Season-long seed dispersal patterns of the invasive weed *Erigeron bonariensis* in south-western Spain

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ABSTRACT

Within-field demography of weeds exhibiting wind-mediated long distance seed movement can be largely governed by extra-field seed-source populations. Thus, for these species, a clear understanding of the temporal and spatial patterns of seed dispersal can benefit the development of effective management options. The spatial distribution of the seeds released from the onset of fruiting, in early summer, to the onset of the rainy season, in early autumn, was studied during 2 years at a Mediterranean-climate locality in *Erigeron bonariensis* L. (Hairy fleabane), a wind-dispersed invasive weed inhabiting ruderal environments and crop fields. Each year, a small source population was established in an open field in SW Spain and seed traps were arranged in the eight cardinal directions at distances up to 100 m (year 1), or in the NE and NW directions at distances up to 65 m (year 2). Counts of trapped seeds were carried out at 4–6 day intervals and the number of seeds released by the source population was estimated each year in most census dates. Four empirical dispersal models based on either thin-tailed or fat-tailed density kernels were tested using year 1 data for their ability to represent the spatial distribution of seeds. To test for anisotropic dispersal, model parameters were allowed to vary according to the wind pattern in each cardinal direction. Based on information criteria, a model including a fat-tailed, Log-hyperbolic secant kernel showing parameter response to the wind pattern, highlighting striking anisotropic dispersal, was selected and evaluated using year 2 data. Distance percentiles 50 and 80 attained by the seed crop released in year 1 season were modeled at 530 m and 10,498 m, respectively. The opposite quadrants encompassing the dominant downwind (N-NE) and upwind directions (S-SW) received 52.5% and 10.8% of seeds. The year 1 population, consisting of 85 plants, generated a modeled seed rain of at least 10 seeds m^{-2} up to 200 m downwind. Implications of results for management of this herbicide resistance-prone species are discussed.

1. Introduction

The ability of plants to move seeds in space is a crucial determinant of population and meta-population spatial extent and dynamics, gene flow, interaction with predators and pathogens, rate of range shift following global change and invasive capacity (Howe and Smallwood 1982; Levin et al., 2003; Beckie et al., 2019). Through wind, plant propagules, either seeds or fruits, can attain long dispersal distances. In these cases, propagules are either minute in size, i.e. "dust" seeds, and thus easily lifted in air, or are provided with hairy, frequently pappus-like appendages reducing their terminal velocity (Cousens et al., 2008). Apart from propagule traits, parent plant traits are also determinant of dispersal ability through wind. These include release height and fruiting phenology (Higgins et al., 2003; Wright et al., 2008), and

wind speed or orientation thresholds for propagule abscission (Greene 2005; Borger et al., 2012; Treep et al., 2018), which can facilitate release under the most favorable seasonal or daily wind conditions for increasing dispersal distances (Schippers and Jongejans 2005; Savage et al., 2014). Wind-mediated dispersal can be markedly directional when the fruiting season exhibits dominant winds. This anisotropic pattern can affect the full seed crop or only some fraction, and in this case the whole crop can still show isotropic dispersal as a result, for instance, of an extended fruiting phenology encompassing different seasons with contrasting wind directional patterns.

Ability for long distance dispersal through wind is frequently correlated with other plant attributes, particularly high fecundity, immediate seed germination under favorable conditions, short-term seed persistence in soil and short life span. This trait set is generally

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associated to a ruderal strategy (Grime 1979) favoring colonization of transient habitats characterized by temporally unpredictable, small-scale disturbance patterns (Lososová et al., 2006), such as urban environments, roadsides, highly disturbed field margins and perennial crops managed under low plant soil cover.

Different species in the genus *Erigeron* L. (Asteraceae), which form pappus-bearing one-seeded fruits, or achenes, in capitula (seed heads) exhibit this trait set and ecological affinities. This is the case of the hairy fleabane, *E. bonariensis* L. (syn. *Conyza bonariensis* (L.) Cronquist; nomenclature follows IPNI, 2021), an annual, South-American native, invasive in warm-temperate and sub-tropical areas worldwide. In south-western Europe it frequently co-occurs with two other introduced, American-native, co-generic annuals, Canadian fleabane, *E. canadensis* L. (syn. *C. canadensis* (L.) Cronquist) and Sumatran fleabane, *E. sumatrensis* Retz. (syn. *C. sumatrensis* (Retz.) E. Walker), from which it is easily distinguished by its much shorter stature and extensive branching, with basal branches overtopping the main stem. In the last decades, following the adoption of no-tillage soil management associated to herbicide-based weed control, *E. bonariensis* has increasingly become a weed problem in different crops in this area, including olive groves, citrus orchards and fruit tree crops (Amaro-Blanco et al., 2018), potentially causing substantial yield reductions (Trezzi et al., 2015). The problem is recently aggravated by the steady appearance of populations exhibiting evolved resistance to various herbicide groups, including glycines, bipyridiliums, ALS and photosystem II inhibitors (Urbano et al., 2007; Heap 2020). Ability for long-distance dispersal has been demonstrated in *E. canadensis* (Dauer et al. 2006, 2009) and, based on simulations at a constant 1 m release height, also in *E. bonariensis* (Savage et al., 2014). It has also been suggested for *E. sumatrensis* (Hao et al., 2009). Long-distance dispersal ability represents a challenge to the design and implementation of control strategies as they should encompass management options at the landscape rather than at the individual field-level (Dauer et al., 2006; Gonzalez-Andujar 2018; Amaro-Blanco et al., 2019; Beckie et al., 2019). This necessary but challenging approach can gain from a throughout knowledge of the dispersal process. With this aim, in this paper we studied the dispersal pattern of the whole seed crop released during summer, the most favorable season for wind dispersal, in source populations of *E. bonariensis* established during two years in an open field in Mediterranean-climate south-western Spain. We asked the following questions: i) compared to taller (>1 m) *E. canadensis* plants (Dauer et al., 2006), is the dispersal curve of shorter-statured (<1 m) *E. bonariensis* plants also fat-tailed, as suggested by a previous simulation study (Savage et al., 2014)? Ii) On a season-long perspective, is the wind pattern impinging an anisotropic distribution of the seed output, dispersal distances, or both? Answers to

these questions can have implications for population and resistance management.

2. Material and methods

2.1. Experimental setting

Seed source *E. bonariensis* populations were established in 2005 and 2006 in a previously tilled, 3 ha flat field within a citrus farm located in Huelva, SW Spain (37° 21′ 44″N, 6° 53′ 57″W; Fig. 1). In late January of the first and second study year, 90 or 60 plants at the 8–12 leaf rosette-stage, previously grown in pots in a greenhouse facility at the nearby La Rábida campus of the University of Huelva, were respectively transplanted within a 2.5 m radius circular area near the centre of the field. Eighty five and 55 plants survived up to flowering in the respective years. Resulting plant densities were low enough to not constraint fecundity (Zambrano-Navea et al., 2018).

In each study year, immediately before the onset of flowering, in early summer, seed traps consisting of 0.4 × 0.225 m adhesive cards (Agrobio S.L, La Mojonera, Almeria, Spain) were arranged around the seed source population. Traps were attached with clips to horizontal wooden frames placed 0.2 m aboveground at the top of wooden poles partially inserted into the soil. In year 1 they were arranged at 1 (8 traps), 5 (8), 10 (8), 20 (14), 30 (14), 40 (14), 50 (14), 65 (13), 80 (10) and 100 m (12). Traps up to 50 m were distributed in the different cardinal directions (Figs. 1 and 2 and) whereas at 65 m they were arranged only within four 45° sectors, N (2 traps), NE (7), SW (1) and W (3), and at 80 and 100 m they were placed only in the N (3 and 4 traps, respectively) and NE sectors (7 and 8 traps) according to the prevailing wind direction in summer in the study site (Fig. 1a). In year 1, at each sampling position further than 5 m an additional trap was placed 1.5 m aboveground using a metal pole. Whereas lower traps were intended to capture the seed deposition pattern, upper traps were used to evaluate the relative magnitude of updrafts in the different cardinal directions, as explained below. In year 2, only lower traps were positioned. At 1 and 5 m one trap was placed in each of the eight cardinal directions whereas at further distances traps were placed only in two 22.5° sectors, NE and NW. In each of these sectors, traps were positioned at 10 (2 traps), 20 (3), 30 (4), 40 (5), 50 (6) and 65 m (8; Fig. 1b).

2.2. Monitoring seed arrival and estimating seed numbers at the source

In both study years, census of trapped seeds (i.e., one-seeded fruits or achenes) were carried out from the onset of seed release to the onset of the rainy season, in early autumn, generally at 4–6 day intervals
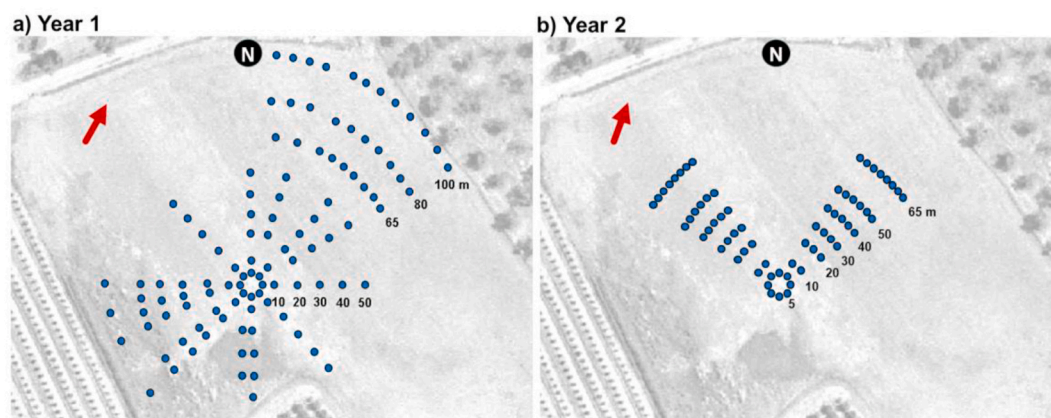
Fig. 1. Arrangement of seed traps around *Erigeron bonariensis* source populations (not shown) in the two study years. The nearest displayed traps were positioned at 5 m distance, as shown in b), and eight additional traps were placed at 1 m (not shown). In year 1 (a), two traps were placed at every position further than 5 m, at 0.2 and 1.5 m aboveground. In year 2 (b) traps were only placed at the lowest height. Arrows indicate the mean wind direction at the study site in each study season. Credit of the background image: SIGPAC GIS system, Government of Spain.
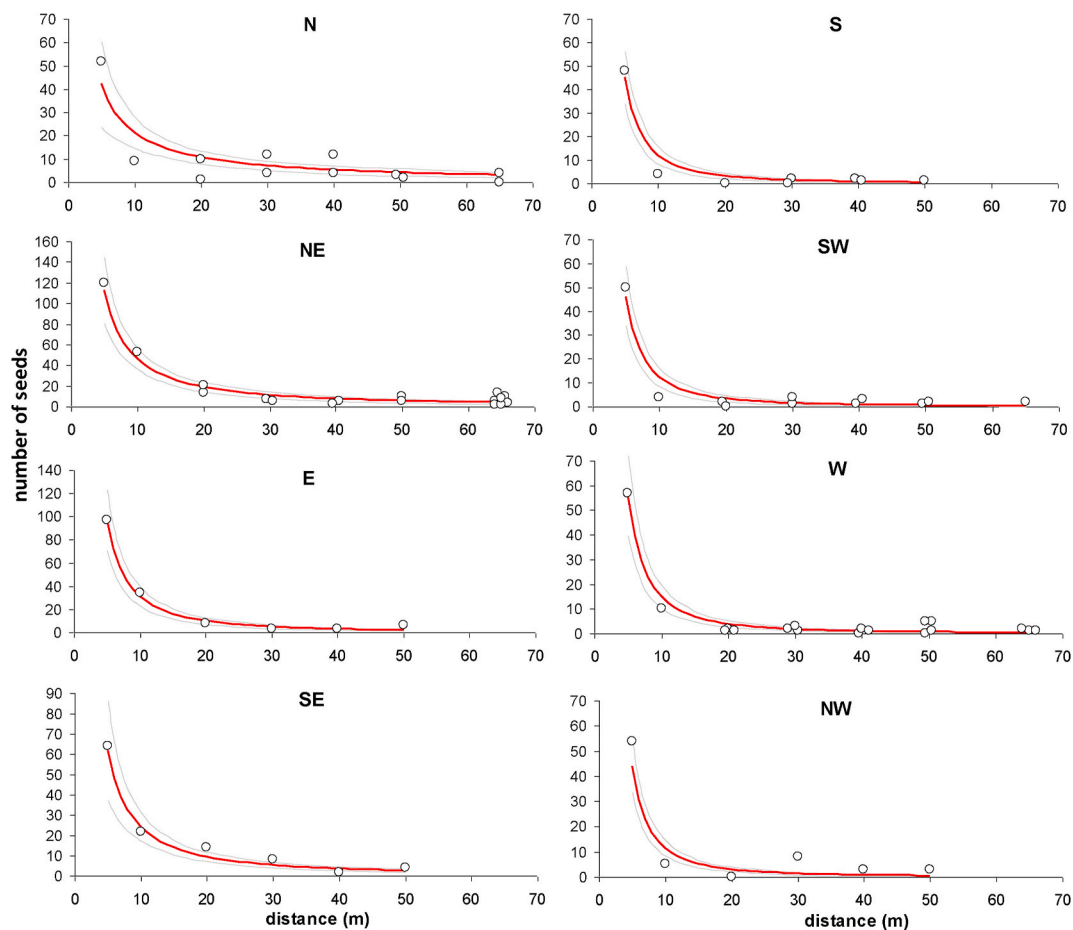
Fig. 2. Observed (dots) and modeled (red lines) seed numbers per trap as a function of distance to the source and direction. Grey lines encompass 95% CI for predicted mean seed numbers. In some cases, dots have been slightly displaced horizontally to facilitate visualization. Note that *y*-axes are not always on the same scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Appendix, Fig. S1). The adhesive cards used as seed traps were replaced after each census.

In addition, we estimated each year in most census dates the number of seeds released by the source population and release height. In year 1, additional visits were made after the onset of the rainy season up to near end fruiting to estimate the full seed crop. In each year, immediately before the onset of seed release, ten *E. bonariensis* plants were randomly selected and tagged. On each visit, we counted in each plant the number of capitula exhibiting less than 1/4 of the seed content, as estimated visually. The cumulative number of seeds released up to each visit was estimated as the mean number of capitula accomplishing seed release per sampled plant multiplied by the number of fruiting plants in the population and by the mean seed content per capitulum (420, F. Bastida et al., unpublished data). The number of seeds released in a given interval was calculated as the difference between consecutive estimates. Mean seed release height in each interval was measured in each plant as the mean height value of the highest and lowest capitulum at the seed release stage.

2.3. Measuring the wind pattern

A meteorological station (Kronos, Instrumentación Quimisur S.L, Sevilla, Spain) was placed in the study field to record at hourly intervals the number of minutes the wind blew to each of the eight cardinal directions (45° circular sectors or octants), the mean and maximum horizontal wind speed at 2.5 m height and rainfall. The horizontal wind pattern in each direction was captured in a single variable by multiplying the time the wind blew toward the corresponding octant (minutes

every hour) by the maximum hourly horizontal speed. These hourly values were summed up to obtain the distance (time x speed) accumulated by the wind in each octant in each interval between consecutive census of trapped seeds. Finally, for the whole season we calculated a weighted sum of these values, with weights being the fractions of the total number of seeds counted in lower traps that were trapped in the different intervals, used as estimates of the intensity of seed release in the source population. This variable was called weighted cumulative wind distance (WCWD).

The relative importance of updrafts in each direction, which are expected in the study area during summer as a result of wind turbulence, either mechanically induced or resulting from thermal convection (Pazos et al., 2013), was evaluated in year 1 season as the quotient between the total number of seeds recorded in upper traps and in lower traps taking into account only sampling points where traps were placed at both heights.

2.4. Modeling the seed dispersal pattern

Four probability density functions, or density kernels, commonly found in the literature (Nathan et al., 2012), were tested for their ability to represent the spatial distribution of the seeds released by the source population during year 1 season. The tested kernels were the thin-tailed exponential and the fat-tailed Logistic, Log-hyperbolic secant and 2Dt curves (Table 1). The kernels include a scale parameter (*a*), describing the curve steepness and, except for the single-parameter exponential, a shape parameter (*b*) describing the curve's tail thickness. Multiplying the kernel, which gives the probability of arrival per unit area as a

Table 1

Density kernels tested in dispersal models. Expressions are according to Nathan et al. (2012). *a* and *b* are the scale and shape parameters, respectively, and *d* is distance to the source. Γ is the gamma function.

density kernel	expression	constraints
Exponential	$\dfrac{1}{2\pi a^2}\exp\left(-\dfrac{d}{a}\right)$	$a>0$
Logistic	$\dfrac{b}{2\pi a^2 \Gamma(\frac{2}{b})\Gamma(1-\frac{2}{b})}(1+\dfrac{d^b}{a^b})$	$a>0,\ b>2$
Log-hyperbolic secant	$\dfrac{1}{\pi^2 b d^2[(\frac{d}{a})^{\frac{1}{b}}+(\frac{d}{a})^{-\frac{1}{b}}]}$	$a>0,\ b>0$
2Dt	$\dfrac{b-1}{\pi a^2}(1+\dfrac{d^2}{a^2})^{-b}$	$a>0,\ b>1$

function of distance (*d*) from the point source, by the number of dispersing seeds (*Q*), probabilities are converted into numbers and, when adjusted by the trap area (*A*), they represent the number of seeds arriving per trap (*n*). Thus, the dispersal model is given by:

$$n_d = A.\ Q.\ g(d) \quad (1)$$

where $g(d)$ is the kernel. We assumed that the number of seeds per trap at distance *d* followed a Poisson distribution with mean $\mu(d)$. Allowing for over-dispersion, the model in Eq. (1) can be reformulated as (Snäll et al., 2007; Bastida et al., 2018):

$$\log(\mu(d)) = \log(A) + \log(Q) + \log(g(d)) + \varepsilon \quad (2)$$

where log is natural logarithm and ε is an over-dispersion term.

To test for anisotropic dispersal resulting from varying wind conditions among octants, we allowed each parameter to be explained by the wind pattern (WCWD values) in each cardinal direction. We tested for linear and curvilinear responses of kernel parameters βs (*a*, *b*) to the wind pattern as:

$$\log(\beta_j) = \beta_1 + \beta_2.\ w_j + \beta_3.\ w_j^2 + \beta_4.\ w_j^3 \quad (3)$$

where w_j is the centered WCWD value in octant *j*, and quadratic and cubic terms allow for curvilinear responses. While *Q* in Eqs. (1) and (2) is usually treated in the literature as an additional parameter to be estimated in the fitting process (e.g. Bullock et al., 2017), the availability in our study of an estimate of the number of seeds released by the source population (*S*) deserves a particular treatment for *Q*, which can differ among octants under anisotropic dispersal. The value of *Q* for an octant *j* is not only dependent on *S* but also on trap efficiency *e*, i.e., the fraction of arriving seeds a trap is able to retain, and on the allocation of *S* among octants, p_j. Thus, Q_j was modeled as:

$$Q_j = 8.\ S.\ e.\ p_j \quad (4)$$

where the constant 8 assures the proper value of Q_j. As trap efficiency should be a value comprised between 0 and 1, we modeled *e* in Eq. (4) using the sigmoid function:

$$e = \exp(k_1) / (1 + \exp(k_1)) \quad (5)$$

with high and low k_1 estimates approaching *e* in Eq. (5) to 1 and 0, respectively. The fraction of the seeds landing in octant *j* was modeled, following the form in Eq. (3), as:

$$p_j = \exp(k_1 + k_2.w_j + k_3.\ w_j^2 + k_4.\ w_j^3) / \Sigma_i \exp(k_1 + k_2.w_i + k_3.\ w_i^2 + k_4.\ w_i^3)$$
$$= \exp(k_2.w_j + k_3.\ w_j^2 + k_4.\ w_j^3) / \Sigma_i \exp(k_2.w_i + k_3.\ w_i^2 + k_4.\ w_i^3) \quad (6)$$

where Σ_i indicates summation over the eight octants. Taking into account possible anisotropy as described, the model in Eq. (2) can finally be expressed as:

$$\log(\mu_j(d)) = \log(A) + \log(Q_j) + \log(g_j(d)) + \varepsilon \quad (7)$$

Fitting of the kernel-specific models based on Eq. (7) was carried out

using the gnm package (Turner and Firth 2018) in R (R Core Team, 2018). As the most distant traps were only placed in a few directions (Fig. 1a), a more balanced data set for model construction was selected including only trap data up to 65 m. The nearest distance to the source (1 m) was also discarded as the point source assumption required for the kernels hardly holds at this short distance (Snäll et al., 2007). For each tested kernel, a complete model allowing a curvilinear response to wind for each parameter was initially fitted, and alternative models with linear responses or with responses, either linear or curvilinear, in only two, one or neither parameter were also fitted. Model selection was based on the Akaike Information Criterion corrected for small samples and adjusted for over-dispersion (QAICc). The dispersion parameter of the complete quasi-poisson model including the best fitting kernel was selected as an estimate of over-dispersion in data (Anderson and Burnham 2002), and this estimate was thereafter used in calculating QAICc values for simplified models and for the set of models based on the alternative kernels. QAICc values were retrieved using the R package MuMIn (Barton, 2018). Checking of the best model, i.e., the model exhibiting the lowest QAICc value, was carried out in two ways. First, systematic departures from observed values were evaluated by plotting Pearson residuals against distance for each cardinal direction and, second, prediction ability of seed deposition at 80 and 100 m within the NE sector, from which observed data were available (Fig. 1a), was tested. Generality of the model for the study site was evaluated using results of the year 2 experiment as independent data.

3. Results

3.1. Seed release patterns and seed counts on traps

From the onset of seed release in early summer to the onset of the rainy season in early autumn, *E. bonariensis* source populations released an estimated number of 5,058,060 seeds (year 1, 3Jun-30Sep) and 6,107,619 seeds (year 2, 26Jun-13Oct; Appendix, Fig. S1). Additional censuses carried out during autumn in year 1 indicated that the referred estimate represented 61.2% of the total seed output up to end November (Appendix, Fig. S1), when the first plants in the source population completed their annual cycle and senesced. In both years, fruiting phenology did not apparently differ from that of spontaneous populations of the species in the area (pers. obs.).

Along the season, mean seed release height increased from 0.33 to 0.53 m (year 1) or from 0.41 to 0.67 m (year 2). This height increase resulted from the switch in capitula production from the short main stem to the taller lateral branches which characteristically develop in *E. bonariensis* plants after the onset of fruiting.

Twenty and 22 censuses of trapped seeds were carried out along the study season in years 1 and 2, respectively (Appendix, Fig. S1). Due to poor attachment of the adhesive cards, a large number of traps were displaced by the wind during the first census interval (3–13Jun) in year 1, so data from this interval were not further considered. During the remaining year 1 season (13Jun-30Sep), the number of seeds released by the source population was estimated at 4,455,360 (*S* value in Eq. (4)). Along this period, a total of 9744 and 461 seeds was recorded in the lower and upper traps, respectively. The number of seeds recorded in the lower traps placed between 5 and 65 m, on which model construction was based, was 960 (Appendix). In year 2, four census intervals were rainy (>1 mm rainfall, Appendix, Fig. S1) and they were discarded from further analyses. In the remaining 18 censuses, 19,632 seeds were counted in traps, of which 6861 and 867 seeds were recorded in the NE and NW sectors, respectively. As expected, the estimated number of seeds released and the total number of seeds recorded in traps in the different census intervals were highly correlated, both in year 1 (*r* = 0.95, *N* = 15; in calculating correlation, seed counts in traps in consecutive censuses were sometimes summed up to match the census intervals of released seeds, as depicted in Appendix, Fig. S1), and year 2 (*r* = 0.91, *N* = 18).

3.2. Daily and seasonal wind pattern

A characteristic daily pattern of the wind consisting of a consistent blowing to N-NE in conjunction with a peak in horizontal speed around midday was observed during summer at the study site in both study years (Appendix, Fig. S2a, b). As expected from this daily pattern, the weighted cumulative distance travelled by the wind (WCWD) during summer in study year 1 (13Jun-30Sep) was highest for the NE (490,597 m) and N (474,209 m) cardinal directions and lowest for the opposite directions (SW, 91,608 m; S, 100,538 m; Appendix, Fig. S2c). In year 2, WCWD values during the study season (26Jun-13Oct) were also higher for NE (269,527 m) than for NW direction (74,764 m). Intensity of updrafts in the different cardinal directions, as measured by the quotient of the total number of seeds recorded in upper and lower traps in year 1, was highly positively correlated with WCWD values ($r = 0.88$, Appendix, Fig, S2c).

3.3. Seed dispersal pattern

Among the four tested kernels, the short-tailed exponential led to the worst-performing models, indicating fat-tailed dispersal patterns, and thus ability for long-distance dispersal in *E. bonariensis* (Table 2). For each kernel, the isotropic model showing parameter independence from the directional wind pattern tended to perform worst than remaining, anisotropic models (Table 2). Models including the Log-hyperbolic secant kernel outperformed the alternative models tested, with the best model showing linear and curvilinear responses to the wind pattern (WCWD values) in parameters Q and b, respectively (Table 2).

Checking of the selected model through Pearson residuals showed that departures from observed values appeared to be related to neither distance nor orientation (Appendix, Fig. S3). In addition, the observed

Table 2
Model selection according to QAICc values. Dispersal models based on four density kernels were compared: exponential, logistic, log-hyperbolic secant (Log-sech) and 2Dt. Wind influence on parameter estimates resulting in anisotropic dispersal was tested as indicated by superscripts: (3) curvilinear response, (1) linear response, (0) no response. See text for details. For the globally best performing kernel, additional models including combinations of parameters with curvilinear and linear responses to wind were also tested when the possibility existed of further reducing QAICc. The lower QAICc value is highlighted. Q, seed number; a, scale parameter; b, shape parameter.

wind influence on parameters	Exponential	Logistic	Log-sech	2Dt
$Q^{(0)}$, $a^{(0)}$	322.84	–	–	–
$Q^{(3)}$, $a^{(3)}$	264.48	–	–	–
$Q^{(3)}$, $a^{(0)}$	277.23	–	–	–
$Q^{(0)}$, $a^{(3)}$	312.75	–	–	–
$Q^{(1)}$, $a^{(1)}$	261.34	–	–	–
$Q^{(1)}$, $a^{(0)}$	277.68	–	–	–
$Q^{(0)}$, $a^{(1)}$	320.65	–	–	–
$Q^{(0)}$, $a^{(0)}$, $b^{(0)}$	–	256.43	228.12	255.97
$Q^{(3)}$, $a^{(3)}$, $b^{(3)}$	–	190.53	169.30	198.87
$Q^{(3)}$, $a^{(3)}$, $b^{(0)}$	–	182.95	180.45	182.49
$Q^{(3)}$, $a^{(0)}$, $b^{(3)}$	–	213.60	162.82	212.02
$Q^{(0)}$, $a^{(3)}$, $b^{(3)}$	–	185.13	167.99	183.90
$Q^{(3)}$, $a^{(0)}$, $b^{(0)}$	–	210.65	185.10	210.24
$Q^{(0)}$, $a^{(3)}$, $b^{(0)}$	–	210.52	187.67	210.30
$Q^{(0)}$, $a^{(0)}$, $b^{(3)}$	–	214.05	168.71	213.36
$Q^{(1)}$, $a^{(1)}$, $b^{(1)}$	–	196.69	176.83	196.25
$Q^{(1)}$, $a^{(1)}$, $b^{(0)}$	–	194.38	181.63	193.97
$Q^{(1)}$, $a^{(0)}$, $b^{(1)}$	–	209.76	174.64	208.86
$Q^{(0)}$, $a^{(1)}$, $b^{(1)}$	–	196.47	176.87	195.35
$Q^{(1)}$, $a^{(0)}$, $b^{(0)}$	–	211.12	185.22	210.70
$Q^{(0)}$, $a^{(1)}$, $b^{(0)}$	–	244.41	237.77	237.93
$Q^{(0)}$, $a^{(0)}$, $b^{(1)}$	–	214.39	192.50	213.56
$Q^{(1)}$, $a^{(1)}$, $b^{(3)}$	–	–	160.32	–
$Q^{(3)}$, $a^{(0)}$, $b^{(1)}$	–	–	176.41	–
$Q^{(1)}$, $a^{(0)}$, $b^{(3)}$	–	–	**158.50**	–
$Q^{(1)}$, $a^{(0)}$, $b^{(1)}$	–	–	174.64	–

mean number of seeds per trap at 80 m (3.4, $N = 7$ traps) and 100 m (3.0, $N = 8$) within the NE octant, not included in the data set used for model construction, were close to modeled values, remaining within the respective 95% CIs, 3.0 (1.8–4.1) and 2.1 (1.2–3.1), respectively. Thus, we judged that the selected model provided an adequate description of seed deposition (Fig. 2).
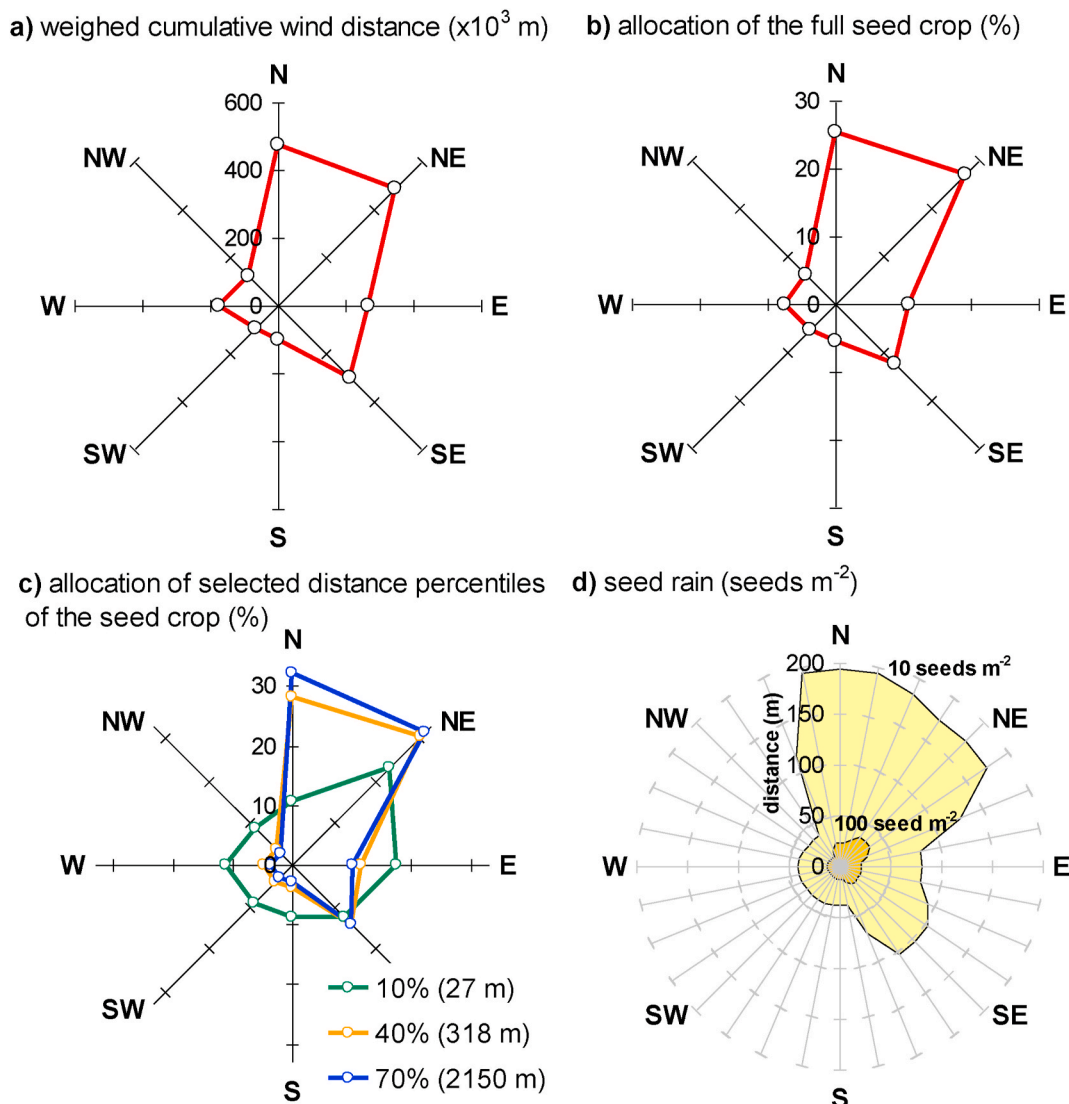
Full trap efficiency ($e = 1$) was modeled, as indicated by the large estimate of parameter k_1 (Appendix). Allocation among cardinal directions of the year-1 seed output released during the most favorable season for dispersal was predicted to parallel the horizontal wind pattern (Fig. 3a and b). The two most favorable 45° sectors in terms of WCWD received a fraction of 27.1% (NE) and 25.4% (N) of seeds, respectively. In contrast, the opposite S and SW sectors received 5.5% and 5.3% of the seeds, respectively (Fig. 3b). Median dispersal distance, as calculated by numerical integration of the density kernel, was modeled at 530 m whereas the distance percentile 80 was predicted at 10,500 m. The degree of anisotropy was predicted to vary for different distance percentiles of the seed output, progressively increasing up to around percentile 70 (2150 m), for which 63.6% of seeds were modeled to land within de quadrant encompassing the N and NE sectors (Fig. 3c), and thereafter decreasing down to the values dictated by the allocation pattern of Q. The seed rain generated by the year-1 source population was predicted to be much higher within the predominant downwind directions at every distance. In the most favorable 45° sector, a seed rain of at least 100 and 10 seeds. m^{-2} was modeled for distances up to 35 and 195 m, respectively (Fig. 3d).

Graphical evaluation of the model using independent data from the year-2 experiment suggested that it was useful enough to predict the number of seeds arriving to each trap according to the wind pattern at the study site (Fig. 4, Appendix). As a consequence, modeled dispersal patterns in year 2 were qualitatively the same as for year 1. For instance, 22.9% and 19.4% of the year-2 seed output were modeled to be allocated to the downwind N and NE octants, respectively, whereas 8.2% and 8.5% of seeds were predicted to land within the opposite S and SW octants.

4. Discussion

In this work we show a large ability for long-distance seed dispersal in *E. bonariensis*. Several attributes apart from seed morphology appear to contribute to this ability. These include very high seed production and an extended fruiting season, which encompasses favorable periods of the year for wind dispersal in the Mediterranean-climate area of introduction. As for the former attribute, large seed production favors dispersal because the number of seeds attaining a given distance is directly proportional to the number of seeds released by a source plant (Q, Eq. (1)). Seed release along the hot, dry summer of the study area ensures continuously favorable conditions for wind-mediated dispersal (Greene 2005; Treep et al., 2018). Additional permissive intervals appear to be the mild, dry periods lasting days to weeks which occur intermingled with rainy intervals along the autumn, a season through which a relevant fraction of the full seed output can be produced and released in *E. bonariensis*, as we have found in this work.

A distinctive daily wind pattern was apparent at the study site during summer. Peaks of horizontal wind speed associated to increased updrafts occurred consistently at around midday. Increased updrafts, evidenced in this work by the higher allocation of seed captures to the upper traps compared to the lower traps in the preferential N-NE directions to which the wind blew at this daily time, can be mainly explained by increased mechanical turbulence near ground level caused by higher wind speed. A plausible, alternative or complementary explanation, namely thermal turbulence resulting from ground surface heating, is expected to have had lesser influence as its effects appear to be evident only under low wind speed (Greene 2005). This correlation between wind speed and updrafts at daily scale appears to be general (Pazos et al., 2013) and favors dispersal because the gain in height above ground level of a seed

a) weighed cumulative wind distance (×10³ m)

b) allocation of the full seed crop (%)

c) allocation of selected distance percentiles of the seed crop (%)

d) seed rain (seeds m⁻²)

Fig. 3. Wind and dispersal patterns during year-1 season (13jun-30sep). A) Weighted cumulative wind distance (WCWD) in the octants defined by cardinal directions. B) Modeled allocation among octants of the seeds produced by the source population. C) Modeled allocation among octants of selected distance percentiles of the seed crop, highlighting a progressively higher anisotropy of seed distribution up to percentile 70. Distances attained by the percentiles are indicated in parentheses. D) Modeled seed rain as a function of distance to the source and direction. Contour lines for 100 and 10 seeds. m^{-2} are presented. Interpolated values for adjacent positions between two octants are given.
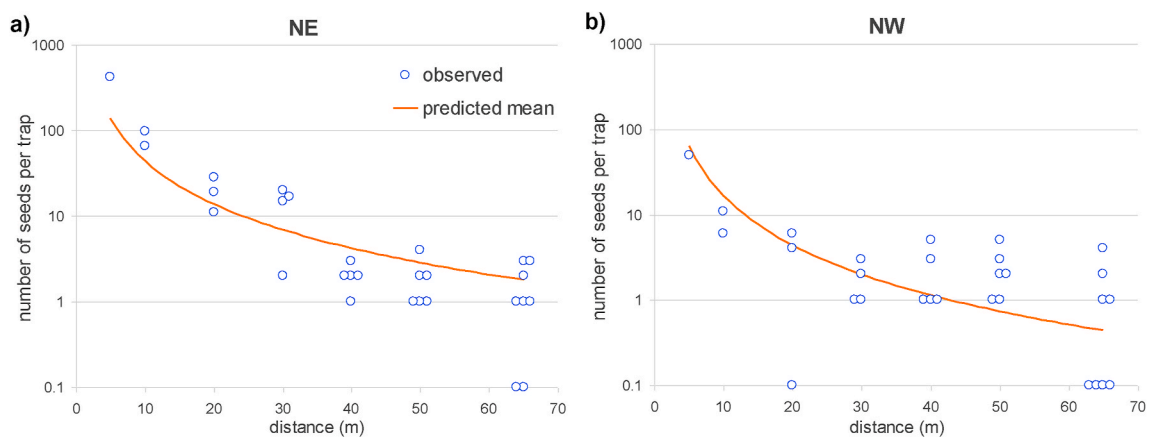
Fig. 4. Observed number of seeds in traps arranged at different distances from the source population within two cardinal directions, NE (a) and NW (b), in the year-2 experiment, and predicted mean values according to the dispersal model including the Log-hyperbolic secant kernel fitted to year-1 data. To facilitate visualization some dots have been slightly displaced horizontally and zeroes in *y*-axes are presented as 0.1 values.

caught in a vertical wind gust exposes it to higher wind speed, thus allowing a higher dispersal distance, as has been shown for *E. bonariensis* (Savage et al., 2014) and for *E. canadensis* (Dauer et al., 2009). Because of this correlation, our WCWD metric should best be viewed as a measure of wind favorability for dispersal. In addition, in different wind-dispersed species seed abscission occurs preferentially after a threshold of wind speed (Borger et al., 2012; Bastida et al., 2018; Treep et al., 2018) or gust orientation on the vertical axis is surpassed (Borger et al., 2012). Indeed, in *E. bonariensis* a larger fraction of the seeds within a capitulum was found to be released under simulated updrafts compared to same-speed downdrafts or horizontal wind (Borger et al., 2012).

Seed release associated to high wind speed or favorable gust orientation can make individual plant traits generally associated to dispersal ability, such as plant height and seed terminal velocity, less informative in explaining the spatial distribution of the seeds released by an individual plant or population migration rates (Soons and Bullock 2008). Although further research would be needed, we argue that this response could attenuate differences in dispersal ability among *E. bonariensis* and co-occurring *E. canadensis* and *E. sumatrensis* plants, which commonly form their capitula largely above 1 m height. This response to the wind could explain the fat-tailed dispersal pattern evidenced in this work in *E. bonariensis*.

On the other hand, we show a striking wind-induced anisotropy in the distribution of the seeds released during summer and early autumn. The selected dispersal model, based on the log-hyperbolic secant kernel, a function ranking among the best-fitting kernels in most studied systems so far (Bullock et al., 2017), clearly indicated that anisotropy resulted from wind effects on both the allocation of the seed output among directions (through effects on parameter *Q*) and on the shape of the dispersal curve (through effects on the kernel's parameter *b*; Eq. (1) and Table 2). The modeled allocation of the seed crop among directions tightly matched the directional wind pattern (Fig. 3a and b). As a consequence, 53% of the seed output released during the year 1 study season was modeled to land within the N-NE quadrant, with the opposite quadrant receiving only 11% of the seeds. Interestingly, this anisotropy, which can be interpreted as a by-product of the species adaptation for preferential use of high wind speed and associated updrafts for seed release and dispersal, appears to be dependent on the distance percentile of the seed output. The seed fraction attaining short dispersal distances, up to some tenths of meters, exhibited a nearly isotropic distribution (Fig. 3c). We speculate that this pattern may be reflecting the effect of capitulum age on wind speed thresholds for seed abscission. Borger et al. (2012) found that more seeds were released under lower mean wind speed in older than in recently opened *E. bonariensis* fruiting capitula. As lower wind speed was associated to lower incidence of updrafts in the study site, seeds released from older capitula should have experienced both reduced dispersal distances and reduced anisotropy.

Results from this study provide useful cues for the management of the study species. Long distance dispersal ability indicates that *E. bonariensis* forms geographically extended populations and metapopulations. Through seed dispersal, genes conferring herbicide resistance can easily spread from the original resistant stand, through the agricultural landscape composed of similarly-managed fields, to landscapes distant hundreds of kilometers with similar or alternative, suitable habitats for the species (Beckie et al., 2019). As pointed out elsewhere for weeds exhibiting long-distance, wind-mediated seed dispersal (Dauer et al., 2006; Evans et al., 2018; Gonzalez-Andujar 2018; Beckie et al., 2019), coordinated control measures among neighboring farmers and other relevant stakeholders, rather than independent within-field management alternatives, appear to be required for effectively reducing abundance and frequency of *E. bonariensis* populations. However, as our study highlights, this necessary approach is also challenging because of easily undetected, tiny stands composed of a few tenths of plants inhabiting road verges, urban wastelands or highly disturbed field margins, escaping control measures, can release several

million seeds able to travel long distances, and can generate an intense seed rain even at several hundreds of meters in downwind directions. A seed rain of 10 seeds m^{-2} at 200 m downwind, as modeled here for a source stand of 85 plants, can lead to the successful establishment of 1–2 plants per square meter in an open, ruderal habitat in a nearby locality in Southern Spain (Zambrano-Navea et al., 2018), this emphasizing the high colonization ability of the study species.

5. Conclusions and implications

Apart from highlighting an ability for long-distance dispersal in *E. bonariensis*, this paper emphasizes a marked wind-driven anisotropy in the spatial distribution of the seed output released during the most favorable season for dispersal in the Mediterranean-climate study site. This anisotropic dispersal concentrates the seed crop in downwind directions, generating a high seed rain up to distances further from the source. Collective, landscape-level, integrated measures including not only alternative herbicides but also avoiding highly disturbed, narrow field margins and promoting high cover of herbaceous plant communities enriched in grasses (Prieur-Richard et al., 2002), or using grass crop residues as soil cover (Loura et al., 2020), can be useful options to reduce the establishment probability or plant performance in *E. bonariensis*, ultimately contributing to diminish the influx of airborne seeds and resistance genes in crop fields.

Credit author statement

FB contributed to conceptualization, methodology, formal analysis, investigation, data curation, writing of the original draft and supervision. JM contributed to editing and resources. DC contributed to investigation. JLGA contributed to conceptualization, methodology, formal analysis, editing and supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2021.105720.

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