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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

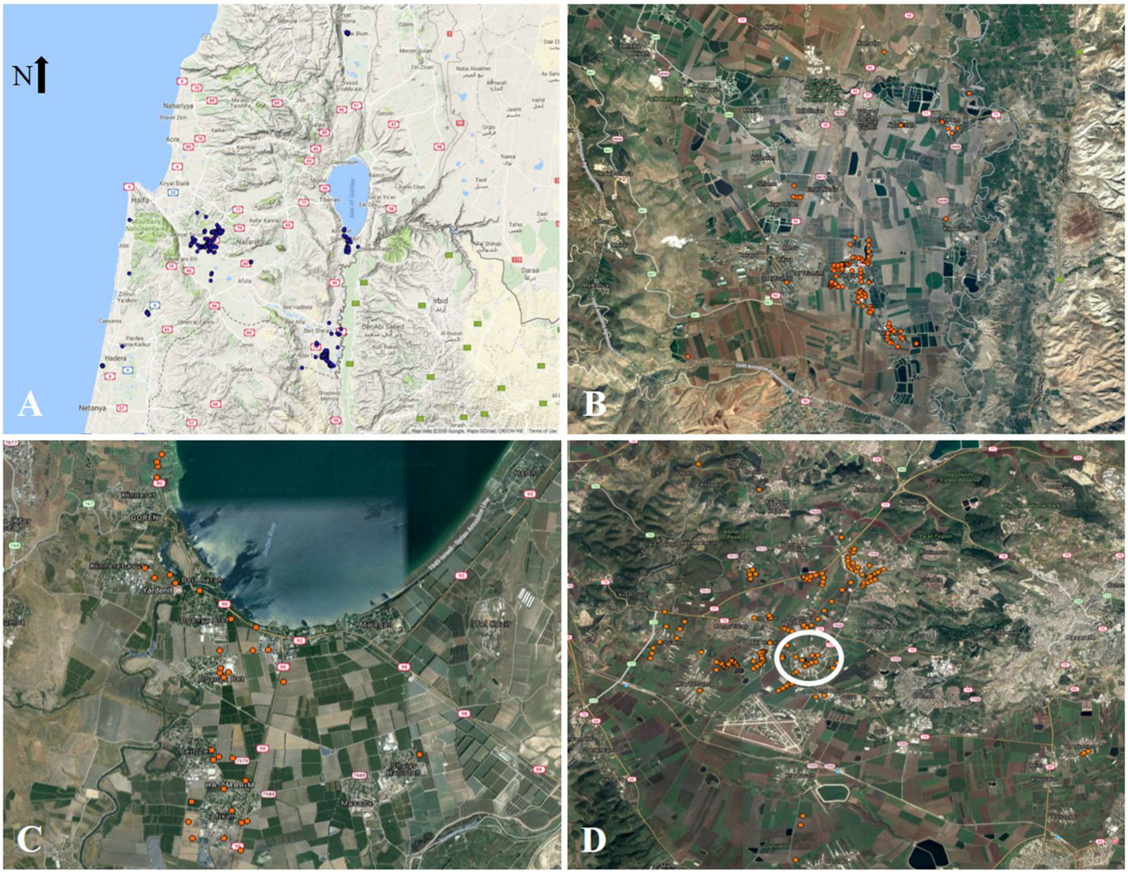

FIGURE 1 | Distribution of *Parthenium hysterophorus* across Israel. **(A)** Overview of the current *P. hysterophorus* distribution region. **(B)** Specific distribution in the Beit Shean Valley, **(C)** the Jordan Valley, and **(D)** the Jezreel Valley.

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):

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

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).

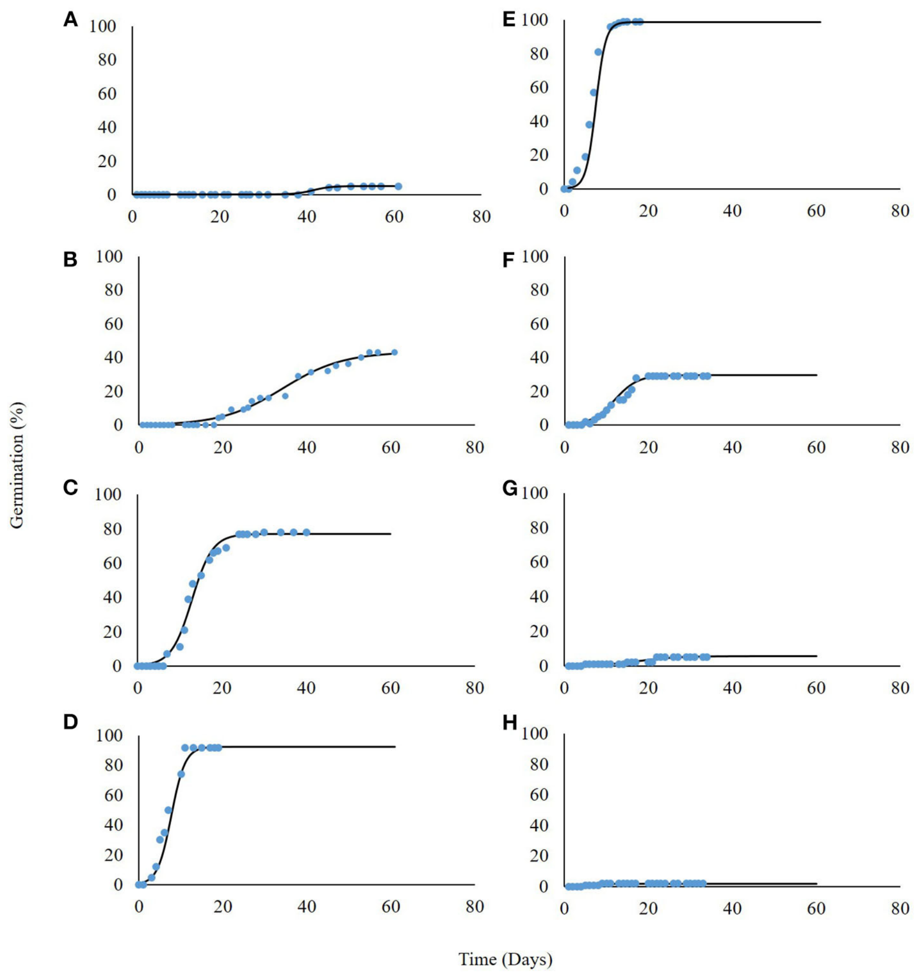

FIGURE 2 | Germination of *P. hysterophorus* seeds under constant temperatures: 5, 10, 15, 20, 25, 30, 35, and 40°C (**A–H**, respectively). The coefficient for non-linear regressions are given in **Table 1**.

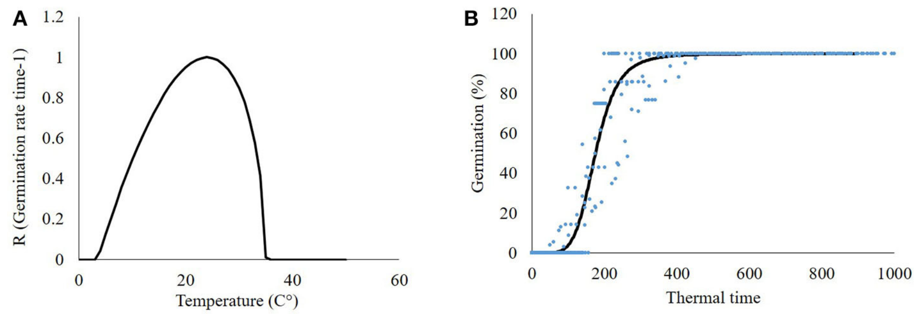

FIGURE 3 | Mathematical models describing the germination dynamics of *Parthenium hysterophorus* seeds. **(A)** Beta-function model describing the rate and maximum temperature-dependent germination and **(B)** seed germination dynamics according to a log-logistic model.

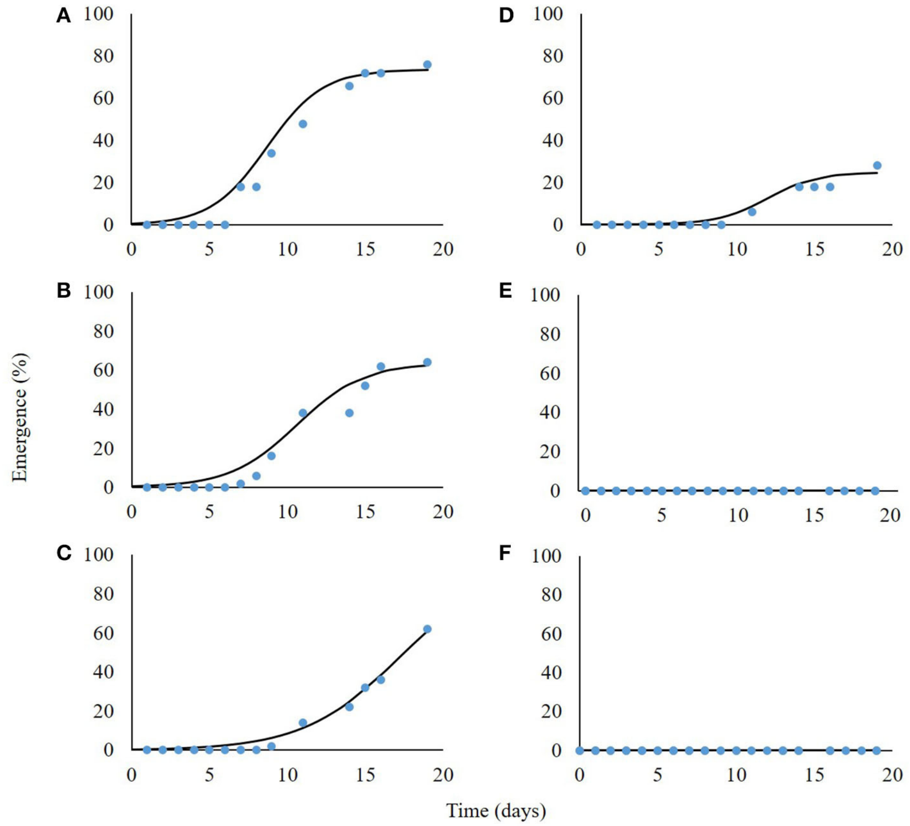

FIGURE 4 | Seedlings emergence of *Parthenium hysterophorus* seeds sown in different soil depths: 0, 1, 2, 3, 4, and 5 cm (**A–F**, respectively). Coefficient data are given in **Table 2**.

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

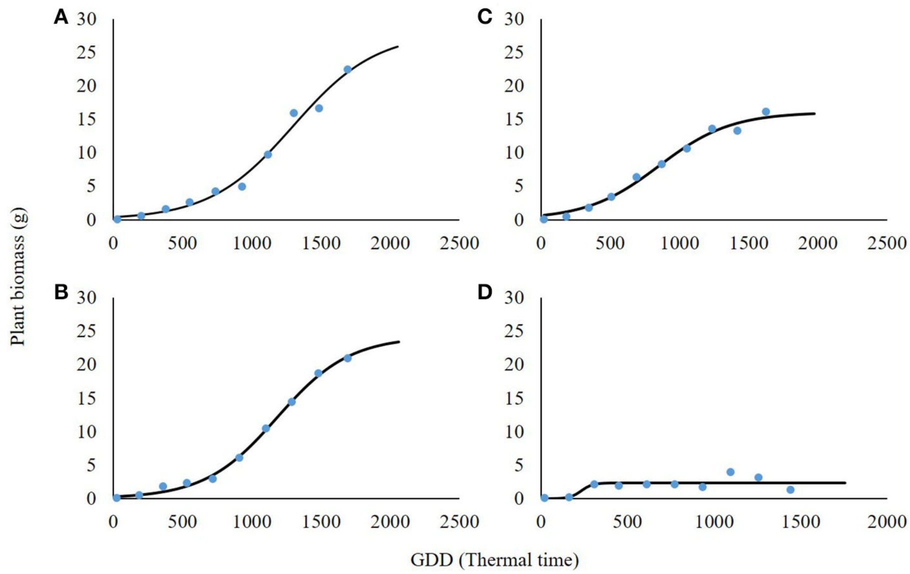

FIGURE 5 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on final shoot biomass of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 3**.

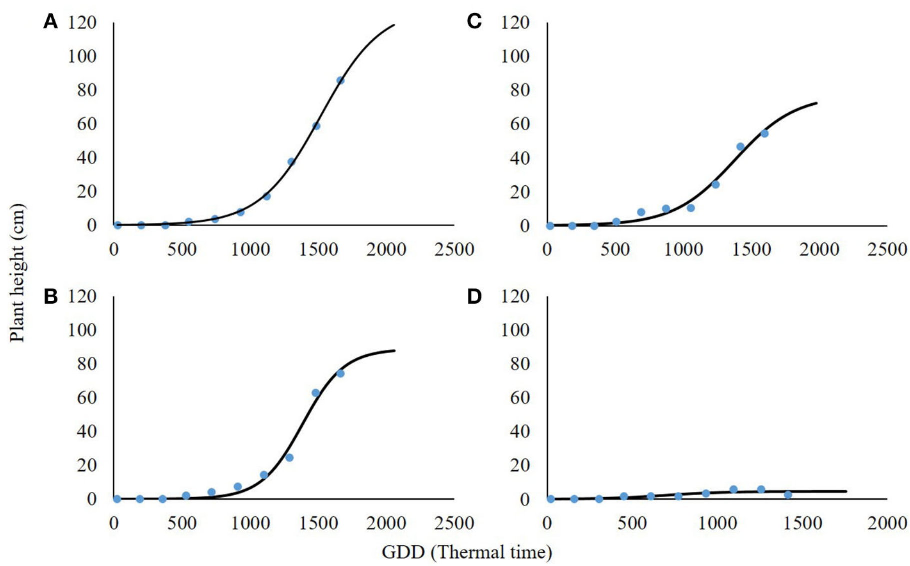

FIGURE 6 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on final plant height of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 4**.

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).

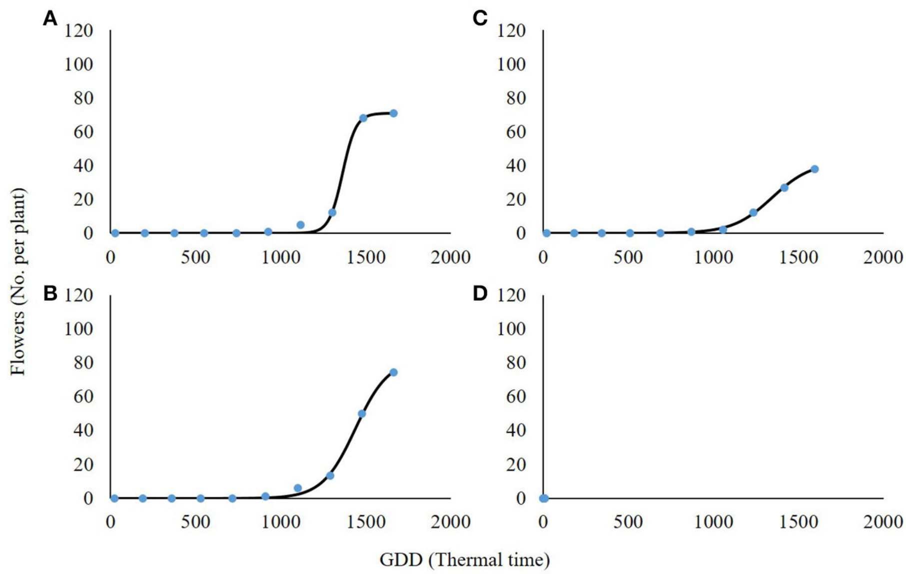

FIGURE 7 | Effect of shade levels (0, 30, 60, and 90%; **A–D**, respectively) on the final number of flowers per plant of *Parthenium hysterophorus*. The coefficient for non-linear regressions is given in **Table 5**.

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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