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Wind dispersal and saltation effect on microinvertebrate propagules: A wind tunnel study

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ABSTRACT

Ephemeral wetland surfaces are preferential locations for wind erosion and repositories for resting stages (propagules) of aquatic invertebrates. Dormant propagules can disperse to new habitats via wind (aeolian transport, or anemochory). Wind transport of invertebrate propagules has been documented at local and regional scales, but prior laboratory wind tunnel tests of propagule anemochory neither replicated the predominant natural processes of wind erosion in drylands, saltation-sandblasting, nor determined the viability of experimentally wind-transported propagules. We used a soil saltation wind tunnel to test aeolian erosion, transport, and subsequent viability of propagules from seven aquatic invertebrate species. A propagule-bearing crusted soil surface was prepared, then abraded by saltating silica sand in the wind tunnel to emit aeolian sand and dust. Sediment was collected from three downstream sections of the wind tunnel, representing different transport distances in the environment, and propagules were quantified for each section by species. The wind-eroded material was rehydrated with sterile media to detect hatching of any propagules which survived the sandblasting. Although survival was much lower than in a control experiment without wind tunnel saltation treatment, and hatching rates were lower than those reported from undisturbed egg banks, viable individuals of all wind-tunnel-tested species were detected after hydration. Larger propagules settled closer to the source of entrainment than smaller propagules, indicating a shorter dispersal distance for larger propagules- although only short-distance anemochory may be necessary for dispersal across drainage basins. These results demonstrate that resting stages of many invertebrates can be wind-bombarded from natural surfaces along with sand and dust, dispersed into and transported through the atmosphere, and remain viable. Future investigations of anemochory of aquatic invertebrates from ephemeral waters should use appropriate wind tunnels to evaluate propagule and surface properties as potential adaptations for wind dispersion.

1. Introduction

The existence of aquatic invertebrates in ephemeral wetlands is precarious: flourishing when basins are filled or wetlands are moistened, but subject to desiccation during drought. At some stage in their life cycle, most zooplankton in ephemeral wetlands produce tough-walled, desiccation-resistant diapausing stages (dormant eggs, resting eggs, tuns, or more generally, propagules) that assemble in a persistent egg bank near the soil surface (Wallace and Smith, 2009; Brendonck et al., 2017) to cope with such unfavorable conditions (Brendonck & De Meester, 2003; Incagnone et al., 2015; Radzikowski, 2013; Walsh et al., 2017; Wilson and Sherman, 2013). These egg banks (propagule banks) play a major role in the success of aquatic invertebrate communities (Hairston, 1996; Lopes et al., 2016; Walsh et al., 2014, 2017). Although aquatic invertebrates have evolved to successfully reproduce during wet conditions and some taxa enter resting stages quickly when the waters that they live in desiccate, they do not possess the ability to actively transport themselves away to new habitats and ensure survival or reproduction if their original environment becomes inhospitable. Aquatic invertebrates inhabiting these ecosystems must develop strategies for their propagules to pass the barrier represented by the surrounding dry land, to disperse and colonize new environments (Incagnone et al., 2015; Walsh et al., 2014, 2017).

The passive dispersal of aquatic organisms occurs by several

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mechanisms including hydrochory involving water as a transport mechanism (Su et al., 2019), and zoochory which is transport by various animal vectors (Incagnone et al., 2015). The other method of passive transport is anemochory- dispersal by the wind (aeolian transport), the focus of this study. Anemochory plays a fundamental role in many ecological processes and provides important connectivity at scales ranging from individual organisms to the globe; however, aeolian transport is under-appreciated in ecological studies because aeolian research is traditionally contained within the geosciences (Field et al., 2010). A growing number of studies mark the role of wind as a dispersal strategy of aquatic invertebrates (e.g., Branchiopoda, Copepoda, Rotifera) (Brendonck and Riddoch, 1999; Nkem et al., 2006; Graham and Wirth, 2008; Vanschoenwinkel et al., 2008, Vanschoenwinkel et al., 2009; Lopes et al., 2016; Moreno et al., 2016; Rivas et al., 2018, 2019; Arenas-Sánchez et al., 2024). Anemochory also provides propagules a way to escape from fungal pathogens (Wilson & Sherman, 2010).

Ephemeral wetlands, especially playas (intermittent lakes), are among the world's dominant sources of aeolian dust emission and sand transport (Prospero et al., 2002; Bullard et al., 2011; Ginoux et al., 2012) and are also sites of egg banks for the diapausing stages of aquatic invertebrates (Anderson and Smith, 2004; Bright and Bergey, 2015; Meyer-Milne et al., 2022). Playas occur in hydrologically disconnected closed basins fed by ephemeral streams which may not hold water for years, suppressing propagule dispersal by hydrochory, leaving zoochory and anemochory as plausible mechanisms for dispersal between drainage basins. As climate change increases human water demand in deserts and natural evaporation, hydrological connectivity of desert wetlands will decrease (Pinceel et al., 2018; Zipper et al., 2021; Sives, 2024), and more desert wetlands likely will desiccate, increasing the extent of aeolian erosion and transport and increasing the importance of anemochory for dispersal. We posit that anemochory via soil wind erosion events is an under-appreciated dispersal process of aquatic invertebrates of ephemeral wetlands of arid and semiarid regions.

While there is evidence of anemochory of invertebrate resting stages via aeolian sand and dust transport in both cold and hot deserts (Nkem et al, 2006; Rivas et al., 2018, 2019; Pinceel et al., 2020; Sives, 2024), little research has considered the mechanisms of *how* propagules are dislodged, entrained, and dispersed by aeolian processes in ephemeral wetlands, and only a few studies have physically tested or simulated anemochory of ephemeral wetland organisms under controlled field or laboratory conditions with wind tunnels or similar devices. Graham and Wirth (2008) used a small portable field wind tunnel to determine threshold velocities for wind entrainment of sediment from potholes on the Colorado Plateau. Parekh et al. (2014) used a wind tunnel to test the threshold velocity for direct aerodynamic entrainment of *Artemia franciscana* cysts from a rough-textured surface, and the wind speed required to disperse 50 % and 80 % of the cysts. Pinceel et al. (2016) investigated the threshold velocity of emission and the effect of propagule size and ornamentation on dispersal potential using propagules adhered to glass or sandpaper using a simple wind tunnel system and similar taxa to those used in our study. Pinceel et al. (2020) tested the effect of wind speed, duration of wind exposure, disturbance and drying on anemochory of propagules, using Petri dishes of sediment in which egg banks of the fairy shrimp *Branchipodopsis wolfi* were embedded. Arenas-Sánchez et al. (2024) tested the effect of propagule size and substrate on wind emission of *Brachionus plicatilis* rotifer propagules placed onto a sandpaper surface.

However, none of these prior experiments entrained the propagules into the air through the predominant terrestrial wind erosion mechanism, generally summarized as "saltation-sandblasting," in which dry, often crusted soil surfaces are turbulently bombarded by saltating (bouncing) sand grains, forming dust- and sand-sized particles and aggregates that are injected into the atmosphere (Kok et al., 2012). Propagules are known to be resilient to certain extents to diverse environmental extremes including salinity, UV, radiation, pH, cold temperatures, desiccation, and fire (Dai et al., 2011; Radzikowski, 2013; Strachan et al., 2015; Bright et al., 2016; Belovsky et al., 2019). We aimed to determine if they are also resilient to the highly energetic process of saltation-sandblasting. We designed wind tunnel experiments to determine whether propagules are transported by and survive this wind erosion process generally required for dispersal by anemochory from ephemeral wetlands.

Rivas et al. (2018) conducted a multi-faceted group of experiments to assess and demonstrate anemochory of diapausing propagules of aquatic invertebrates across regional scales (10^2–10^5 km) in the Chihuahuan Desert of North America. The work included wind tunnel experiments on simulated playa-surface egg banks, and data indicated that after wind erosion by saltation and downwind aeolian transport, propagules could be viably rehydrated (See Supplemental Document S2 and Table S2 in Rivas et al., 2018). Here, we re-evaluate the original wind tunnel data of Rivas et al. (2018, Supplemental Document 2) to consider additional insights and implications, as well as describe a control experiment to investigate whether the aeolian processes affected the viability of the propagules as they were dislodged and transported.

2. Materials and methods

We prepared propagule-bearing soil surfaces mimicking natural wetland conditions, then subjected them to saltation in a wind tunnel to assess wind erosion and transport of the propagules. We applied resurrection ecology methods to propagules collected in the tunnel to determine survival after experiencing energetic aeolian processes. The aim was to better understand how wind disperses aquatic invertebrate propagules in ephemeral aquatic systems. Some experimental methods were previously summarized in Rivas et al. (2018; primarily in Supplemental Document S2.2). A fuller description of the methods and the wind tunnel is provided in Appendix A (Supplementary Information) of this publication.

We used a laboratory-scale suction-type wind tunnel designed and widely used for simulation of wind erosion of soil surfaces (Van Pelt et al., 2009; Khatei et al., 2024) at the United States Department of Agriculture- Agricultural Research Service (USDA-ARS) Big Spring Field Station, Big Spring, Texas. The experiment simulated saltation-forced wind detachment of desiccated wetland soil aggregates from the soil surface, aeolian dust/sand generation and transport, and downwind deposition of particles and aggregates containing aquatic invertebrate propagules; thus, it investigated the effects of the saltation-abrasion process, typifying wind erosion in nature, on the entrained propagules, which were then tested for viability.

Diapausing stages (propagules) were obtained of seven species of aquatic invertebrates: Tadpole shrimp (*Triops longicaudatus* (LeConte, 1846)), water fleas (*Daphnia* sp., whose ephippia contain two embryos each), clam shrimp (*Eulimnadia texana* (Packard, 1871)), red-tail fairy shrimp (*Streptocephalus* sp.), brine shrimp (*Artemia salina* (Linnaeus, 1758)), and two rotifer species (*Brachionus plicatilis* (Müller, 1786) and *B. calyciflorus* (Pallas, 1776)). Propagules were obtained from commercial sources (see Table S1 in Appendix A). Due the large number of propagules needed for the wind tunnel experiments, it was not feasible to harvest them ourselves directly from natural playas. The commercial propagules of branchiopods (*Daphnia*, clam shrimp, fairy shrimp, tadpole shrimp) obtained are from playas/ephemeral wetlands in Arizona, and the species present likely overlap with those in the Chihuahuan Desert. The rotifer propagules we used are the only two species that are commercially available in large numbers. *Brachionus plicatilis* is frequent in saline playas in the Chihuahuan Desert while *B. calyciflorus* is found in some freshwater playas (see data repositories for Brown et al., 2020, 2022). Average propagule size was determined before wind tunnel exposure by measuring 20 propagules from each of the seven species using a Zeiss Axioscope equipped with a SPOT camera and SPOT imaging software v 5.0 (Table 1).

Twenty-one artificial soil surfaces in trays for placement in the wind tunnel (Fig. 1A.) were assembled at the Big Spring Field Station. The soil

Table 1
The approximate number of propagules of each taxon added to the soil pans used in the wind tunnel experiments, and their size.

Aquatic Invertebrates	Propagules (#/kg of soil)	Propagule size (μm) Mean ± SD
Artemia salina (brine shrimp)	2,000	221 ± 15.2
Eulimnadia texana (clam shrimp)	100	121 ± 10.7
Triops longicaudatus (tadpole shrimp)	100	376 ± 20.5
Daphnia sp. (water flea)	100	1285 ± 148.5
Streptocephalus sp. (Redtail Fairy Shrimp)	1,500	239 ± 22.7
Brachionus plicatilis (brackish water rotifer)	20,000	92 ± 10.1
Brachionus calyciflorus (freshwater rotifer)	10,000	123 ± 18.7

used for all trays was Pullman clay loam (fine, mixed, superactive, thermic Torrertic Paleustolls), which commonly occurs on the edges of natural playas and wind-erodible surfaces in the semiarid Southern High Plains of Texas (Van Pelt et al., 2017) and has been used for wind tunnel tests of soil erosion by wind abrasion (Tatarko et al., 2020). The soil tray surfaces had polygonal crusts simulating playa soil surface structure (Nelson et al., 1983) (Fig. 1B.), and each tray had a specific number of propagules of a given species (Table 1) mixed into the top 2 mm of soil.

Three replicate soil pans containing propagules from each species were included in each run of the wind tunnel, operated at 10 ms^{-1} centerline wind speed for 30 min. Quartz sand, necessary for saltation which bombards and dislodges material from the soil surface into the air, preferentially generating airborne particles along the edges of playas (e.g., Lee et al., 2009), metered from a hopper attached to the upwind end of the wind tunnel, acted as the supply of abrader material to saltate on the crusted simulated playa soil surfaces.

Entrained aeolian sediment was collected from within the wind tunnel after each run at three downstream locations in the instrument's aspirated sampling system: 1) a transfer section for coarse sediment, 2) a settling chamber for finer saltation-sized sediment, and 3) two borosilicate glass microfiber paper filters (HI-Q Environmental Products Company, Part No. FP2061-810), for suspension-sized sediment. These three sections represent analogs of environmental dust/sand transport distances from source areas downwind in meters (transfer section), tens of meters (settling chamber), and hundreds to thousands of meters (paper filters), respectively (Hagen et al., 2007). Each section of the wind tunnel was cleaned with pressurized air prior to each run.

A second wind tunnel experiment was conducted solely to investigate dispersal of the propagules throughout the wind tunnel sections and examine a labeling technique that could be useful for future experiments. For this experiment, propagules of the same taxa were coated with a colored non-toxic fluorescent solution derived from commercial multicolor office highlighter markers, allowed to dry, and quantified using a UV light prior to rehydration (Fig. 2). The procedures were the same as described in the first experiment with a soil pan with propagules of *Brachionus plicatilis and B. calyciflorus* mixed together, a pan with *Eulimnadia texana* only propagules, and a mixed replicate consisting of propagules of all seven species mixed together with the soil in one pan. Collected windblown propagule-bearing sediment was brought to the University of Texas at El Paso (UTEP) for subsequent analyses.

Particle size analysis by laser diffraction was performed on small subsamples of the material collected from each section of the wind tunnel from each of the two experiments (for details see Appendix A (Supplementary Information)). The purpose of these analyses was to verify dry aggregate size reduction of the soil transported downstream through the wind tunnel system, as should be observed in natural aeolian processes (Hagen et al., 2007). Sediment recovered from within the wind tunnel was sieved using a U.S.A. Standard Testing Sieve to remove most of the abrader sand, but to allow propagules to remain in the transported soil for rehydration. Because *Daphnia* sp. propagules were larger than the sieve opening, they were physically picked out of the sieve and added back to the wind-transported soil. Due to the size variation of *Triops* propagules (329 μm – 422 μm), two sieves were used to remove propagules. Samples were then divided into 10 subsamples for each wind tunnel experiment; three subsamples of collected material from the transfer section, five subsamples for the settling chamber, and one subsample from each of the two filters.

Approximately 1.75–2.50 g of each subsample recovered from each section of the wind tunnel was rehydrated to document hatching and thus determine viability of propagules of each species. A control experiment was performed to examine the hatching rate of propagules

Fig. 1B. Polygonal crust formation of Pullman soil that occurred after wetting soil with distilled water and allowing it to dry.

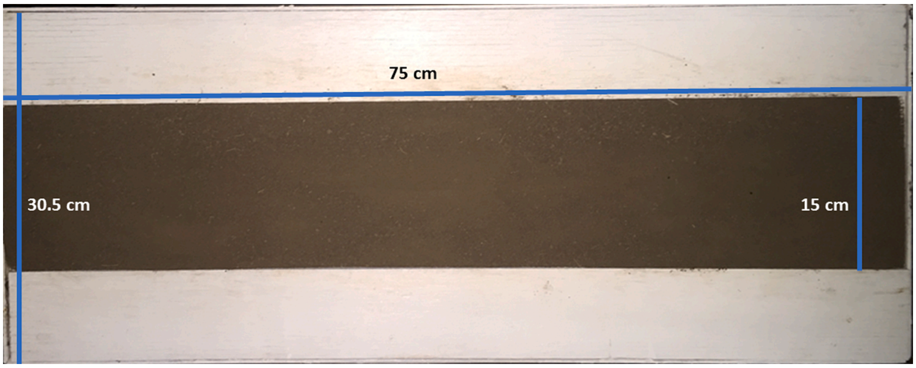

Fig. 1A. Example of a soil tray used in the wind tunnel experiments. Tray dimensions are shown and the tray depth was about 1.6 cm. Approximately 1 kg of sterilized soil was added to this area.

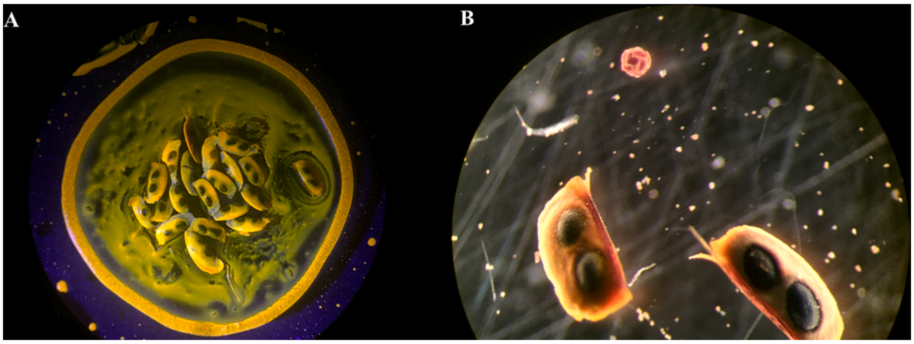

Fig. 2. Example of fluorescent coating of *Daphnia* propagules shown under UV light (a) prior to transport through wind tunnel, (b) after collection from sediments transported. A *Streptocephalus* propagule (pink) is also shown.

that were not subjected to aeolian transport, to determine whether passing through the wind tunnel (simulated dust event) resulted in lower viability of diapausing stages. For details of rehydration/ hatching rate experiments, see Appendix A (Supplementary Information).

3. Results

3.1. Wind tunnel testing and rehydration experiment

Results of initial wind tunnel and rehydration experiments, not including the control experiment, were provided in Supplemental Document S2 and Table S2 in Rivas et al. (2018). Full results are presented in Tables 2-6 and summarized in this section.

Wind-eroded sediment and propagules of all seven taxa tested were transported to and recovered from all sections of the wind tunnel sampling system. In the first experiment, viability after wind tunnel transport was confirmed in five of the seven species: *A. salina*, *T. longicaudatus*, *E. texana*, *Streptocephalus* sp., and *Daphnia* sp. Propagules of *Brachionus plicatilis* or *B. calyciflorus* collected in any part of the wind tunnel in the first experiment all proved unviable. It is possible that the diapausing embryos of the rotifers used in the first experiment were no longer viable when purchased. In the second experiment, in which propagules of the same seven species (including a new supply of the rotifer species) were fluorescently labeled, we recovered viable propagules of all taxa in each section of the wind tunnel (Table 2).

The percentage of propagules present in each section of the sediment sampling system for the first rehydration was also calculated (Table 3). For *Brachionus plicatilis* and *B. calyciflorus,* propagule counts were from the second experiment only due to their lack of viability in the first experiment. Most propagules of all taxa were found in the settling chamber (equivalent to ambient wind transport of tens of meters); however, propagules of *Artemia salina* and *Triops longicaudatus* had high percentages of propagules in the transfer section, representing short distance ambient aeolian transport (meters) (see Tables 3 and 4). No viable organisms were found in the rehydrated abrader sand, confirming that it did not provide any contaminating propagules. Table 4 shows the results from the second experiment, which contained a pan with clam shrimp propagules, two more pans with *Brachionus plicatilis* and *B. calyciflorus* propagules, and a mixed treatment pan where propagules of all species were combined together. As in the first experiment, most of the propagules were found in the settling chamber.

Table 2
Number of transported but unviable propagules [], hatched organisms (), and total dispersers (hatched organisms + unviable propagules) {} recovered in the different sections of the wind tunnel for both experiments. Viable rotifers were counted as adults and nauplii for the other taxa. For the mixed treatment, rotifer diapausing embryo counts were for both species considered together. (Modified from Rivas et al. 2018, Supplemental Document S2.2).

	Wind tunnel sections			
Taxa	Transfer Section	Settling Chamber	Filter Section	Total Transported
B. plicatilis[2]	[39] (46)	[266] (309)	[78] (56)	[383] (411) {794}
Eulimnadia texana[1]	[24] (4)	[509] (72)	[44] (12)	[577] (88) {665}
B. calyciflorus[2]	[5] (1)	[21] (5)	[5] (2)	[31] (8) {39}
Artemia salina [1]	[1655] (1173)	[15885] (6228)	[1761] (20)	[19,301] (7421) {26,722}
Streptocephalus sp. [1]	[1164] (249)	[11,501] (7133)	[5699] (384)	[18,364] (7766) {26,130}
Triops longicaudatus [1]	[3] (0)	[15] (2)	[2] (0)	[20] (2) {22}
Daphnia sp.[1]	[4] (0)	[131] (6)	[0] (0)	[135] (6) {141}
Mixed Treatment[2]				
FS = *Streptocephalus* sp.	[2] (1) E	[5] (1) E	[2] (1) E	[9] (3) {12} E
TS = *Triops longicaudatus*	[2] (0) BS	[24] (2) BS	[0] (0) BS	[26] (2) {28} BS
BS = *Artemia salina*	[5] (0) FS	[22] (2) FS	[11] (0) FS	[38] (2) {40} FS
DE = *B. calyciflorus* and *B. plicatilis* diapausing embryo	[2] (0) DE	[13] (0) DE	[3] (0) DE	[18] (0) {18} DE
E = *Daphnia* ephippia	[0] (1) TS	[3] (1) TS	[0] (0) TS	[3] (2) {5} TS
CS = *Eulimnadia texana*	12 CS	28 CS	4 CS	44 CS

[1] Results from the first experiment for each pan which had propagules from one taxon incorporated into the soil.

[2] Results from the second experiment which included *B. plicatilis* and *B. calyciflorus* only pans. In addition, pans with propagules from all taxa mixed in the soil (mixed treatment) were run.

3.2. Control experiment

In all cases, large numbers of individuals hatched from diapausing propagules in the control experiment (Table 5). It should be noted that in some cases the number of hatchlings exceeded the apparent number of eggs rehydrated. This is likely a result of the manufacturer providing excess propagules to compensate for any that were not viable and/or because the eggs are relatively small and difficult to accurately count. In addition, the large brachiopod eggs and *Daphnia* ephippia were likely difficult to separate from sediment as they were packaged with a small amount of playa sediment. The low rate of hatching of brine shrimp may be due to the relatively low salinity of BPM/2 as opposed to the concentration given by the manufacturer for optimal hatching success. Nonetheless, substantially higher rates of hatching were observed for those propagules that were not transported through the wind tunnel when compared to the low hatching success of the abraded, wind-transported propagules, indicating that aeolian processes, particularly sandblasting, render a large percentage of propagules unviable.

Table 3
Percentage of total dispersers (unviable propagules + hatched organisms) collected in each section of the wind tunnel from Experiment 1.

	Transfer section	Settling chamber	Filter section	Total dispersers
Eulimnadia texana	4.2	87.4	8.4	665
Artemia salina	10.6	82.7	6.6	26,722
Streptocephalus sp.	5.4	71.3	23.3	26,130
Triops longicaudatus	13.6	77.3	9.1	22
Daphnia sp.	3.0	97.0	0	202

Table 4
Percentage of propagules and viable taxa collected from the mixed pan treatment in Experiment 2. An additional pan consisting of rotifer diapausing embryos from both species were combined in a separate treatment (shown as bottom row).

	Transfer section	Settling chamber	Filter section	Total dispersers
B. plicatilis	10.7	72.4	16.8	768
B. calyciflorus	15.3	66.6	17.9	39
Artemia salina	7.1	92.8	0	28
Streptocephalus sp.	12.5	60.0	27.5	40
Triops longicaudatus	20.0	80.0	0	5
Eulimnadia texana	27.2	63.6	9.0	44
Daphnia sp.	25.0	50.0	25.0	12
B. plicatilis + *B. calyciflorus*	11.1	72.2	16.7	18

Table 5
Hatching success of diapausing eggs that were not subjected to the wind tunnel procedure.

Species	Replicates	Number of diapausing eggs[*]	Number of live offspring (Mean ± SD)	Number of dead or partially hatched offspring (Mean ± SD)
Brachionus calyciflorus	6	1,000 to 1,667	943.7 ± 586.1	–
Brachionus plicatilis	4	1,000 to 1,667	684.0 ± 375.1	–
Fairy shrimp	4	1 g	2636 ± 859.8	–
Clam shrimp	4	25	158.3 ± 26.2	9.8 ± 6.4
Tadpole shrimp	6	20	16.5 ± 6.4	0.5 ± 0.5
Brine shrimp	3	>200,000	1316.7 ± 132.1	–
Daphnia sp.	6	100	85.8 ± 29.5	–

[*] Number of eggs according to the supplier. *Daphnia* ephippia contain two embryos each.

Table 6
Undispersed dry aggregate textural analysis for material recovered from each section of the wind tunnel. Sediments collected from transfer section, settling chamber, and the filter section were analyzed after transport through the wind tunnel section. Also shown is the mean dry aggregate size for the Pullman soil. Numbers are percentages in each USDA soil texture class, with the exception of the mean aggregate size values.

Dry Aggregate Size	<2 μm	2–50 μm	>50 μm	Grain Size Mean ± SD (μm)
Transfer section	0	5	95	463 ± 6
Settling Chamber	0	12	88	184 ± 7
Filter section	2	48	50	53 ± 6
Pullman soil	0	9	91	463 ± 6

3.3. Grain size analysis

Particle size analysis of soil aggregates from each section of the wind tunnel sampling system indicated a decrease in aggregate size downstream (downwind) through each sequential section of the wind tunnel. This is consistent with the expected decrease in aggregate size (increase in proportion of clay and silt sized aggregates via breakdown through saltation bombardment) with increasing distance of wind transport (Anderson et al., 1991; Avecilla et al., 2018), indicating that the wind tunnel experiments realistically simulated ambient aeolian transport. Dry aggregate size measurement indicated that aggregate size fractions in the transfer section were 0 % <2 μm (clay sized aggregates), 5 % between 2 and 50 μm (silt sized aggregates), and 95 % > 50 μm (sand sized aggregates). Dry aggregate size fractions from the settling chamber were 0 % clay, 12 % silt, and 88 % sand. Filter section results indicated 2 % clay, 48 % silt and 50 % sand. The abrader sand used as the supply of material for saltation onto the propagule-bearing experimental dry playa surfaces had a mean grain size of 512 μm, larger than the size of propagules except for those of *Daphnia* (so that the sand could be sieved out of the windblown sediment, leaving the windblown soil from the tray and the propagules), consistent with measured grain size of material available for saltation in Chihuahuan Desert playas (Klose et al., 2019). The Pullman clay loam soil mean dry aggregate size prior to running through the wind tunnel was 460 μm (19 μm wet-dispersed particle diameter)(see Table 6). The Pullman soil aggregates in the transfer section were essentially not broken down from their original dry aggregate size; but by the time they reached the filter section downstream the mean dry aggregate size was approximately an order of magnitude smaller, with some clay-sized (<2μm) grains present, again consistent with wind erosion and transport in the ambient air.

4. Discussion

4.1. Viability of propagules

In at least one experiment, viable propagules of all seven species of aquatic invertebrates were successfully transported along with aeolian (windblown) sediment to all sections of the laboratory wind tunnel in a 10 ms^{-1} wind with abrading saltating sand, analogous to soil wind transport in ambient air for meters to kilometers. Mean grain size of dry aggregates deposited in the transfer, settling chamber, and filter sections sequentially downstream in the wind tunnel decreased from 483 μm to 184 μm to 53 μm, and the grain size of the transported sediments fell within the size ranges of the propagules of the different taxa. Thus, these experimental results in the laboratory are a reasonable replication of the saltation-sandblasting driven dust emission process in nature (Hagen et al., 2007) and indicate that invertebrate propagules can be injected into the atmosphere by saltating sands abrading dried ephemeral wetland soil surfaces in which they are embedded and travel short to long distances (meters to potentially many kilometers) downwind, while remaining viable. The kinetic impacts of saltating (bouncing) sand grains, sufficiently energetic to sandblast sediments and propagules out of crusted playa surfaces, reduced the viability of the diapausing stages, but did not render all the propagules unviable.

Viability of propagules recovered from wind tunnel transport ranged from ∼ 4 % (*Daphnia*) to ∼ 52 % (*B. plicatilis* in experiment 2); most viable taxa collected fell between the two (Table 2). Hairston et al. (1995) found viability ranging from ∼ 10—50 % of copepods in egg banks from freshwater lakes, and Garcia-Roger et al. (2006) found approximately 50 % viability in *B. plicatilis* eggs collected from egg banks in ponds in Spain. However, other studies have observed higher hatching rates from resting stages in egg banks: Hulsmans et al. (2006)

observed up to an 85 % hatching rate from the fairy shrimp *Phallocryptus spinosa* (Milne-Edwards, 1840) dormant eggs in Sua Pan sediments from Botswana, Brede et al. (2007) found hatching rates up to 80 % for *Daphnia* rehydrated from various egg banks, and Allen (2010) found up to 90 % hatching rate in *Daphnia* dormant eggs from ponds in the midwestern USA. Thus, the viability of propagules having undergone aeolian transport appears to be somewhat lower than those remaining in egg banks.

4.2. Implications of propagule size, shape and location

Propagules of smaller size (< ~250 μm) (e.g., *Brachionus*, *Eulimnadia, Artemia, Streptocephalus*) – equivalent to the diameter of fine sand grains- were more likely to be collected in the settling chamber and filter section, representing medium to long transport distances and thus higher potential to disperse into a different basin. In the first experiment, the largest propagules, *Triops longicaudatus* and *Daphnia,* were preferentially recovered from the transfer section or settling chamber, representing short to medium dispersal distances. In the second experiment, *Artemia salina* and *Streptocephalus* propagules were collected in larger numbers in the settling chamber, and propagules of *Triops longicaudatus* were transported to the transfer and settling chamber sections only. However, in the second experiment some *Daphnia* propagules were recovered from the filter section, suggesting the potential for longer-distance dispersal. According to Cohen & Shurin (2003), aquatic invertebrates are fast dispersers over short distances, consistent with collection of most of the propagules in the settling chamber (representing tens of meters of dispersal). However, even short distance anemochory may be consequential for dispersal if, for example, it crosses a drainage divide, as was suggested for *Triops* by Ridings et al. (2010).

Aquatic invertebrate propagules are much lower in density and higher in sphericity than sand grains of equivalent size, and thus more aerodynamic and likely to be more easily entrained by the wind, injected higher into the atmosphere, and transported farther than mineral aerosols. Wind tunnel experiments by Iturri et al. (2017) showed that the lower-density organic components of soil were preferentially carried at greater heights and would be mixed higher in the atmosphere under aeolian transport (and thus be more likely to be transported greater distances downwind than the mineral component of soil). Thus, our extrapolations of environmental transport distances of propagules from these wind tunnel tests may represent lower bounds.

In our investigations, soil particles and propagules were eroded from a crusted surface of a typical playa wetland soil (with propagules embedded into naturally-desiccated soil peds, simulating a propagule bank) and ejected into the air by saltation bombardment, which is the principal mechanism for the natural entrainment of aeolian sediment (Shao et al., 1993), including on playa surfaces (Baddock et al., 2011). Meiobenthic organisms such as bdelloid rotifers and gastrotrichs preferentially colonize sandy sediment layers near the ground surface (Ricci and Balsamo, 2000), thus these organisms and their propagules would tend to initiate their anemochory journey within a cloud of saltating sand-sized grains and must survive this energetic process to disperse successfully.

4.3. Constraints on laboratory testing and representation of wind erosion mechanisms

Wind tunnels are physical models that replicate the processes involved in wind erosion and transport. As such, they do have limitations including lack of wind gustiness and issues of fluid flow and turbulent interaction scaling between laboratory and nature (Bauer et al., 2004; Bauer, 2009). Nevertheless, wind tunnel experiments have revealed a great deal about the mechanics of aeolian transport (Bauer, 2009), with the fundamental processes including saltation and suspension being the same in the wind tunnel and in nature. In our experiment, the saltation cloud in the wind tunnel abraded the soil and propagules in the trays and emitted dust and propagules into the free air stream such that they could be found in all sections of the sediment recovery system. Coupled with the finding of viable propagules in clouds of windblown sand and dust far above the surface (Rivas et al., 2018, 2019), these wind tunnel observations provide agreement with field data indicating that viable propagules can be transported various distances in the atmosphere.

Wind tunnels provide an ideal experimental method to study aeolian processes (Bauer et al., 2004; Bauer et al., 2009; Gardner et al., 2012; Avecilla et al., 2018; Marston et al., 2020; Khatei et al., 2024) and anemochory (Graham & Wirth, 2008; Parekh et al., 2014; Pinceel et al., 2016, 2020; Arenas-Sánchez et al., 2024). However, care must be used to consider the design of the wind tunnel and experiment in consideration of the mode of wind transport being simulated. Factors include reproduction of the flow processes causing natural wind erosion (Raupach and Leys, 1990), development of a wind profile similar to that in nature, and realistic dispersion of suspended sediment (Raupach and Leys, 1990; Sweeney et al., 2008). Only a few prior wind tunnel anemochory studies have used aquatic invertebrate propagules as the tested material, and of the published descriptions of the wind tunnels and experimental setups suggest that none of them simulated the saltation-sandblasting process, nor does it appear that prior investigations analyzed the sediments transported along with the propagules to confirm results consistent with ambient aeolian transport of sand and dust, or investigated the viability of the wind-transported propagules after transport was completed.

The wind tunnel systems and sample preparation techniques of prior published wind tunnel propagule anemochory experiments simulated the physical process of “direct aerodynamic entrainment”, the lifting of materials sitting freely on the land surface without saltation. Direct aerodynamic entrainment is locally important as a process of aeolian sediment emission (Parajuli et al., 2016), but saltation bombardment is the globally dominant mechanism (Shao et al., 1993). Surfaces of playas are generally crusted, direct aerodynamic entrainment is limited due to the lack of loose particles, and saltation bombardment is required for significant emission of dust and sand into the air (Baddock et al., 2011; Tan et al., 2023). Pinceel et al. (2020) reported that in their experiments (without saltation), “few eggs were picked up when the egg bank (embedded into soil) was dry prior to exposure, even at winds of 70 km h^{-1}.” On the other hand, our experiments showed sand saltating in winds of half that velocity would naturally abrade the crusted surface and release large amounts of dust, sand. and propagules.

4.4. Ecological and management implications

Resting stages of *Triops longicaudatus*, one of the species evaluated, are resistant to at least low-intensity fire sweeping across dry grassy playa basins (Bright et al., 2016). After a fire in such an environment, the underlying soil surface becomes exposed and the playa basin often becomes increasingly susceptible to wind erosion for some months until the vegetative cover is re-established (Stout, 2012). Thus, resting stages of playa invertebrates that survive fire will be more exposed to potential wind dispersal.

Triops longicaudatus may become an agricultural pest, if it enters fields of wetland crops such as rice (Grigarick, 1984), and *Eulimnadia* has been described as a pest in aquaculture facilities (Luzier and Summerfelt, 1996). Rotifers have dispersed into outdoor algal biomass production facilities and decreased algal yields (Day, 2013: Thomas et al., 2017). The potential of propagules of these species to be viably dispersed at least short distances (such as across a levee or subtle drainage divide) by the wind has implications to intensively used river basins (such as anemochory to or from floodplains) and agricultural lands and human settlements downwind of playas in arid zones. Anemochory of wetland species such as these would also be possible during dry spells in non-desert regions with more intensive land use, such as the agriculture-dominated midwestern North America (with its numerous prairie potholes, playas, and floodplains) and coastal and valley environments downwind of rice fields. For example, the eastward spread of *Triops* into the USA states of Missouri and Illinois (Tindall et al., 2009; Ridings et al., 2010) was hypothesized to occur in part through anemochory across levees from river floodplains (Ridings et al., 2010).

4.5. Suggestions for future research

In our experiments, all propagules were fixed to the same soil with the same surface structure. However, different physical textures, structures, and chemical compositions of ephemeral wetland soil surfaces have different abilities to be transported by the wind (Glennie, 1987). For example, Sweeney et al. (2016) observed that mud aggregates at Yellow Lake, Texas produced 2–3 orders of magnitude more airborne dust than typical playa sediments when eroded in a field wind tunnel. Any taxa whose propagules are preferentially contained in or affixed to such extremely wind-transportable sediments might be preferentially adapted for anemochory. Thus, future field investigations should determine whether egg banks of some taxa are preferentially located in sedimentary environments and structures with the highest (or lowest) wind erosion potential, and future wind-tunnel tests could quantify rates of wind entrainment and post-transport viability of taxa bound to different sediment types and substrates. Future wind tunnel experiments could also evaluate the roles of different soil types, soil conditions (soil moisture, extent and strength of crusting, saltating particle grain size, etc.), and different wind speeds on the ability of propagules to be transported by the wind and survive that transport.

The experiments of Elliott et al. (2019) on soil microbes led them to hypothesize that some taxa are particularly adapted for dispersal by wind and preferentially air-entrained, being primary colonizers of newly exposed niches and possessing structures and morphologies to facilitate and prolong anemochory. Angiosperm seeds with a low weight /volume ratio and an aerodynamic structure are believed to be selected for buoyancy and enhanced wind dispersal (Leake, 1994). In addition, microbial taxa possess adaptations to resist airborne desiccation and radiation (Makarova et al., 2001), and fungal spores with such adaptations dominate samples collected from the air (Al-Subai, 2002). Given the field and mechanistic evidence of invertebrate propagule anemochory, such adaptations for aerial dispersion should be investigated for aquatic invertebrate propagules of ephemeral wetlands.

Pinceel et al. (2016) and Meyer-Milne et al. (2021) suggested that anemochory would be correlated to propagule morphology and size. In our experiments, taxa with smaller propagules were more likely to be transported to the further-downstream reaches of the wind tunnel, suggesting that travel distances via anemochory resulting from saltation-sandblasting are inversely correlated with propagule diameter. However, Arenas-Sánchez et al. (2024) observed that larger propagules were aerodynamically entrained to a greater extent than those of the smaller one. In addition to size, propagule shapes, densities, and ornamentations vary between taxa: these variations have been suggested to modulate their aerodynamic diameters, affecting their propensity to disperse by the wind and/or their relative distance of dispersal (Jenkins et al., 2007; Brendonck et al., 2017; Iturri et al., 2017; Pinceel et al., 2020). Additional controlled saltation wind tunnel experiments on propagules with different morphologies, densities, dimensions, ornamentations, and adhesion tendencies could shed light on whether they might represent adaptations to anemochory and, when combined with numerical modeling of wind flow, help quantify potential dispersal distances.

5. Conclusions

Our wind tunnel experiments provided evidence that propagules of various aquatic invertebrates embedded within dry, crusted soil surfaces can be injected into the atmosphere by the energetic saltation / bombardment mechanism- the dominant process of wind erosion of ephemeral wetland sediments- and some will remain viable after transport. Propagule viability after experimental anemochory was lower than that of undisturbed egg banks, but viable individuals of all tested species were found after saltation wind tunnel testing. Aeolian transport (anemochory) of aquatic invertebrates is thus shown to be a physically feasible pathway for successful movement to new habitats, potentially helping explain observed downwind dispersal of some species (Ridings et al., 2010; Sives, 2024) and providing additional insights on wind transport of organisms from desiccated wetlands. Direct aerodynamic entrainment of propagules into the atmosphere, which prior wind tunnel experiments simulated, certainly occurs, but is likely a minor component of dispersal by anemochory, since it would require propagules resting loosely atop wetland surfaces with minimal cohesion.

Tesson et al. (2015) pointed out that it is much easier to sample organisms or descendants after they have dispersed than to monitor them during dispersal, calling for collaborations between biologists, atmospheric scientists and modelers to “clarify the role of wind dispersal for macroorganisms – for example, how far can zooplankton propagules of different sizes be dispersed by this means?” We believe that our experiments begin to close this gap and hope that they will inspire others to more vigorously pursue follow-up investigations.

Disclaimers

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CRediT authorship contribution statement

Jose A. Rivas: Methodology, Investigation, Visualization, Formal analysis, Writing – original draft, Writing – review & editing. **R. Scott Van Pelt:** Supervision, Investigation, Methodology, Conceptualization, Visualization, Validation, Resources, Writing – review & editing. **Elizabeth J. Walsh:** Conceptualization, Investigation, Methodology, Supervision, Funding acquisition, Writing – review & editing, Resources, Project administration. **Thomas E. Gill:** Conceptualization, Methodology, Resources, Supervision, Funding acquisition, Project administration, Writing – review & editing.

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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 material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2024.108560.

Data availability

Data used for this study not otherwise listed in this publication or in Appendix A (Supplementary Information) are available at the UTEP Bioinformatics Data Repository at https://datarepo.bioinformatics.utep.edu/getdata?acc=ACIEJDV41U1ZN5I.

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