favorable environments. For example, warmer-region palms such as *Trachycarpus fortunei* have successfully established in open fields in temperate European ecosystems while surviving the winters (Walther et al., 2007; Finch et al., 2021). Climate change has increased the spread of the aquatic weed *Ranunculus trichophyllus* into new lakes in the Himalaya region (Lacoul and Freedman, 2006). In Sri Lanka, the aquatic invasives *S. molesta* and *E. crassipes*, which are also in the list of WONS (**Tables 3**, **4**) have been reported in Gregory's lake in the Nuwera Eliya city of Sri Lanka (Shirantha et al., 2010), a location that has recorded an increase of annual air temperature at a rate greater than the global average during the period 1906–2005 (De Costa, 2008). These results have indicated the threats of alien plants becoming IAPs with range expansion in a warming world, in turn impacting irrigated agro-ecosystems.

Furthermore, as reported by Hou et al. (2014), the seed germination and seedling growth stages of *Mikania micrantha*, a WONS in Sri Lanka (**Table 3**), have better tolerated day/night temperatures of 34/29°C by allocating more biomass to shoot growth compared to that of native plant species. Hou et al. (2014) also reported that *M. micrantha* seedlings had short-term tolerance to extreme high day/night temperature (40/35°C). These results suggest that IAPs have higher chances of survival and rapid colonization in a changing climate with different growth stages showing differential responses to high environmental temperature regimes.

Some IAPs could also indirectly support the spread of other alien invasives. For example, *Arundo donax*, gorse (*Ulex europaeus*), kikuyu grass (*Pennisetum clandestinum*), and old world climbing-fern (*Lygodium microphyllum*), with their ability to increase fire loads and heat intensity, could result in higher

TABLE 5 | Invasive behavior of alien plants as affected by climate change and resulting changes in the environment (this is a representative list; the outcomes are based on scientific studies and observations).

Parameter	Influence on weeds and IAPs	Source
Higher environmental temperatures	Increases seed production and population densities of *E. crus-galli*	Marambe and Amarasinghe, 2002
Higher CO_2 levels	Increased prevalence of *M. pigra* and *P. juliflora*	Marambe et al., 2003; Wijesundara, 2010
RCP 4.5 and 8.5 emission scenarios	A projected increase in population sizes by 2050 of *M. pigra* and *P. hysterophorus*	Kariyawasam et al., 2019a
RCP 4.5 and 8.5 emission scenarios	A projected decrease in population sizes by 2050 of *P. maximum* and *L. camara*	Kariyawasam et al., 2019a
Climate change induced disequilibrium in the ecosystem	Facilitate spread into protected areas: *C. odorata*	Iqbal et al., 2014
Floods	Facilitate spread into new habitats*: M. pigra*, *M. invisa*, *E. crassipes*, *S. molesta*	Iqbal et al., 2014
Increase in diurnal temperatures	Facilitate extension of temperature boundaries for growth: *Tithonia diversifolia*, *Eupatorium riparium*	Iqbal et al., 2014
El Nino La Nina (ENSO) years	Increase weed infestation in paddy	Sathischandra et al., 2014
Temperatures above 35°C	Enhanced seed germination and growth of paddy field weeds: *E. crus-galli*, *L. chinensis*, *Lindernia rotundifolia*, and *Monochoria vaginalis*	Bandara et al., 2017
High temperatures and moisture limited conditions	Higher population densities: *P. repens, Echinochloa* spp., *C. rotundus, L. chinensis,* and *Ischaemum rugosum*	Malaviarachchi et al., 2019
Increasing environmental temperature	Shift of weed flora from annuals to perennials in sugarcane	Witharama et al., 1997
Variation in rainfall	Changes critical period of weed competition in pole bean	Premalal et al., 1999

mortality rates in some fire-intolerant native species thus opening up more space for invasion by IAPs (Wijte et al., 2005). Though a direct inference cannot be drawn, *P. trichocladum* is a potential IAP (Wijesundara, 2015) that has shown a rapid spread in the central province of Sri Lanka over the past few decades.

At the global scale, the cost of IAS including IAPs was recently estimated to be around US$ 1.288 trillion for the period 1970–2017 (Diagne et al., 2021). These estimates clearly indicate an unprecedented pressure to the economies, with annual average cost of US$ 26.8 billion. Diagne et al. (2021) also reported that in 2017 alone the global cost of IAS was US$ 162.7 billion. Furthermore, Cleland et al. (2007) showed that climate change could provide opportunities for aliens to become invasive by changing plant growth rates, reproductive capacity, and the plant physiology and phenology thus shifting their range.

CONCLUSION

Many agro-ecosystems in Sri Lanka are vulnerable to the changes in climate. Such vulnerable ecosystems with already low biodiversity, would be the first to demonstrate interactions between weeds, IAPs and climate change. Determination of the relationship between the environment parameters and species characteristics is important to estimate the spread and persistence of agriculturally important weeds and IAPs under changing and variable climate. Detailed studies on niche shifts of weeds and IAPs are a necessity to understand the underline processes of such changes in agro-ecosystems. Continuous monitoring of the shifts in species populations of weeds and IAPs are thus a necessity. As highlighted by Iqbal et al. (2014) and Marambe et al. (2009, 2015a), climate impacts could be aggravated further by IAPs, if they are not considered as a significant component of the environment, especially in the climate action dialogue in Sri Lanka. Prioritizing actions against weeds and IAPs under a changing and variable climate, especially using the provisions granted by the NWS, NAP-CC, and National Invasive Alien Species Policy, Strategy and Action Plan is an urgent need in order to protect its fragile agro-ecosystems and ensure optimum use of its agro-biodiversity.

AUTHOR CONTRIBUTIONS

BM developed the initial concept and outline. BM and SW collectively expanded the content, contributed, and edited the manuscript. Both authors contributed to the article and approved the submitted version.

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Screening Diverse Weedy Rice (*Oryza sativa* ssp.) Mini Germplasm for Tolerance to Heat and Complete Submergence Stress During Seedling Stage

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Rice is a staple food for more than 3.5 billion people worldwide, with Asia producing almost 90% of the global rice yield. In the US, rice is primarily produced in four regions: Arkansas Grand Prairie, Mississippi Delta, Gulf Coast, and Sacramento Valley of California. Arkansas currently accounts for more than 50% of the rice produced in the US. As global temperatures continue to rise and fluctuate, crop-breeding programs must continue to evolve. Unfortunately, sudden submergence due to climate change and unpredictable flash flooding can cause yield reduction up to 100% and affect 20 million ha of agricultural farmlands. Similarly, it has been demonstrated that temperatures higher than 34°C can cause spikelet infertility resulting in up to 60% reduction in yield. One major drawback to developing abiotic stress-tolerant rice is the loss of critical traits such as vegetative vigor, spikelet fertility, and grain quality, which are essential in increasing economic return for farmers. To replace traits lost in past breeding endeavors, weedy rice (WR) has been proposed as a source for novel trait discovery to improve rice breeding programs. Therefore, the goal of this study was to screen and identify heat- and submergence-tolerant WR accessions. A WR mini germplasm consisting of seedlings at the 3–4 leaf stage was exposed to heat (38°C) and complete submergence for 21 days. After each treatment, height was recorded every 7 days for 28 days, and biomass was collected 28 days after treatment. The average height reduction across all accessions was 19 and 21% at 14 and 28 days after treatment (DAT) for the heat-stress treatment. The average height reduction across all accessions was 25 and 33% for the complete submergence stress. The average biomass reduction across all accessions was 18 and 21% for heat and complete submergence stress, respectively. Morphologically, at 28 DAT, 28% of the surviving WR accessions in the heat-stress treatment with <20% height reduction were straw-colored hull types without awns. Under complete submergence stress, 33% of the surviving WR accessions were blackhull types without awns. These specific biotypes may play a role in the increased resilience of WR populations to heat or submergence stress. The results presented in this paper will highlight elite WR accessions that can survive the effects of climate change.

Keywords: abiotic stress, weed physiology, weed control, rice breeding, crop improvement, climate change, weedy rice, *Oryza sativa* ssp.

INTRODUCTION

Rice, *Oryza sativa*, is a major food staple and arguably one of the most essential crops feeding close to half of the world's population and providing more than 50% of the daily calories (Muthayya et al., 2014; Kim et al., 2015; Dong and Xiao, 2016). Rice is primarily grown in major river deltas of Asia and Vietnam, and it is a rapidly growing food source in Africa (Kuenzer and Knauer, 2013). Cultivated rice is separated into two species: *O. sativa* (subspecies *japonica* or*indica*) and *O. glaberrima,* with origins from North Asia, South Asia, and West Africa, respectively (Vaughan et al., 2008). In the US, *japonica* cultivars are primarily grown in the southern rice belt while *indica* cultivars are primarily grown California (USDA ERS, 2021). China and India consume more than 50% of the rice produced worldwide, while the US exports more than 4,000 tons of rice annually (USDA ERS, 2021).

In the US, rice yields continue to increase annually due to the adoption of optimum management practices and the introduction and adoption of hybrid rice varieties, but rice production systems still struggle against increased weed pressure and impacts of climate change (Espe et al., 2016; Fargione et al., 2018). Of the significant abiotic stresses, rice can be impacted by salinity, drought, flooding, and high/low temperatures (Hasanuzzaman et al., 2018). In crops such as maize, soybeans, and rice, climate extremes explain 18–43% of the yield variance from year to year (Vogel et al., 2019). In rice, temperatures above 33°C can negatively impact all stages of plant growth and development with temperatures above 37°C causing a complete loss of plants at the reproductive stage (Jagadish et al., 2007; Aghamolki et al., 2014; Kilasi et al., 2018). Temperatures above this threshold are typical in the summer months in the southern US, but US rice is able to withstand these temperatures notwithstanding some yield losses (Tenorio et al., 2013; Chiang et al., 2018).

Although many studies have been conducted to evaluate the effects of heat stress at the reproductive stage, rice's increased sensitivity to heat and the direct correlation to grain yield lead Kilasi et al. (2018) to screen rice seedlings for heat stress tolerance (37°C) as a comparative means to identify genes controlling heat tolerance (2018). By opting to screen at the seedling stage, Kilasi et al. (2018) used the root and shoot growth as a percentage of the control to identify tolerant lines that can be genotyped quickly. Bewley (1997) noted that stored reserves are mobilized during post-germination, radicle cells elongate, cells divide, and DNA is synthesized. These processes happen rapidly and can be considerably affected by heat stress (Kilasi et al., 2018). In the case of complete submergence, Adkins et al. (1990) reported that submergence stress tolerance in rice is associated with the seedling stage as older plants are more tolerant than younger ones. Additionally, most rice plants that are submerged for more than 3 days are severely injured or dead, and few cultivars can survive complete submergence for 10–14 days (Gao et al., 2007). Survival and tolerance of rice cultivars have been associated with semi-dwarf cultivars and suppressed leaf elongation and decreased carbohydrate consumption while submerged (Gao et al., 2007).

In an effort to mitigate the effects of climate change, there has been a shift in research to study genetically similar weed species to uncover stress-tolerant traits to improve crop systems (Barrett, 1983; Ghanizadeh et al., 2019; Hopper et al., 2019). In rice, studies have turned to weedy rice (WR), *Oryza spp.* (also commonly referred to as red rice or weedy red rice), to understand the evolutionary pathways that lead to increased competitiveness (Olsen et al., 2007). In the US, WR infestations are most prominent in the Arkansas and Mississippi delta leading to a reduction in rice yield by up to 80% (Estorninos et al., 2005). As one of the major weeds in rice, WR can reduce both the quality and quantity of cultivated rice as WR is adapted to rice production agroecology (Jia and Gealy, 2018).

WR has numerous characteristics similar to that of cultivated rice, but the contrasting differences such as increased height, seed shattering, and seed dormancy, coupled with its ability to mimic cultivated rice, make WR challenging to control. At the same time, WR can be a source of genetic variation previously lost through the domestication of cultivated rice (Bevilacqua et al., 2015; Nadir et al., 2017). WR also possesses competitive characteristics to produce more tillers and culms and be taller than rice while accumulating more nitrogen and sucrose, leading to increased biomass production (Kwon et al., 1992; Burgos et al., 2006).

WR grows taller and faster than cultivated rice even when planted deeper, suggesting that it may harbor some traits that could overcome cold stress (Gealy et al., 2000). Research has shown that weedy rice has increased tolerance to cold stress; however, those accessions identified as cold tolerant still exhibited a height reduction of 29–37% compared to non-stressed controls (Bevilacqua et al., 2015). Currently, the US primarily grows *japonica* rice cultivars, which are more tolerant to cold stress than *indica* type rice varieties. However, farmers have to adhere to an appropriate rice planting window to ensure good crop stand and crop development (Xu et al., 2008). While *japonica* rice cultivars are planted in the US, Bevilacqua et al. (2015) determined that more than 90% of WR found in the US is of the *indica* biotype. Challenges exist in the hybridization of *japonica* x *indica* rice; one being the predominance of sterile offspring when breeding for cold tolerance (Borjas et al., 2016). To combat these challenges, it may be useful to cross cold-sensitive *indica* rice cultivars with cold-tolerant WR biotypes.

WR had also shown tolerance to high salinity during germination, with levels only dipping below 50% germination when salinity was >16 dS m^{-1} (decisiemens per meter) (Hakim et al., 2011). In the same study by Hakim et al. (2011), WR species exhibited $<20\%$ shoot length reduction at 4 dS m^{-1}, and increased shoot lengths were recorded up to 24 dS m^{-1}. WR also boasts broad-spectrum resistance to rice blast disease, with ∼18 of the 60 screened WR accessions were resistant to 3–10 blast races (Liu et al., 2015). Of the 18 resistant WR accessions, one accession demonstrated complete resistance to 10 blast races, although the 14 blast races present had a virulence rate of 98.3% (Liu et al., 2015).

Weedy rice exhibit differential tolerance to herbicides. For example, the Arkansas WR germplasm showed 30–100% injury when treated with a commercial rate of glyphosate at 900 g a.e. ha^{-1}(Burgos et al., 2011). Moreover, studies have shown that weedy rice is highly variable, genetically and phenotypically (Gealy et al., 2002; Cao et al., 2006; Burgos et al., 2014; Chen et al., 2014). Burgos et al. (2014) reported seven hull colors in imazethapyr-resistant WR, indicating the phenotypic diversity of WR populations. The same study presented six genetic groups of WR in the surveyed fields. Cao et al. (2006) used AMOVA analysis to confirm that ∼35% of total genetic variation existed among WR regions. Using microsatellite markers, an average genetic diversity of 0.63 across 89 weedy rice accessions in Arkansas was reported (Gealy et al., 2002). Studies also point to a significant amount of diversity amongst and within weedy rice populations and between weedy rice and cultivated rice (Ferrero, 2003; Londo and Schaal, 2007; Tseng et al., 2013).

This study aimed to identify heat- and submergence-tolerant WR accessions and characterize the competitive traits of stress-tolerant accessions.

MATERIALS AND METHODS

Plant Materials

Seeds of 200 different WR accessions were collected from the major rice-growing counties in Arkansas in 2008-09 and grown in a commong garden at the Rice Research and Extension Center, Stuttgart and at the Main Agricultural Research Center, Fayetteville, AR. Various morphological characteristics were evaluated (Tseng et al., 2013) and using these morphological data, 54 weedy rice accessions (**Supplementary Table 1**) were selected based on desirable competitive traits including height and high tillering. Four rice cultivars specific to the southeastern United States (CRL-Thad, CRL-Rex, CRL-CL163, and CRL-PM), and four rice-breeding lines (RBL) with traits for heat and submergence, were obtained from the Delta Research and Extension Center, Mississippi State University, Stoneville, Mississippi, for inclusion in the study. Each experiment consisted of 54 weedy rice lines (**Supplementary Table 1**), two rice-breeding lines (heat-stress specific), and three cultivated rice lines. After completing one run with all 54 WR accessions, 10 WR accessions with $<20\%$ height reduction and biomass reduction, and five (four in the case of the heat-stress treatment) accessions with $>80\%$ height reduction and biomass reduction were selected for runs two and three.

Heat Tolerance Screening

These experiments were conducted in 2016, 2017, and 2019 in the weed physiology laboratory located on the Mississippi State University campus (MS State, MS). Each experiment consisted of three treated replicates and three non-treated controls. Four seeds from each WR accession, rice-breeding-line, and cultivated rice line (CRL) were sown in a 72-well planting tray (Greenhouse Mega Store) containing potting soil (SunGro Professional Growing Mix; 3.8 cu. ft.) in a completely randomized design. Plants were covered with clear domes (Propagation domes; Greenhouse Mega Store) and grown under optimum conditions (28°C /16 h light, 24°C /8 h dark) in a growth chamber (Percival Scientific, Perry, IA) until germination, after which the clear domes were removed. After 21 days, 3–4 leaf stage sized plants were thinned to two plants per well, and plant height was measured. The plants were then transferred to a similar growth chamber set at 38°C and incubated for 21 days with a 16/8 h light/dark cycle. After 21 days, plants were returned to the growth chamber set at optimum growing conditions, and plant height was measured at 14 and 28 days after treatment (DAT). Plant height was measured from the soil surface to the tip of the healthiest, fully emerged leaf. The plants were cut at soil level, oven-dried for 7 days at 50°C, and weighed.

Submergence Tolerance Screening

Submergence experiments were conducted in 2016, 2017, and 2019 in the weed physiology laboratory at the Mississippi State University campus (MS State, MS). The plants were prepared following the same procedure as the heat tolerance experiment. Once emerged, plants were thinned to two plants per well and covered with a modified 72-well tray. Wells were cut from the bottom of the 72-well tray to allow roots to grow through. Twenty-one days after planting, the plants were completely submerged for 21 days within 102 liter ($78.4 \times 51.5 \times 36.9$ cm) black totes (Command XL; Lowes). Water levels were maintained at 20–30 cm (submergence depth) above the plant canopy to ensure complete coverage of plants throughout the experiment. After 21 days of submergence, water was drained to maintain 5–10 cm depth in each plastic tote, simulating normal flood conditions. Plant heights were recorded at 0 DAT and every 7 days for 28 days. Plant height was measured from the soil surface to the end of the healthiest, fully emerged leaf blade. After the experiment (28 DAT), plants were cut at the soil level, oven-dried for 7 days at 50°C, and weighed.

Statistical Analysis

Data was collected from a completely randomized design with three replicates and two plants per replicate to evaluate the effects of heat and complete submergence on a WR population. The reduction in plant height was obtained by subtracting the individual heights of the treated plants (HTP) from the height of the control plants (HCP), then dividing by the HCP and multiplying by 100 to obtain a percent (Equation 1). For biomass reduction, Equation (1) was used where height was replaced with biomass of the corresponding plant. Data were analyzed using ANOVA to compare treated WR accessions and corresponding untreated controls, rice-breeding lines, and cultivated rice lines based on individual mean height and biomass reduction. Where factor effect was significant, treatment means were compared Tukey's multiple comparisons test in JMP 14©. The LSD values were separated at a 0.05 level of significance. Additionally, the data were subjected to principal component analysis (PCA) with 16 agronomic traits alongside mean height and biomass reduction. K-means clustering with hierarchical clusters was used to separate the WR population into groups based on these traits.

$$\frac{Height\ of\ Control\ Plants\ (HCP) - Height\ of\ Treated\ Plants\ (HTP)}{Height\ of\ Control\ Plants\ (HCP)} \times 100 \qquad (1)$$

RESULTS AND DISCUSSION

Heat Tolerance Screening

Due to the high vigor of WR, seedlings were kept at 38°C for 21 days. Heat stress effect was manifested as reduced plant height and biomass at 14 and 28 DAT. The WR population showed substantial differences in response to sustained heat stress at 38°C during the seedling stage. Approximately 57 and 42% of the 14 WR populations showed 20% or less reduction in plant height at 14 and 28 DAT, respectively. This indicates that severe heat stress could kill rice seedlings. In an experiment with rice mutants, Bahuguna et al. (2015) found that mean temperatures ranging from 36 to 45°C resulted in a loss of 53% of the seedling population within 15 days after transplanting resulting in only eight seedlings surviving the stress (Bahuguna et al., 2015). In the current study, consistent temperatures of 38°C allowed for the survival of 14 WR accessions treated at the 3–4 leaf stage. Selecting a temperature within the range provided by

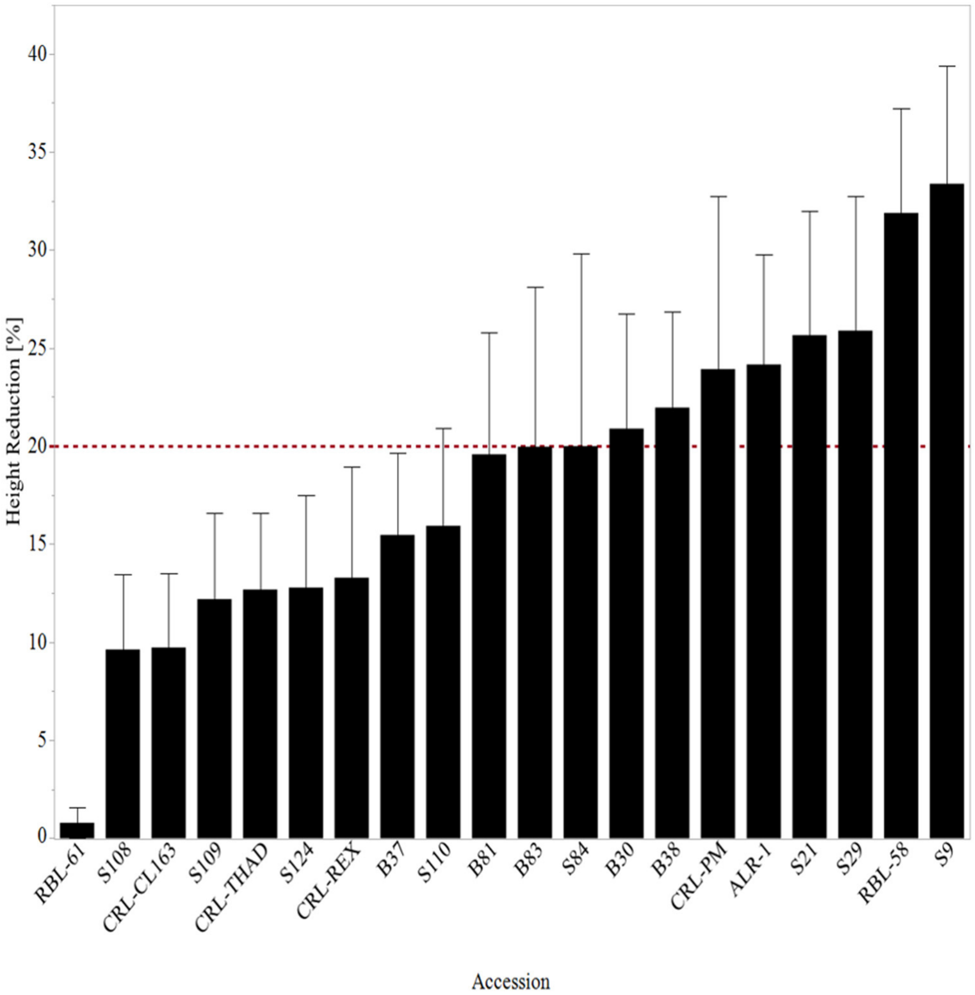

FIGURE 1 | Mean height reduction 14 days after heat stress treatment arranged from lowest reduction to the highest reduction in height. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

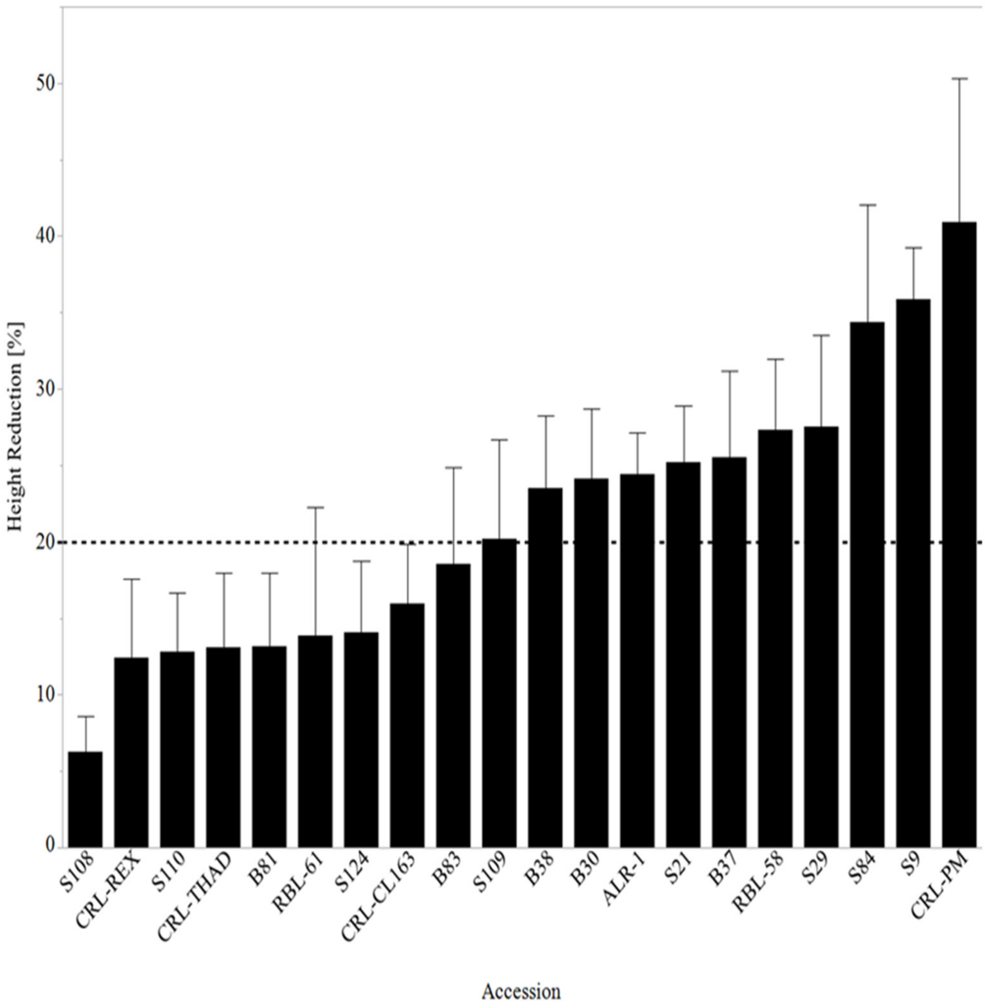

FIGURE 2 | Mean height reduction 28 days after heat stress treatment arranged from lowest reduction to the highest reduction in height. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

Bahuguna et al. (2015) provided sufficient stress to plants while maintaining a consistent population size. In another study, Kilasi et al. (2018) found that *aus* variety N22 had ∼30% longer root and shoot lengths compared to the heat-sensitive variety IR64 after only being exposed to heat stress (37°C) for 4 days during germination. These results are similar to findings in this study as rice seedlings were just 21 days old before the onset of heat stress.

In this study, plant height reduction ranged from about 1 to 33% at 14 DAT (**Figure 1**). At 14 DAT, RBL-61 (0.8%) showed the least reduction in height, followed by WR accession S108 (10%) and CRL-CL163 (10%). Rice-breeding line, RBL-61, is a commercial indica type rice from Pakistan often used as a reference for tolerance to heat stress (Pervaiz et al., 2010). RBL-61 is a semi-dwarf variety (≤110 cm tall) that matures in 116–130 days (Pervaiz et al., 2010). WR accession S108 is a high-yielding, straw-colored, awn less ecotype from Randolph County, Arkansas. The WR accessions were collected from random fields across the rice-producing counties in the Arkansas Delta and were characterized morphologically in a common garden (Tseng et al., 2013). WR accession S9 showed the most height reduction at 33% at 14 DAT. This WR accession was collected from Arkansas County, Arkansas, and is a straw hull, awn less ecotype. Poli et al. (2013) also reported stunting of heat-stressed rice "N22." Findings showed that plant height increased by only 5% although the current study resulted in few plants with decreased height but the 3-week heat stress treatment (Poli et al., 2013).

At 28 DAT, mean plant height reduction across cultivars and WR accessions ranged from 6 to 41% (**Figure 2**). This increased stunting with time is a manifestation of long-term effects of heat stress, especially reduced photosynthetic processes, reduced cell growth, and even cell death. Injury and cell death due to extreme heat stress can occur within a few minutes of exposure to heat and is characterized by foliar senescence and inhibition of root and shoot growth (Nievola et al., 2017). In our study, WR accession S108 had the least reduction in height (6%), while CRL-PM was most stunted (41%). As previously mentioned, WR

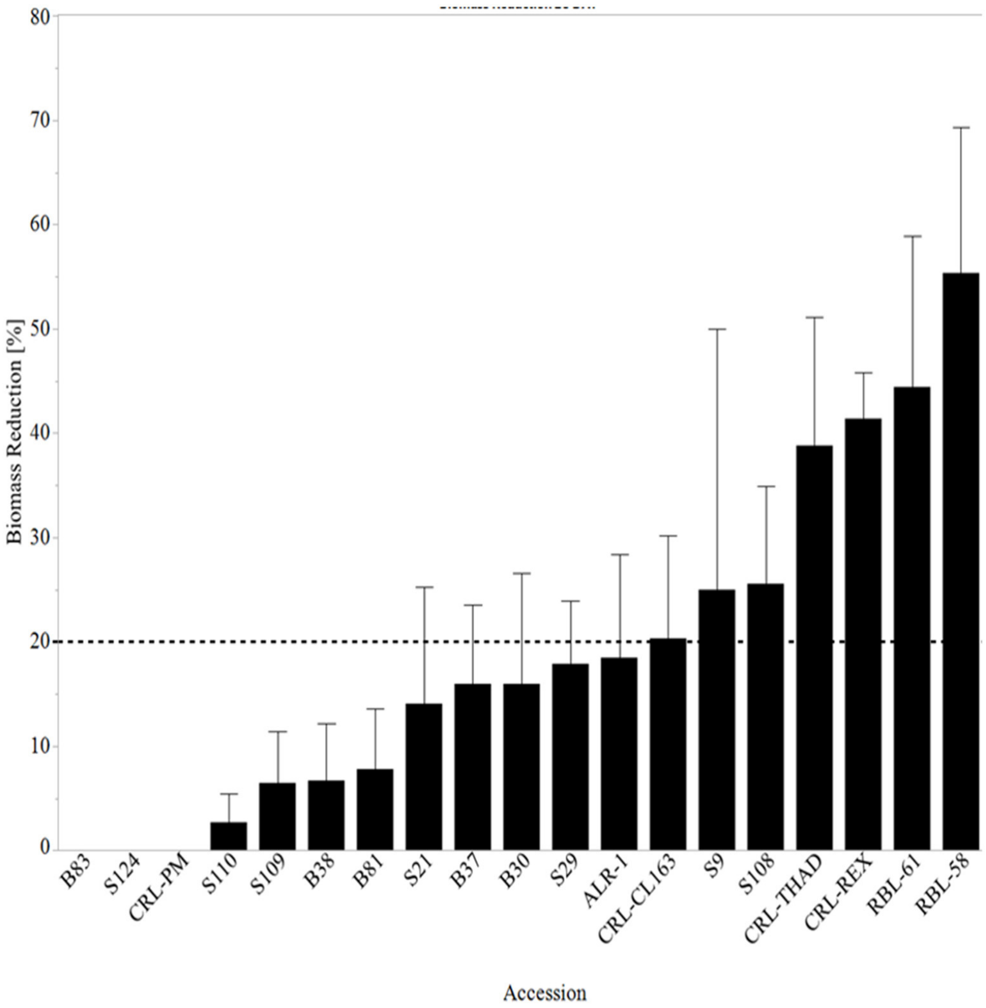

FIGURE 3 | Mean biomass reduction 28 days after heat stress treatment arranged from lowest reduction to the highest biomass reduction. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

accession S108 showed significant recovery and continued to grow taller after being exposed to heat stress for 21 days. The height reduction for S108 was 10% at 14 DAT compared to the control, which decreased to 6% at 28 DAT. Severe heat stress can also reduce panicle length, contributing to yield loss. Research by Wu et al. (2016) showed that high-temperature stress reduced the length of exerted panicles by ∼60%.

After 21 days of exposure to 38°C temperatures, the mean biomass reduction ranged from 0 to 55%. Rice is a grain crop that has demonstrated the ability to continue to grow new leaves after the senescence of older leaves (Inada et al., 1999). Extended leaf exposure to high temperatures leads to the degradation of chloroplasts and the rapid decline of soluble proteins and chlorophyll (Inada et al., 1999). Considering this cycle of production and loss of proteins and chlorophyll under heat stress, some WR plants demonstrated the ability to continue producing biomass even after prolonged exposure to high temperatures. WR accessions B83 and S124 did not show biomass reduction whereas RBL-58 lost 55% of biomass after the 3-wk heat stress (**Figure 3**). Interestingly, CRL-PM had the highest height reduction (38%) at 28 DAT but had no biomass reduction at 28 DAT. CRL-PM is commonly used in breeding programs to visually distinguish cross changes in early generation breeding programs (Gravois et al., 2005). This line lodges readily and has high degree of seed dormancy, but has been used as the parental line in many breeding efforts from the early 90's to 2000's (Roche et al., 2005).

Yoshida (1981) identified the threshold temperature for rice seedlings to be 35°C. Heat stress is characterized by irreversible damage that impacts plant growth and activity (Xiao et al., 2011). Reduced growth due to severe heat stress had been reported before, causing up to 90% height reduction (Yoshida, 1981). In this study, three lines (BKN6624-46-2, IR7478-2-6, and N22) were stunted and showed 90–100% reduction in spikelet fertility at temperatures from 35 to 31°C (Yoshida, 1981). At temperatures just above 25°C, both spikelet number and tiller number declined with further increase in temperature (Yoshida, 1973). Heat stress (38°C) during flowering time can cause 50–80% reduction in spikelet fertility (Cheng et al., 2012). A study of rice mutants using crosses between heat-sensitive, high-yielding rice variety, IR64, and drought- and heat-tolerant mutant, *aus* variety, N22, found that mutants had a 13% increase in plant height at 38°C when compared to parents (Poli et al., 2013). Increases in plant height can increase the transpiration cooling effect seen in many plants under heat stress (Weerakoon et al., 2008; Hasanuzzaman et al., 2013). Similar results may be valid in heat-tolerant WR as two (2) WR lines had no height reduction at 28 DAT. In this study, height reduction was a significant focus as plant height is a critical characteristic for breeding rice cultivars with increased yield (Jeng et al., 2012).

To further assess the variability and performance of those lines with low and high height and biomass reduction, a principal component analysis (PCA) was employed using hierarchical

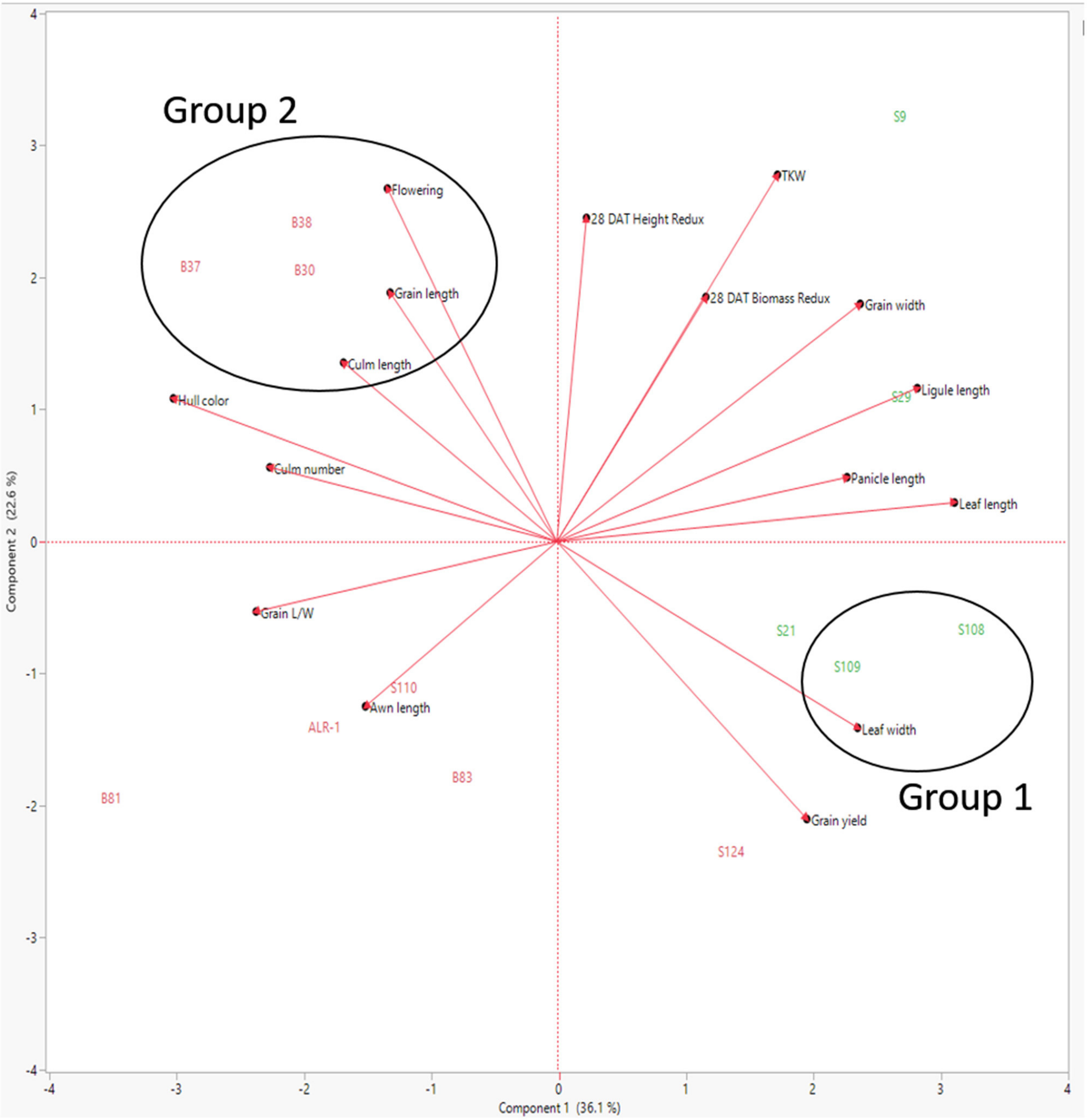

FIGURE 4 | Principal component analysis (PCA) of 16 agronomic traits, including plant height reduction and plant biomass reduction 28 days after heat stress treatment.

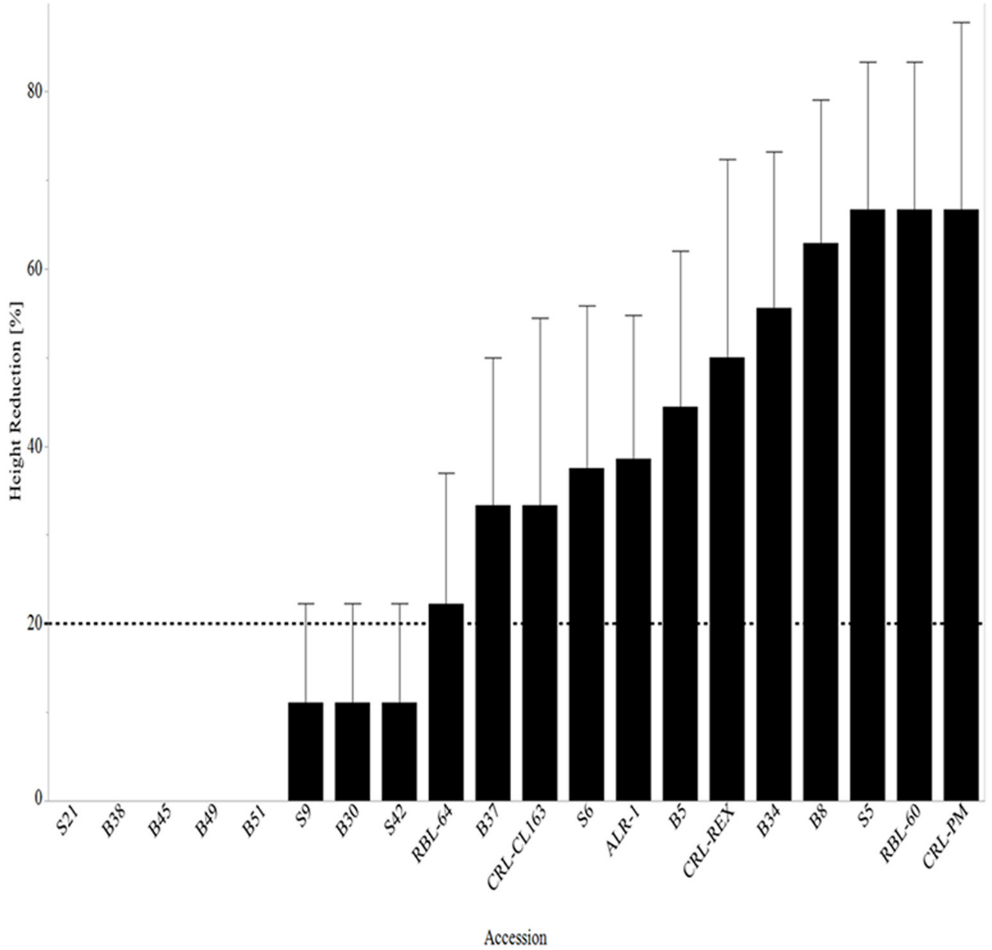

FIGURE 5 | Mean height reduction 14 days after complete submergence stress treatment arranged from lowest reduction to the highest reduction in height. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

clustering (Tseng, 2013). In the PCA, 16 agronomic traits were used to access the variability captured in components 1 and 2. The PCA revealed that 36% variation in heat-stress-tolerant WR accessions was attributed to component 1 compared to just 23% in component 2 (**Figure 4**). When PCA was paired with hierarchical cluster analysis, WR accessions S108 and S109 formed an independent group (Group 1) associated with leaf width (mean = 1.4 cm). These leaves are wider than the population average of 1.26 cm. While WR accession S108 did have a reduction in biomass 28 DAT, the accession consistently had <20% reduction in height at 14 and 28 DAT. Group 1 is also comprised of WR plants with straw-colored hulls without awns. A second grouping (Group 2) consisting of accessions B30, B37, and B38 had above average measurements in flowering time (mean = 105 days), grain length (mean = 6 cm), and culm length (mean = 129 cm), but the PCA reveals that these agronomic traits are not associated with heat-stress tolerance. These selected agronomic traits are associated with increased plant height while culm length is directly related to plant height (Jeng et al., 2012). Additionally, agronomic associations can be made related to increased ligule length, panicle length, and leaf length in similar PCA planes. Similar results are observed in Arkansas weedy rice as PCA attributes hull color as the primary trait separating the population (Kanapeckas et al., 2018).

Submergence Tolerance Screening

At 14 DAT, ∼33% (five out of 15 WR accessions) of the WR accessions had no height reduction, while 53% (eight out of 15 WR accessions) of WR had <20% height reduction (**Figure 5**). The accessions with no height reduction, S21, B38, B45, B49, and B51, are predominantly black-pericarp, awned WR accessions. Although Setter and Laureles (1996) found a negative correlation between shoot elongation and plant survival, stating that increased elongation in flooded rice was characteristic of low surviving seedlings after exposure to complete submergence for 14 days, the effects have not been studied in WR. In this study, varying effects were observed where those accessions that had no reduction in height continued to survive the effects of submergence stress 28 DAT. This trend was observed at 7 and 14 DAT, but at 28 DAT, 40% of the WR had <20% reduction in

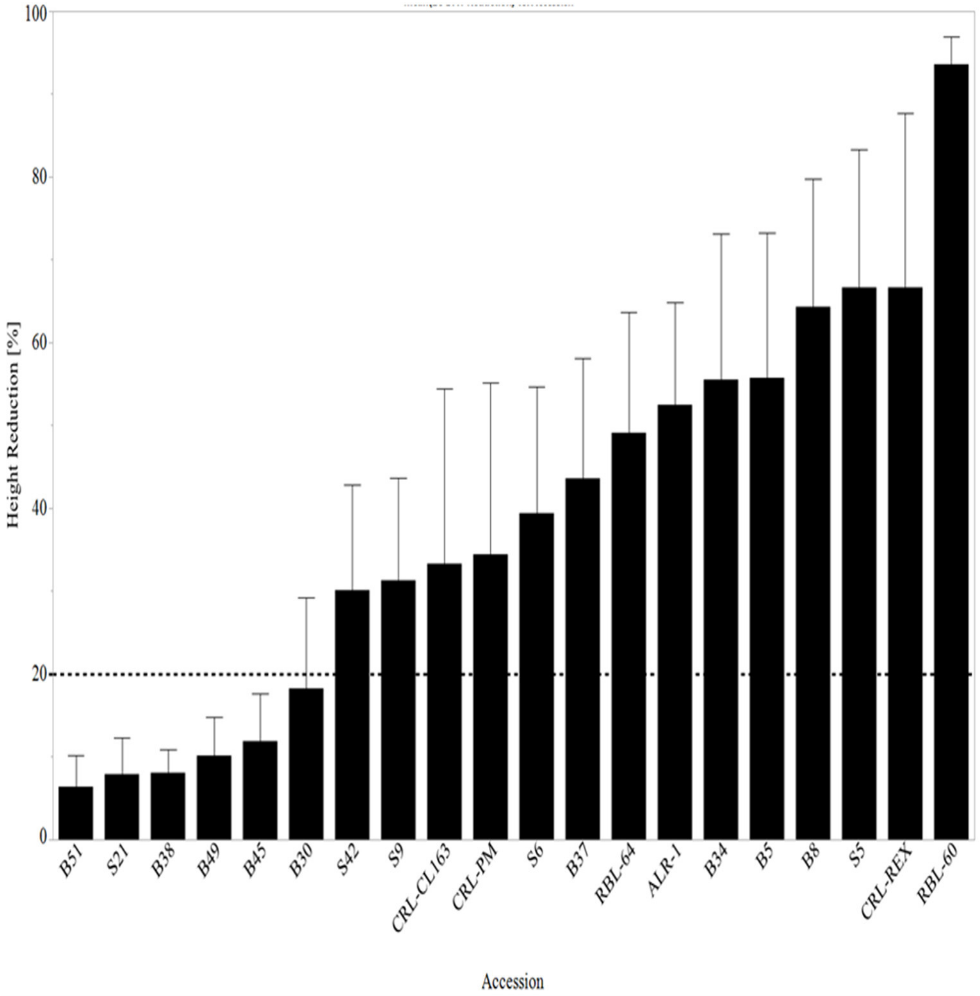

FIGURE 6 | Mean height reduction 28 days after complete submergence stress treatment arranged from lowest reduction to the highest reduction in height. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

height, but no WR accessions had no height reduction (**Figure 6**). Moreover, it is worth noting that those lines that had <20% height reduction at 14 DAT, surviving weedy rice accessions seemed to recover after de-submergence and maintain <20% height reduction at 28 DAT while CRL-Rex and RBL-60 remained stunted at 28 DAT.

Unsurprisingly, when these WR accessions were compared to cultivated rice lines and rice breeding lines, CRL-REX and RBL-60 had more than 70% height reduction 28 DAT. It is worth mentioning that tolerant rice cultivars are commonly known to suppress leaf elongation and maintain higher carbohydrate levels under complete submergence, but it is unknown if this is true about its weedy counterpart (Gao et al., 2007). This ability may account for the increase in height reduction compared to untreated controls. CRL-REX is a Mississippi developed, conventional, semi-dwarf cultivar with excellent yield performance, good straw strength, milling, and stand ability (Solomon et al., 2012). CRL-REX is also known to be susceptible to rotten neck blast and sheath blight disease (Hardke et al., 2013). Disease susceptibility could also be why increased height reduction in this rice cultivar as flooded waters can contribute to an increase in these diseases. RBL-60 is a submergence-tolerant rice breeding line developed at the Delta Research and Extension Center in Stoneville, MS. RBL-60 is a derivative of IR49830 developed as a converted mega variety with the *Sub1* gene to increase submergence stress tolerance (Septiningsih et al., 2009).

At 28 DAT, 27% of WR accessions (S21, B30, B38, and B45) did not show biomass reduction while 67% of accessions had <20% reduction in biomass (**Figure 7**). Three of the four accessions with no biomass reduction were awned blackhull types. In submergence-tolerant rice, biomass increased by 60% compared to sensitive rice after exposure to complete submergence for 10 days (Das et al., 2009). Das et al. (2009) also found that biomass reduction (23%) was only observed when silt was introduced into the flooding environment suggesting that silt has a negative impact on plant biomass.

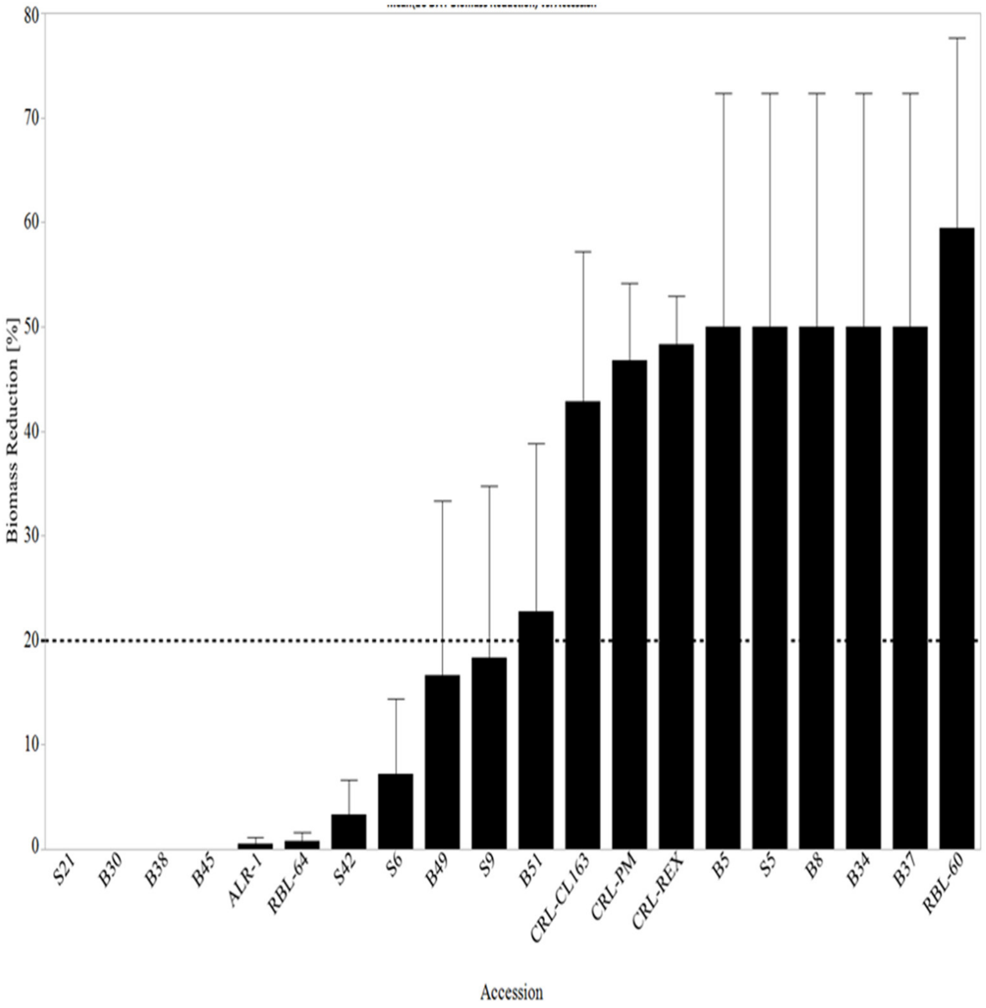

FIGURE 7 | Mean biomass reduction 28 days after complete submergence stress treatment arranged from lowest reduction to the highest biomass reduction. The line at 20% represents all lines with ≥20% reduction in height. RBL, Rice breeding line; CRL, cultivated rice line.

Although rice is well-known for withstanding flooded conditions due to its ability to germinate without CO_2 and aerobically escape slow rising waters, limitations still arise in rice's ability to escape and survive sudden and complete submergence due to flash flooding (Jackson and Ram, 2003). Severe injury has been reported when rice coleoptiles, leaves, or stems cannot escape flooding conditions, resulting in sustained complete submergence (Pearce and Jackson, 1991). In instances of sudden flooding, it has been reported that rice height can increase by 25 cm per day, but drastic increases in water levels can reduce plant survival (Vergara et al., 1976). Rice seedlings have demonstrated the ability to survive complete submergence for up to 20 days, but seedling survival rate strongly depends on the age of seedlings and the growth stage at the time of submergence (Richharia and Parasuram, 1963). Kotera and Nawata (2007) reported ≥60% yield loss when complete submergence occurred 17 days after transplanting. Although plants were completely submerged for only 2 days, yield loss was high (Kotera and Nawata, 2007).

While many studies have been performed to assess rice survival rate and performance when exposed to complete submergence stress at the seedling stage, few studies have evaluated the WR performance under submergence at the seedling stage. In our study, many WR seedlings died after 21 d of submergence. Those that did survive were significantly stunted and incurred severe loss of biomass at 14 and 28 DAT. The survivors showed clear signs of exposure to long duration of complete submergence stress such as chlorosis, reduced leaf extension and growth resulting in loss of biomass. In addition, submergence survivors produced more ethylene and had reduced respiration (Jackson et al., 1987).

The PCA and hierarchal clustering of WR accessions using 16 agronomic traits in response to complete submergence stress produced two distinct clusters (**Figure 8**). Cluster 1 was comprised of WR accessions with more than 20% height and

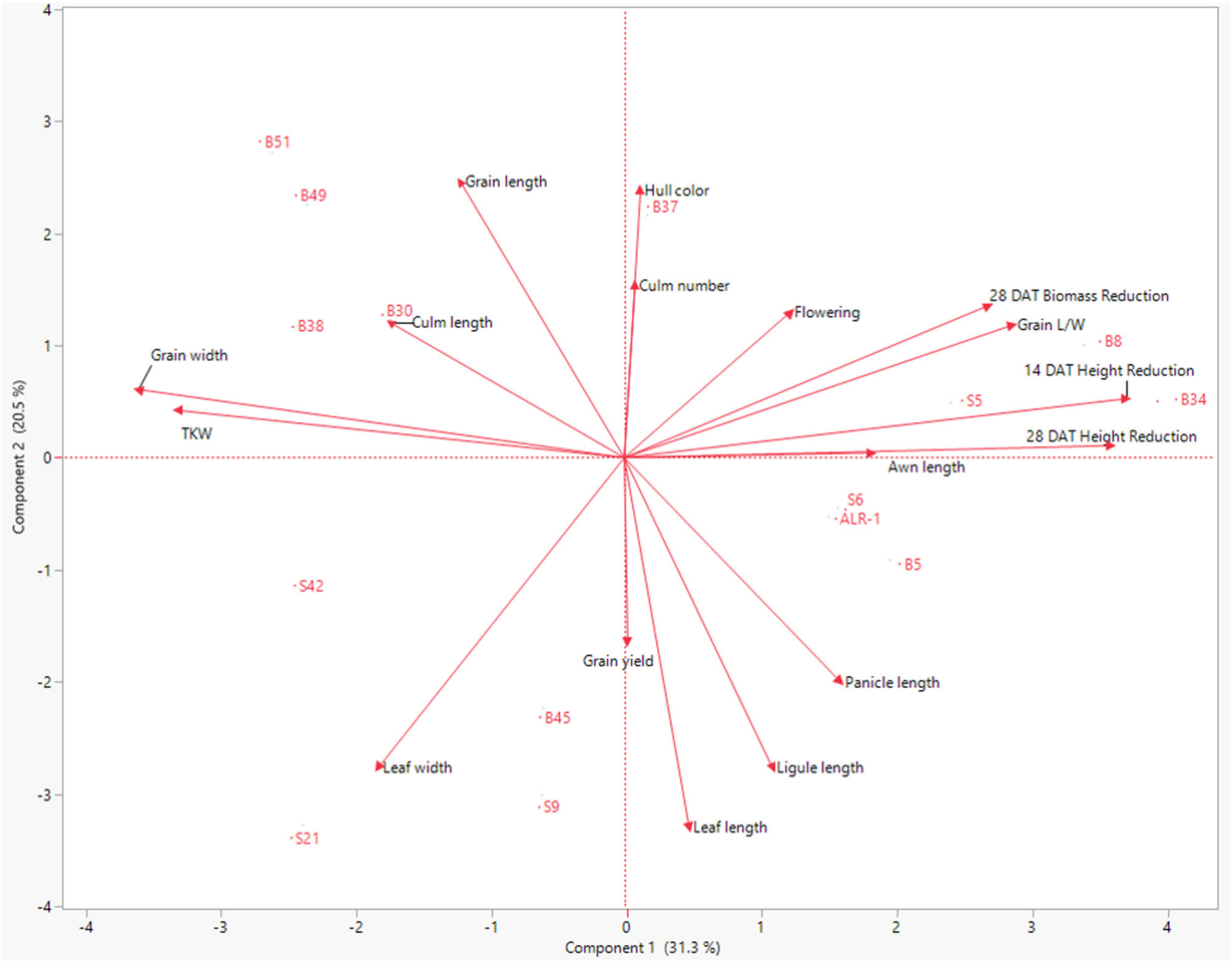

FIGURE 8 | Principal component analysis (PCA) of 16 agronomic traits plus plant height reduction 28 days after complete submergence stress treatment and plant biomass reduction 28 days after complete submergence stress treatment.

biomass reduction 28 DAT, while cluster 2 consisted of accessions with <20% height and biomass reduction 28 DAT. Component 1 explained 28% of the variation in the data, while component 2 captured 22%. Because rice is known to escape complete submergence with decreased survival rates, agronomic traits such as awn length and grain length/weight may not be significant indicators of submergence stress tolerance. Submergence stress-tolerant WR accessions had increased culm length (mean = 134 cm) and grain yield (mean = 97 g), suggesting that these can be agronomic indicators of submergence stress tolerance.

CONCLUSION

This study aimed to highlight the increased competitiveness of a diverse WR population compared to cultivated rice lines and developmental rice breeding lines. By analyzing plant height and biomass reduction and associations of agronomic traits, we can see why weedy rice continues to be a challenge in rice production in the US and elsewhere. Some WR accessions, such as S21 and B28, were more tolerant to heat and submergence stress than the reference tolerant rice cultivar. Given their survival to both heat and submergence-stress, these lines may be useful in the discovery of abiotic stress tolerant traits.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

All authors equally contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fagro.2021.642335/full#supplementary-material

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