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Testing mechanistic models of seed dispersal for the invasive *Rhododendron ponticum* (L.)

Catriona M. Stephenson[a,b,*], Deborah D. Kohn[b,c,d], Kirsty J. Park[b], Rachel Atkinson[b,f], Colin Edwards[g], Justin M. Travis[c,e]

[a] *Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St. Andrews, Fife KY16 9LZ, Scotland, UK*
[b] *Centre for Conservation Science, University of Stirling, Stirling, UK*
[c] *Centre Ecology & Hydrology, Banchory, Scotland*
[d] *Royal Botanic Garden, Edinburgh, UK*
[e] *School of Biological Sciences, University of Aberdeen, Aberdeen, UK*
[f] *Charles Darwin Research Station, Galapagos, Ecuador*
[g] *Forest Research, Northern Station, UK*

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Abstract

Rhododendron ponticum (Ericaceae) is a serious invasive alien plant in the British Isles and is of considerable conservation and economic concern. While optimal control strategies for single individuals and small stands of *R. ponticum* are well described, effective regional control of the plant demands an improved understanding of its spatial dynamics, in particular its dispersal ecology. Here, we describe the results of two field experiments designed to quantify the dispersal pattern of *R. ponticum* seeds: (1) controlled release over a few seconds at known windspeeds and (2) natural release over the peak dispersal period. We then use these results to assess the potential use of two different mechanistic wind dispersal models (WINDISPER and WALD) as descriptors of seed dispersal ecology for this species. Results from both the controlled and natural release experiments indicate that in open landscapes the vast majority of *R. ponticum* seeds travel less than 10 m, but that a very small proportion (0.001% in controlled trials; 0.02% in natural release) travel more than 50 m. The WINDISPER model provided the best description of seed dispersal for the controlled releases that took place over a few seconds under known windspeeds, but neither model performed well when used to predict seed dispersal from a natural stand over the peak period of dispersal. We suggest that this is due to a lack of knowledge of the exact windspeed at the time of seed release and the poor spatial and temporal resolution of the wind data available to us. The development of mechanistic wind dispersal models offers great potential for helping develop efficient control programmes for invasive alien plants, but further work to investigate the conditions under which seeds are released and the appropriate spatial and temporal resolution of wind data to use is required.

Keywords: Abscission; Dispersal kernel; Invasive alien species; Spatial spread; Wind dispersal

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[*] Corresponding author. Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St. Andrews, Fife KY16 9LZ, Scotland, UK. Fax: +44 1334 461800.
E-mail address: cms@mcs.st-and.ac.uk (C.M. Stephenson).

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Introduction

Invasive alien plants are increasingly recognised as important drivers of ecological change, with consequences for ecosystem processes, biological diversity, economics and human health (Earth Summit, Rio Convention, 1992; Vitousek et al., 1996; IUCN Council, 2000; Le Maitre et al., 2002). For newly arrived alien species that may become invasive, detection and removal constitute the best way of preventing establishment (Simberloff, 2003). For more established species, eradication may be difficult, and constructing population models can help in assessing the planning and feasibility of such a task, highlighting important areas of uncertainty in the species' ecology (Buckley et al., 2005). For many species, dispersal is the key parameter determining spatial dynamics (Bullock et al., 2002; Lockwood et al., 2007) but is one of the life history parameters about which we have least information. Significant advances have been made recently in the field of seed dispersal modelling and these offer considerable promise for the field of invasion biology. In this paper, we describe the results of experiments designed to improve our knowledge of the dispersal ecology of one of the most significant invasive plants in the UK, *Rhododendron ponticum*. We assess the ability of two mechanistic wind dispersal models to describe the dispersal process and consider their potential usefulness in the design of more effective regional control programs.

The dispersal ability of both plants and animals introduced into novel environments is an important factor determining their rate of spread (Clark, 1998; Clark et al., 1999; Bullock et al., 2002; Greene and Calogeropoulos, 2002). Characterising the shape of the dispersal function (seed kernel) and, in particular, quantifying long distance dispersal events at the tail of such kernels, however, is problematic (Levin et al., 2003). Phenomenological models, in which curves are fitted to empirical data, have been used to characterise dispersal patterns, resulting in three common functional forms for distribution: the Gaussian, the negative exponential and the inverse power law (Levin et al., 2003), or a combination of these (Bullock and Clarke, 2000; Nathan and Muller-Landau, 2000). However, in order to understand observed dispersal and generate predictions of patterns across species and contexts (e.g. different landscapes), mechanistic models are required (Nathan and Muller-Landau, 2000; Levin et al., 2003). For mechanistic models of seed dispersal by wind, the three most important variables are the seed's terminal velocity, the height of release and wind velocity (Okubo and Levin, 1989; Nathan et al., 2001). The terminal velocity of seeds, a critical determinant of their potential dispersal distance, is defined as their rate of fall in still air and relates to morphological characteristics such as the surface area to mass ratio (Askew et al., 1997). The height of release determines both the length of time a seed spends in the air and the wind conditions it may encounter. By far the most complex variable acting on dispersing seeds is the movement of air. While the horizontal component of windspeed is of obvious importance, for some species the frequency and severity of vertical windspeeds and turbulence can be important to long distance dispersal events (Tackenberg, 2003; Soons et al., 2004; Katul et al., 2005). For example, Katul et al. (2005) found that simple mechanistic models could not explain the dispersal distances observed for *Calluna* seeds without implying hurricane force winds (Bullock and Clarke, 2000), whereas the WALD model, which incorporates the effects of air turbulence, predicted seeds to land at the observed long distances under much less extreme wind speeds ($\sim 10\,\mathrm{m\,s^{-1}}$).

There have been few independent calibration studies and tests of mechanistic wind dispersal models (Okubo and Levin, 1989; Greene and Johnson, 1989; Andersen, 1991; Bullock and Clarke, 2000; Nathan et al., 2001; Tackenberg, 2003), and difficulties exist in achieving correspondence between models and field data (Bullock and Clarke, 2000; Stoyan and Wagner, 2001). In particular, mechanistic models show varying success in predicting the shape and tail of dispersal curves (Bullock and Clarke, 2000). This is important to the understanding and management of plant invasions because the predictions of invasion models are very sensitive to changes in the tail of the dispersal distribution and different distributions can predict quite different rates of spread (Clark, 1998; Bullock et al., 2002). In addition, some seeds may only be released once the windspeed has exceeded a critical limit (the "release threshold", Schippers and Jongejans, 2005), and the implications that this may have for the dispersal distances of wind-dispersed seeds has been highlighted in a number of recent studies (e.g. Greene, 2005; Schippers and Jongejans, 2005).

R. ponticum is thought to have been first introduced into Britain in 1763 from Iberia although plants have also been introduced from the Balkan peninsula (Cross, 1975; Shaw, 1984; Milne and Abbott, 2000). Since then, it has become well established throughout the British Isles (Cross, 1981, 1982; Rotherham, 1986; Thomson, et al. 1993; Gritten, 1995). It is now considered a major invasive weed, particularly in the west of Britain and Ireland and its presence is of great conservation and economic concern (Cross, 1982; Dehnen-Schmutz et al., 2004). *R. ponticum* has many of the characteristics that have been identified as good indicators of high invasive potential in a species (Higgins et al., 1996; Rotherham, 2001), especially the ability of mature *R. ponticum* to produce hundreds of thousands of seeds every year (Cross, 1975). The morphology and small size of the seeds suggest wind as the primary dispersal agent

(Brown, 1954; Cross, 1975; Shaw, 1984). It has been suggested that in strong winds *R. ponticum* seeds could be dispersed effectively over distances of about 100 m but very occasionally 1000 m or more (Shaw, 1984). To date, however, there is no quantitative information, available on either short or long distance seed dispersal for this species.

Management decisions on invasive species often need to be made in the face of considerable uncertainty regarding the factors that influence the establishment and spread of a species. In order to predict the speed of plant invasions and the effectiveness of control work, there is a need for techniques that can quantify the movement of plant populations given readily available or easily inferred input. Here, we quantify seed dispersal in *R. ponticum* using a combination of controlled and natural release seed trap trials at sites in Scotland, UK. We compare the results of these trials with predictions from a simple mechanistic model, WINDISPER (Nathan et al., 2001) and a more complex mechanistic model, WALD (Katul et al. 2005). To the best of our knowledge this is the first dispersal study to examine the capacity of a known invasive species to disperse seeds up to 100 m under field conditions. Specifically, the aims of the study were to:

1. quantify short and long distance dispersal (i.e. characterise the shape and the tail of the seed kernel) for the invasive plant species, *R. ponticum*;
2. test the ability of two different mechanistic models to describe instantaneous and natural releases of *R. ponticum* seeds given windspeed, habitat type, terminal velocity and the height of seed release; and
3. compare patterns of seed dispersal during instantaneous releases with those produced over a longer period of seed release under natural conditions.

Methods

Terminal velocities

Seeds were collected from four geographically distinct *R. ponticum* infestations within Scotland. Terminal velocities for 90 randomly selected seeds were measured under controlled conditions at the NERC/University of Sheffield's purpose-built facility (Askew et al., 1997). The same collection of seeds was used in the controlled dispersal trials.

Dispersal experiments

After flowering, mature *R. ponticum* release seeds from small capsules between late winter and June (Cross, 1975, 1981; Shaw, 1984). We carried out two field experiments between February and April, the peak period of natural seed dispersal.

Controlled release

A total of 10 controlled trials were carried out in a site near Achnamara on the west coast of Scotland (56°00′N, 5°35′W) over 3 days in April 2003. At the release site we erected a wooden platform supported by scaffolding for the seed releases and attached a portable anemometer (Davis, Wireless Vantage Pro Plus 6160), which registered horizontal windspeed and direction every 2 s, to the scaffolding at a height of 1.85 m. Seed traps made of sticky bookbinding paper, cut in 10 cm wide strips, were laid out along transects in the eight compass directions from the release point. At each distance on the logarithmic scale 0.5, 1, 2, 5, 10, 20, 50 and 100 m the total area of traps equalled 6% of the area of a 10 cm ring at that distance (Bullock and Clarke, 2000). This method ensured trapping effort was constant at each trap distance, and enabled the use of raw seed counts rather than requiring the conversion of count data to densities. The study site allowed the full 100 m transect distance in six of eight compass directions, with the remaining two running to 50 m to avoid setting traps in the dense plantation forest. This meant that trapping effort was only 4.5% of the 10 cm ring at 100 m.

Seeds were released alternately from two heights, 2 and 3.5 m. The lower of these corresponded to the mode of capsule heights measured on a nearby *R. ponticum* thicket, and the greater height of 3.5 m represented the stature of mature *R. ponticum* stands and a plausible release height for seeds from stands on banked ground. Approximately equal numbers of seeds (200,000–237,000) were released during each trial. The number was calculated by weighing a sample of capsule contents (including unfilled seeds, capsule ribs and dried flower parts) and estimating the number of filled seeds per gram (ca. 14,5000; Kohn, unpublished data). Seeds were poured into a strainer held at the requisite height, and the strainer was agitated until all seeds had fallen through the holes, a procedure that took approximately 10 s. The seeds were released from the leeward edge of the scaffolding, i.e. in the direction of wind travel in order to prevent large numbers of seeds landing on the platform. From the moment of release, the anemometer readings were transcribed every 2 s until all seeds were released. Collection of the sticky paper traps began 15 min after release with those traps within 5 m of the platform, and continued with the more distant traps after 25 min. The sticky traps were examined under a microscope at 12 × magnification for counting and for discriminating between filled and unfilled seeds. Only counts of filled seeds were analysed.

Natural release

The second field experiment trapped seeds released over $6\frac{1}{2}$ weeks from an established stand of *R. ponticum* at the edge of an estate in southern Scotland (55°43′N, 3°27′W). Most of the woodland and roadsides on the estate contained *R. ponticum*, with the chosen bank of *R. ponticum* representing a front. The bank was 35 m long and reached a height of 6 m. Sticky traps were laid out in three near-parallel transects within a 20° arc in an open short-grazed field. Individual traps were identical in area to those in the controlled experiments but the sampling intensity at each distance equalled approximately 5% of the area of a 10 cm ring in the half-circle that the field represented. Traps were set out in late February 2003, checked three times and cleared of leaves in March, and collected in mid-April. Again, the sticky traps were examined under a microscope at 12 × magnification to count the filled seeds.

Simulated seed dispersal

A simple mechanistic model for seed dispersal (WINDDISPER, Nathan et al., 2001) was parameterised to generate expected seed dispersal curves for comparison with the observed seed distributions. Full details of this model and its derivation are provided in Nathan et al. (2001). The movement of each seed is modelled using the following equation:

$$D = \frac{u_*}{(K \times F)}\left((H-d)\ln\left(\frac{H-d}{ez_0}\right) + z_0\right),$$

where D is the distance travelled by the seed, u_* is the friction velocity, K is the von Kármán constant ($=0.40$), F is the seed's terminal velocity, H is the height at which the seed is released and, d and z_0 are two roughness parameters, termed roughness length and displacement height, respectively. In all the results shown we have used $d = 0.066$ and $z_0 = 0.03$, these values being appropriate for the vegetation height (~5–15 cm) in the fields over which the seeds were being dispersed (Raupach, 1994). We have, for simplicity, assumed there to be no vertical (either upwards or downwards) wind speed in our implementation of WINDISPER, but this can be readily incorporated if data for paramaterisation are available (see Nathan et al. 2001).

A key feature of WINDDISPER is that it takes a Lagrangian approach, in that it focuses on the movement of individual seeds each of which have slightly different characteristics (e.g. height of release, terminal velocity). Nathan et al. (2001) set the model up such that it 'calculates the postdispersal deposition of individual seeds by randomly selecting the values of all operative parameters from their empirical distributions'. Our approach is identical and for each simulation 200,000 seeds were randomly allocated a windspeed from a distribution derived from the mean and standard deviation of windspeeds observed in the corresponding field trial (Table 1). Similarly each seed was randomly allocated a terminal velocity from a distribution derived from the mean and standard deviation for the 90 seeds tested (Table 1). Seeds that were predicted to land ±0.05 m either side of one of the trap distances (0.5, 1, 2, 5, 10, 20, 50 or 100 m) were counted and used for comparison with the observed data.

WINDISPER is a relatively simple mechanistic model, essentially a 'ballistic' model (Katul et al., 2005), and because it neglects the potential effects of turbulent air flow it is likely to underestimate the tail of the dispersal kernel. Recent progress has seen the development of more complex, and substantially more computationally demanding, mechanistic models (e.g. Hsieh et al., 2000; Katul and Chang, 1999; Tackenberg, 2003) that are much better able to capture long distance dispersal events (Nathan et al., 2002; Soons et al., 2004; Tackenberg, 2003). However, for most applications, particularly those modelling population dynamics over regional scales, these models would be impracticable due to the high computational costs. The need for a model that captures complexities in seed trajectories due to air turbulence, but that can more readily be applied to pressing ecological issues, motivated the development of the Wald analytical long-distance dispersal (WALD) model (Katul et al., 2005). This model is derived from a simplified 3-D stochastic dispersion model retaining the essential physics contained within the computational simulations. The lengthy derivation can be found in Katul et al. (2005), and it is beyond the scope of this paper to repeat details here. Reassuringly, following some daunting maths, the analytical model reduces to the following Wald (or inverse Gaussian) distribution (Eq. (5b) in Katul et al. 2005):

$$p(x_l) = \left(\frac{\lambda'}{2\pi x_l^3}\right)\exp\left[-\frac{\lambda'(x_l-u')^2}{2\mu'^2 x_l}\right]$$

where u' and λ' are dispersal kernel parameters that depend only on the wind velocity statistics (both horizontal and vertical components), seed terminal velocity and seed release height. The standard deviation of the vertical component windspeeds (σ_w) is a potentially key parameter (Katul et al., 2005). We have no empirical data with which to paramaterise this value for our simulations, and therefore tested the sensitivity of the model output to σ_w values between 1 and 6 m s^{-1}. Very little difference was found between results (data not shown), and so we have shown results using the value of 3 m s^{-1} from the parameterisation of WALD for *Calluna* as described by Katul et al. (2005). We implemented the WALD model and conducted an identical set of simulation experiments to those carried out using WINDISPER. Two hundred thousand seeds

Table 1. Summary statistics table for controlled and natural release experiments and simulations (omitting Trial 4; see text)

Trial/simulation no.		Release height (m)	Mean wind speed $(\mathrm{m\,s^{-1}}) \pm$ S.D.	No. of seeds recaptured	Dispersal distances (m)	
					Mode	Max
Controlled seed release						
1	Observed	2	2.20 (±0.583)	349	0.5	5
	WINDDISPER				2	5
	WALD				5	10
2	Observed	3.5	1.47 (±0.815)	523	5	50
	WINDDISPER				5	10
	WALD				5	20
3	Observed	2	3.04 (±0.832)	63	2	10
	WINDDISPER				5	10
	WALD				5	10
5	Observed	2	2.08 (±0.699)	140	2	5
	WINDDISPER				2	5
	WALD				5	10
6	Observed	3.5	1.71(±0.591)	236	5	10
	WINDDISPER				5	10
	WALD				5	10
7	Observed	2	2.96 (±0.917)	69	2	10
	WINDDISPER				5	10
	WALD				5	20
8	Observed	3.5	3.26 (±0.258)	235	10	10
	WINDDISPER				10	10
	WALD				10	20
9	Observed	2	3.66 (±0.974)	22	10	10
	WINDDISPER				5	10
	WALD				5	20
10	Observed	3.5	3.30 (±1.42)	175	5	10
	WINDDISPER				10	20
	WALD				10	20
Natural seed release						
Observed				552	1	100+
No release threshold		5±1				
1	WINDDISPER		5.24 (±3.75)		5, 10[a]	50
	WALD				10	100+
2	WINDDISPER		9.26 (±5.84)		10	100+
	WALD				20	100+
3	WINDDISPER		9.27 (±6.86)		20	100+
	WALD				10	100+
4	WINDDISPER		14.99 (±9.58)		20	100+
	WALD				50	100+
$2\,\mathrm{m\,s^{-1}}$ release threshold		5±1				
1	WINDDISPER		5.24 (±3.75)		10	100+
	WALD				10	100+
2	WINDDISPER		9.26 (±5.84)		20	100+
	WALD				20	100+

In all simulations the number of seeds was kept constant at 200,000, mean terminal velocity was $0.98\,\mathrm{m\,s^{-1}}$ (±0.14) and vegetation roughness was open, short grass.

[a] For this simulation the same number of seeds were predicted for both distances.

were randomly assigned windspeeds and terminal velocities, and the distance each seed travelled was drawn at random from the inverse Gaussian distribution with the form shown in the above equation.

Both models were implemented in R 2.4.1 (R Development Core Team, 2006), with the use of an additional package to provide the Inverse Gaussian distribution (SuppDists version 1.1, Wheeler, 2006). The code is available upon request.

Controlled release

For both models, the simulated number of seeds on each trap was scaled to equal the number of seeds captured in the field (Table 1). Negative log likelihood ($-\ln L$) values were used to determine the likelihood of observing the data given each model (Clark et al., 1999; Skarpaas et al., 2004). The values of $-\ln L$ were calculated for each trap distance in each trial for both models. It was assumed that the errors were Poisson distributed for these calculations, though it is recognised that this assumption may be flawed in some circumstances. For example, applying a Poisson distribution to the data assumes that the mean is equal to the variance; therefore in cases where a zero is observed at a given trap distance under the model predictions but a single seed is observed in the field, the $-\ln L$ will tend to infinity and lead to the conclusion that the field observation is impossible given the model. We do not believe that the models should be discounted solely on the basis of such infinity values and have therefore presented overall likelihood values for each trial with and without these values. The likelihood analysis provides a relative measure of fit that allows comparison of the performance of both models. To provide an absolute measure of fit for each model, we also generated R^2 values using the square of the correlation between observed values from the field and the scaled values predicted to land on each trap distance under each model (Agresti and Franklin, 2007).

Natural release

We used local windspeed data supplied by the British Atmospheric Data Centre, from Meteorological Office Land Surface Observation Stations, for the period of the natural release observations. Daily 24-h means were obtained from a weather station 5.2 km from the study site, hereafter referred to as the "near" station. In addition to daily means, finer resolution data (hourly mean and gust speeds) were obtained from a weather station 21.9 km from the study site, referred to as the "far" station. All wind measurements were horizontal windspeeds recorded at 10 m elevation. Both models correct for the difference between the height of the wind measurements (10 m) and the height of release of the seeds (5.0 m ±1.0 m).

We used wind data of varying resolution in a number of different simulations to examine which dataset resulted in model output that best fit the observations. In each simulation, each of 200,000 seeds was released from a random location within the 35 m long × 4 m wide bank of *R. ponticum* plants, from a mean height of 5.0 m (±1.0 m), and allocated a windspeed drawn at random from the relevant windspeed dataset. With an area source, the distance a seed has to disperse in order to land on a trap will depend on the exact release location within the bank of plants. We accounted for this by simulating the distance travelled by each seed and then calculated which trap it would land on if it travelled towards the trap line: For example, if a seed dispersed 7.3 m from a plant 2 m behind, and 2 m to the left of the start of the trap line, the seed would land on a 5 m trap. In the first two simulations the seeds were allocated one of 48 daily mean windspeeds recorded from the "near" and "far" weather stations, respectively. In the third and fourth simulations, they were allocated one of 1632 hourly mean windspeeds and hourly maximum gust speeds, respectively, from the "far" station. Two of the simulations were repeated to investigate the role of release thresholds (e.g. Schippers and Jongejans, 2005): therefore in a set of additional simulations seeds were only released on windspeeds greater than a threshold of $2.0\,\mathrm{m\,s^{-1}}$ (Table 1). For comparative and goodness of fit purposes, data were treated as for the controlled release trials. Throughout the paper, errors are expressed as Standard Deviations unless otherwise stated.

Results

The distribution of the measured terminal velocities had a mean of $0.98 \pm 0.14\,\mathrm{m\,s^{-1}}$ (Fig. 1), and it was

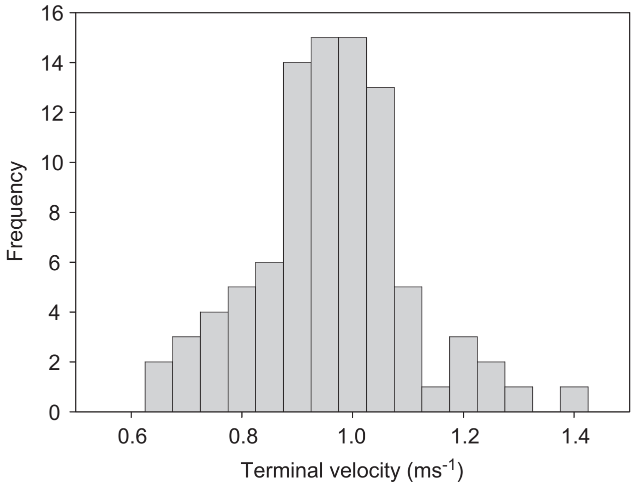

Fig. 1. Frequency distribution of *R. ponticum* seed terminal velocities ($n = 90$) measured at the University of Sheffield.

this distribution that was used to parameterise both WINDISPER and WALD.

Controlled release

In eight out of the ten controlled release trials, more than 60 seeds were captured on the sticky traps. In trial 9, 22 seeds were recovered and in trial 4, only 3 seeds were found; trial 4 was excluded from analyses. Over all trials 99.8% of seeds were found on traps less than or equal to 10 m from the release point, with the greatest number of seeds at 5 m and only 0.001% travelling 50 m or more (Fig. 2, Table 1). The mean distance of seeds released from 2.0 m height was 3.36 ± 2.87 m ($n = 5$) compared with 6.54 ± 2.29 m ($n = 4$) from a release height of 3.5 m, but the sample size was too small to test this difference statistically.

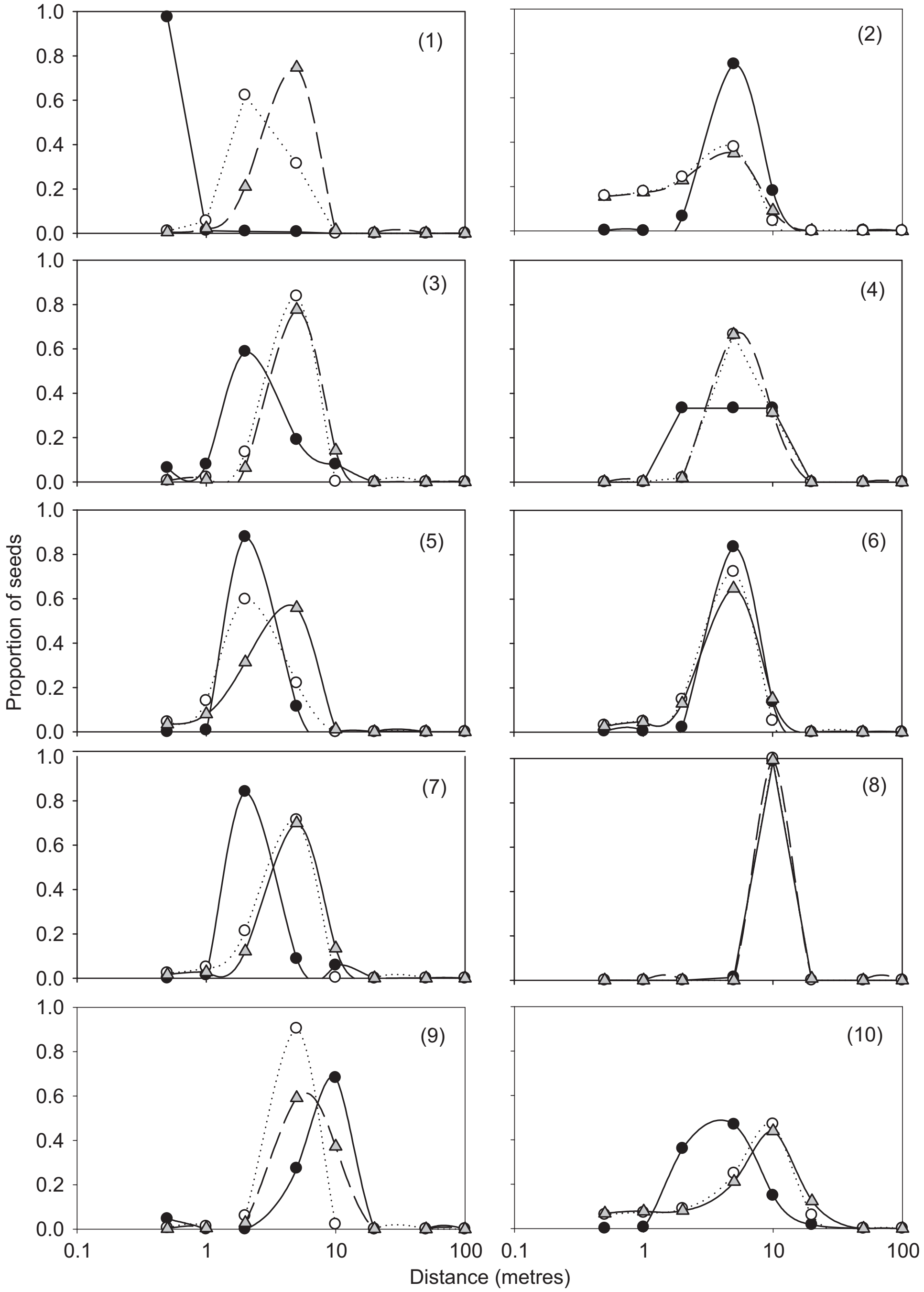

Fig. 2. The observed (●) and predicted proportion of seeds dispersing up to 100 m from release point during 10 controlled release trials for the models WINDDISP (○) and WALD (▲). Seeds for trials 1, 3, 5, 7 and 9 were released 2 m from the ground, and for trials 2, 4, 6, 8 and 10 were released from 3.5 m.

Table 2. Negative log likelihood ($-\ln L$) of the predictions of the WINDISPER (WND) and WALD (WLD) models of dispersal for each of the controlled trials (omitting Trial 4; see text)

Distance	Trial 1		Trial 2		Trial 3		Trial 5		Trial 6		Trial 7		Trial 8		Trial 9		Trial 10	
	WND	WLD	WND	WLD	WND	WLD	WND	WLD	WND	WLD	WND	WLD	WND	WLD	WND	WLD	WND	WLD
0.5	Inf	Inf	77.8	76.4	7.7	8.2	6.2	4.9	5.2	4.8	1.6	1.1	0	0	2.4	3.3	10.8	11.9
1	10.6	2.8	92.8	91.3	4.7	7.2	16.6	8.8	8.9	8.4	2.2	1.3	0	0	0.24	0.1	10.0	10.9
2	202.6	62.3	50.6	45.7	28.8	51.4	11.4	50.8	21.8	18.2	39.4	65.5	0	0	1.3	0.6	43.7	48.4
5	100.6	250.5	78.1	94.1	25.2	22.2	6.6	39.2	5.5	9.4	32.4	31.6	Inf	Inf	8.5	4.2	16.7	23.5
10	0	5.0	63.7	20.5	17.1	2.8	0	1.7	13.8	2.8	10.6	3.6	3.7	3.6	39.8	4.5	28.9	25.2
20	0	0	0	0.1	0	0	0	0	0	0	0	0.03	0	1.8	0	0.03	5.3	14.2
50	0	0	Inf	Inf	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total for trial	**313.9**	320.6	363.0	**327.9**	**83.4**	91.8	**40.8**	105.4	55.2	**43.2**	**86.2**	103.1	**3.7**	5.44	52.3	**12.8**	**115.3**	134.1

In three cases, for each model $-\ln L$ tended to infinity (Inf). As these instances were identical for both models, these values were excluded in the calculation of the total $-\ln L$ for each trial. Bold indicates the better fitting model for each trial (lower $-\ln L$).

Quantitative comparisons of the characteristics of the observed versus expected dispersal kernels however, were possible (Fig. 2, Table 1). The observed and simulated data from each model under the conditions of each trial were treated as paired data for the following comparative analyses. For the WINDISPER model, in four of the nine pairs, the observed and simulated modal distances were the same and for those five that differed, the differences were not greater than 5 m (Table 1). Overall, the differences between the observed and WINDISPER simulated modal dispersal distances were not significant (Wilcoxon signed rank test $= 4.5$, $p = 0.5$, $n = 9$). Maximum distances were equal for seven of the nine pairs, one had a higher simulated maximum compared to the corresponding observed value, and one had a lower simulated maximum (Table 1). Again, these differences were not significant (Wilcoxon signed rank test $= 2.0$, $p = 1.0$, $n = 9$). The mean R^2 value over the 9 trials was 0.42 (min $= 0.04$; max $= 0.99$).

For the WALD model, in three of the nine pairs, the observed and simulated modal distances were the same and, as with the WINDISPER model, for those six that differed, the differences were not greater than 5 m (Table 1). Overall, the differences between the observed and WALD simulated modal dispersal distances were not significant (Wilcoxon signed rank test $= 5.5$, $p = 0.35$, $n = 9$). Maximum distances were equal only for two of the nine pairs, six had higher simulated maximum values compared to the corresponding observed value, and one had a lower simulated maximum (Table 1), but these differences were not significant (Wilcoxon signed rank test $= 7.0$, $p = 0.27$, $n = 9$). The mean R^2 value over the 9 trials was 0.39 (min $= 0.009$; max $= 0.99$).

In six of the nine controlled release trials, the WINDISPER model provided a better fit to the data than the WALD model (Table 2), however the differences between $-\ln L$ were small for most trials. The within-trial likelihood values show that both models provide a better fit to the observed data at the start and end of the kernel, and provide a poorer fit to the peak of the kernel. Three observed values were deemed highly improbable by both models ($-\ln L =$ infinity), but the distance at which these observations occurred was variable and therefore did not indicate any consistent bias in the model predictions. In all trials both models predicted zero seeds dispersing 50 or 100 m which agrees with all but one of the observed trials, suggesting that neither model under predicted the maximum dispersal distance.

Natural release

More seeds were recaptured during the natural release than during any of the controlled trials (Table 1) but it can be assumed that the number of seeds released from the bank of *R. ponticum* over the period of study greatly exceeded 200,000. When data from the three transects were combined, 97.1% of seeds were found on traps less than or equal to 10 m from the release point, with the greatest number of seeds at 1 m (Fig. 3), 0.02% travelling 50 m or more and 0.01% landing on traps at 100 m. Wind recorded at the nearest weather station over the $6\frac{1}{2}$ weeks of the experiment had a mean of $5.23\,\mathrm{m\,s^{-1}}$ with gusts up to $50\,\mathrm{m\,s^{-1}}$ and was predominantly from the west. As seeds were trapped at the maximum trapping distance (100 m), we do not know what the real limit of dispersal distance is (Table 1).

The range of windspeeds in the hourly datasets is greater than that for daily mean windspeeds, and the mean and standard deviation of windspeeds for hourly gusts are greater than those for the three mean windspeed profiles (Table 1). Under all four wind datasets, both models had a higher modal dispersal distance than was observed (Table 1). The observed kernel peaked at 1 m and decreased sharply to 20 m, with a small proportion of seeds landing at 50 and 100 m, whereas the WINDISPER and WALD models predicted much flatter distributions with fatter tails reaching out as far as 100 m (Fig. 3a and b). In all but one case, both models predicted seeds landing on the 100 m trap. Both models predicted that seeds would travel much further than 100 m. WINDDISPER predicted that seeds would travel up to 113 m under the daily mean windspeed and 296 m under the daily maximum windspeeds, whereas the WALD model predicted that seeds would travel up to 204 m under the daily mean windspeed and 472 m under the daily maximum windspeeds (data not shown). Visual inspection alongside the R^2 values indicates that neither model fits the observed data particularly well (mean R^2 for WINDISPER = 0.2 (min = 2.78×10^{-5}; max = 0.45); mean R^2 for WALD = 0.09 (min = 0.005; max = 0.22). In all but one case the WINDISPER provides the better fit when the two models were compared using the $-\ln L$ values (Table 3).

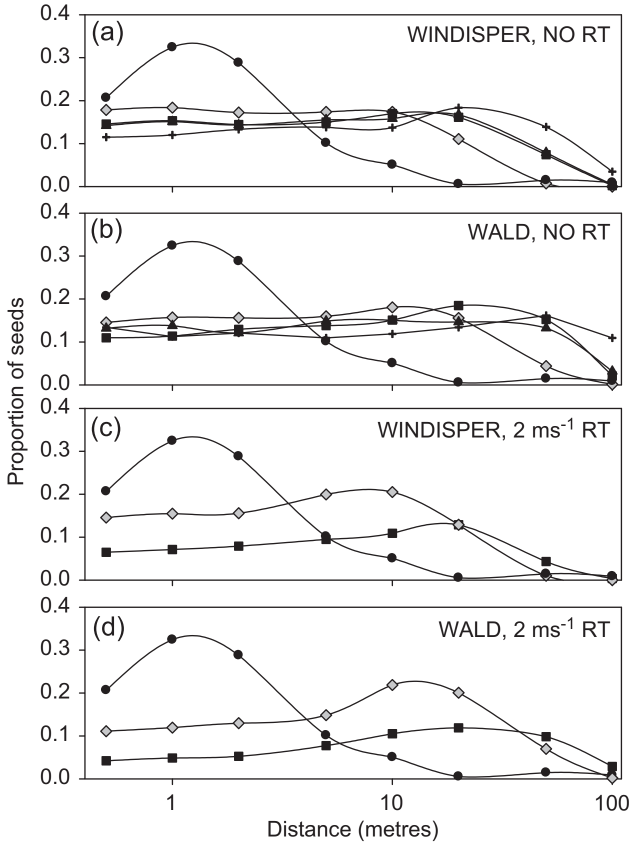

Fig. 3. The observed (●) and predicted proportion of seeds dispersing up to 100 m from an *R. ponticum* bank in southern Scotland (a) WINDISPER assuming no release threshold (RT), (b) WALD assuming no release threshold, (c) WINDISPER incorporating a release threshold of $2\,\mathrm{m\,s^{-1}}$ (using daily mean windspeeds only) and (d) WALD incorporating a release threshold of $2\,\mathrm{m\,s^{-1}}$ (using daily mean windspeeds only). Model predictions are shown using four different sets of wind data from two weather stations: daily mean windspeed ("near" station, simulation 1) = ◆, daily mean windspeed ("far" station, simulation 2) = ■, hourly mean windspeed ("far" station, simulation 3) = +, hourly maximum windspeed ("far" station, simulation 4) = ▲.

Incorporating a release threshold of $2\,\mathrm{m\,s^{-1}}$ made little difference to the predictions of the two models in terms of the modal and maximum distances (Fig. 3c and d, Table 1) but made a large difference to the goodness of fit measures. The $-\ln L$ values for both models were much larger when the release threshold was included, indicating a worse fit to the data and, under the two

Table 3. Total negative log likelihood ($-\ln L$) of the predictions of the WINDISPER (WND) and WALD (WLD) models of dispersal for the natural trial under four different wind data sets from two stations, "near" (NR) and "far" (FAR), summed over all distances

	Total $-\ln L$	
	WND	WLD
Daily mean windspeed (NR)	Inf **(156.78)**	**218.2** (210.7)
Daily mean windspeed (FAR)	**233.7**	326.6
Hourly mean windspeed (FAR)	**235.6**	277.8
Hourly maximum windspeed (FAR)	**308.4**	328.9
Daily mean windspeed (NR) with release threshold = $2\,\mathrm{m\,s^{-1}}$	Inf (1970.3)	**1017.7** **(1204.7)**
Daily mean windspeed (FAR) with release threshold = $2\,\mathrm{m\,s^{-1}}$	1206.5	**722.2**

The models were repeated for the two daily mean windspeed datasets with a release threshold included. In two instances under the WINDDISPER model $-\ln L$ tended to infinity (Inf), the value in brackets is the total $-\ln L$ when the infinity was excluded. For the WALD model the value in brackets is the total $-\ln L$ when the value corresponding to the infinity under WINDISPER was excluded for comparative purposes. Bold indicates the better fitting model for each trial (lower $-\ln L$).

windspeed datasets tested, the WALD model provided the better fit.

Discussion

This is the first study to describe in detail the pattern of seed dispersal for *R. ponticum*, an important characteristic contributing to the invasive potential of this species. Techniques to remove individual *R. ponticum* are now well tested (e.g. Eşen et al., 2006; Edwards, 2006), and there have been great improvements in our ability to clear relatively localised areas in the short term. Assessing the effectiveness of different control strategies for invasive plants in general, however, is currently hampered by the limited information available on different approaches and their long term results (Hulme, 2003), and this situation is no different for *R. ponticum* (but see Groundwork Ireland 2000 for information on a long-term management and monitoring programme: http://www.groundwork.ie/). For invasive plant population models, information on some of the basic ecological requirements and characteristics of such species is often lacking. Recent work has increased our understanding of *R. ponticum* pollination (Stout et al., 2006), germination (Erfmeier and Bruelheide, 2005), and establishment and growth (Eşen et al., 2004; Stephenson et al., 2006). Here we have investigated both short and long-distance dispersal of *R. ponticum* under controlled and natural field conditions and have assessed whether two previously published mechanistic models (Nathan et al., 2001; Katul et al., 2005) can adequately predict the patterns of seed dispersal for this invasive species. These results, alongside data recently presented on *R. ponticum* establishment probabilities (Stephenson et al., 2006), will help enhance the predictive abilities of models designed to assess control strategies and inform managers on future needs for preventing re-establishment.

The results from the controlled release experiments give little indication that *R. ponticum* seeds have the potential to disperse long distances, as almost all seeds landed within 20 m of the release point. However, the windspeeds measured during all the controlled release trials were likely to be too low to observe long distance dispersal events, particularly since *R. ponticum* seeds have a relatively high terminal velocity compared to seeds of other species that have a high potential for long distance dispersal (Tackenberg, 2003). This meant that here we could only assess the performance of the mechanistic model against observed dispersal at low windspeeds. Ideally, we would have conducted the trials under a much greater range of windspeeds, but unusually, for the west coast of Scotland in April, the wind was consistently light throughout the period of the fieldwork.

At low windspeeds, the R^2 values indicated that both models performed well in reproducing the distribution of distances travelled by the seeds in the controlled experiment. In almost all trials the key features and the shape of the observed dispersal patterns were reproduced by both models, and by the WINDISPER model in particular. It is worth highlighting that in any sampling strategy there is the possibility for misidentification of key features of the dispersal distribution. The kernels derived from the observed data are limited to the distances and directions of the sticky traps and may in some instances have missed the precise values of, for example, the modal distance of the dispersing seeds. However, given that the data from the mechanistic models, when allocated to equivalent trap distances, approximately resemble the observed, it is likely that the experimental design captured the important characteristics of the real kernel under the conditions of our controlled release experiment.

In six of the nine controlled trials analysed, WINDISPER provided the better fit to the observed data. The WALD model over-predicted the modal and maximum values of the dispersal kernels more often than did WINDISPER, and from the likelihood analyses it was noted that the WALD model predicted seeds at 20 m on three occasions when no seeds were observed this far in the field. This tendency to over-predict is likely due to the vertical wind velocity and turbulence characteristics that are accounted for in the WALD model (Katul et al., 2005).

The results of the simulations parameterised for the conditions of the natural release experiment indicate longer dispersal distances than could have been observed during the field trial, where the maximum trap distance was 100 m. For example, when WINDISPER was parameterised with the daily mean wind data from the nearest weather station, the maximum dispersal distance was 113 m, whilst for WALD it was 204 m. When maximum dispersal distances were investigated under the different wind data sets, it became apparent that the WALD model consistently predicted seeds to travel further than WINDISPER, under the conditions of the natural release trial. The fact that we could not observe dispersal events at these distances means that we cannot assess which of the two models provides the most realistic predictions in relation to the tail of the dispersal kernel under high windspeeds and from an area source. Anecdotal evidence points to occasional dispersal events for *R. ponticum* of several hundred metres and while it is certainly possible that these rare events may be mediated by other dispersal agents (animal or human), our results suggest that we should not discount the possibility that wind may occasionally disperse a seed several hundred metres. We can conclude from the $-\ln L$ analyses that WINDISPER provided the better fit at distances up to 100 m but the large differences in the tail of the predicted dispersal kernels between the two models raises a number of interesting questions relating to the design of future trap experiments and modelling the spread of this species. A suggested improvement to the experimental design would be to amplify greatly the sampling effort at distances greater than 50 m and possibly use simulations or sequential sampling (Bullock et al., 2002; Skarpaas et al., 2005; Pielaat et al., 2006) to inform the design of the sampling strategy. However, due to the differences in the tails of the simulated kernels, the sampling strategy is likely to be heavily influenced by the mechanistic model employed.

The wind data from the weather station nearest the location of the natural trial differed considerably from those obtained from the more distant weather station, and generated a kernel with a shorter tail compared to the kernels generated using the ''far'' wind data at any resolution. Neither WINDISPER nor WALD, when parameterised with the four different wind datasets, fitted the observed kernel particularly well, even at distances less than 100 m. In all cases both models over-predicted the modal distances of the kernel. The lack of model fit in the case of the natural trial is more likely due to the wind datasets used than the models themselves. It does not seem unusual in the literature for researchers to have needed to make compromises on the wind data used to parameterise models, for example Skarpaas et al. (2004) carried out wind measurements in the 2 weeks following dispersal and paramaterised their model using that, whilst Bullock and Clarke (2000) used data from a weather station 21.75 km from their release site. We feel that it is important to discuss the problems associated with spatial and temporal resolution of the wind data used in this study, and by others, when parameterising models to recreate observations in the field.

Firstly, the closest available wind data came from 5.2 km away from the release site. The general conditions at the weather station and release site are likely to have been similar in terms of the range of windspeeds experienced over the course of each 24 h period, but there may have been site-specific differences in wind conditions that may have influenced the model predictions. Secondly, several studies have carried out dispersal experiments in the field, trapping seeds over the period of peak seed release, and then parameterising mechanistic models with corresponding wind data that is averaged over time (e.g. 6 h in Schippers and Jongejans, 2005; 24 h in Tackenberg et al., 2003). As Greene (2005) points out, averaging time is an important consideration when parameterising dispersal models because long averaging times, say 24 h, are likely to include windspeeds from periods when factors such as humidity may prevent abscission. The lack of fit of either model to the data highlights the need for local, high temporal resolution data to be collected alongside future dispersal experiments. Finally, weather data was collated for the entire six-week period that the traps were situated in the field. The combination of factors required for abscission and dispersal (e.g. mature and open seed capsules, humidity, windspeed), however, may have only been suitable over the course of a few days within the 6 weeks. The range of windspeeds incorporated into the simulations may therefore have been greater than those experienced by dispersing seeds, and a better understanding of the timing and requirements for the abscission and dispersal of seeds in nature would be useful in this respect.

The observed dispersal kernel from the natural release trial was platykurtic, i.e. the distribution is flatter than would be observed under a normal distribution, whereas the controlled release dispersal kernel was leptokurtic. One reason for the difference in the shape of the kernels is the fact that in the natural release trial seeds were being released from a three-dimensional area, rather than a point source. Area sources have been shown to result in flatter distributions with greater median dispersal distances than point sources (Greene and Calogeropoulos, 2002; Shaw et al., 2006). The other causative factor for the differences is that the wind conditions were very different between the controlled and natural trials; the controlled trial was carried out under very light wind conditions whereas the natural trial was carried out over more than 6 weeks during which the wind conditions were highly variable. The resulting kernel had a lower modal distance compared to all controlled releases except trial 1, and a greater maximum distance compared to all controlled trials (Table 1).

The importance of release thresholds, where the windspeed must be above a certain strength for seeds to be released, in determining patterns of seed dispersal is increasingly being recognised (Greene and Johnson, 1989, 1992, 1996; Greene, 2005; Schippers and Jongejans, 2005; Skarpaas et al., 2006). Where a threshold exists for a given species, it is likely to affect its dispersal kernel because seeds released only in conditions of higher windspeeds could travel greater distances than if they were released more easily (Schippers and Jongejans, 2005). Whether a threshold windspeed exists for the release of *R. ponticum* seeds is unknown and has never been investigated empirically. We examined whether simulation models parameterised with a release threshold of $2\,\mathrm{m\,s^{-1}}$ fitted the observed data better than those assuming no release threshold. Under the conditions of the two wind datasets used, the simulated dispersal kernels from both the WINDISPER and WALD models produced a much worse fit to the data when a release threshold was incorporated. Although this result does not rule out a release threshold entirely, a low threshold for this species is likely given the low modal dispersal distance observed in the natural experiment, and the apparent lack of a strong physical attachment of the seed to the parent plant (in contrast with species such as thistles and dandelions, described in previous release threshold studies; Skarpaas et al., 2006; Greene, 2005, respectively).

In this paper we have used one of the simplest mechanistic wind dispersal models, WINDDISPER (Nathan et al., 2001), alongside the WALD model (Katul et al., 2005), which has been developed more recently and incorporates complex interactions between horizontal and vertical windspeeds, and turbulence. There seems little doubt that these processes play an important role in nature in determining the exact shape of the dispersal kernels for most species, but at least for *R. ponticum* dispersal at distances up to 100 m, the added complexity leads to over-estimation and a worse fit to the data compared to the simpler model. The results from the controlled experiments suggest that the simple WINDISPER model performs better for *R. ponticum* over this range of distances. It is possible that for wind-dispersed seeds with relatively high terminal velocities, such as *R. ponticum*, the incorporation of turbulence by WALD leads to overestimation of the tail, and further work is required testing WALD for a variety of species with a range of seed characteristics. However, as we continue work incorporating seed dispersal modelling into spatial population models for *R. ponticum* we will continue to use both models. Management of an invasive species such as *R. ponticum* should be precautionary in nature, and the WALD model, with its prediction of somewhat longer tails may better achieve this objective by reducing the chance of failing to predict the extent of occasional long distance dispersal. Quantifying dispersal up to 100 m, and identifying the best fitting model at these distances has taken us a significant step forward in our ability to model the spread of this invasive species. One of the most pressing remaining questions, however, is the identification of the maximum distance under a greater range of windspeeds than was experienced under the controlled trials. The importance of understanding the longer dispersal distances for determining the rates of spread of invading species is discussed by Bullock et al. (2002). The large difference in the maximum dispersal distances that resulted from parameterising the two mechanistic models for the natural release with different sources and resolutions of wind data highlights the uncertainty surrounding the tail of the dispersal kernel for *R. ponticum*.

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