Active Aerial Dispersal of Minute Wingless Arthropods: Exploitation of Boundary-Layer Velocity Gradients

Abstract. *The wingless first instars of the coccid* Pulvinariella mesembryanthemi *exhibit active aerial dispersal behavior by standing on their hind legs. This behavior is an age-specific response to the ambient wind velocity by which the instars are able to capitalize on air velocity gradients in the thin boundary layer surrounding the host plant substrate. This dispersal tactic may be a convergent evolutionary strategy for many minute terrestrial arthropods.*

Dispersal of living organisms results in the expansion of the range and distribution of species through colonization of new habitats and reduction in the risk of extinction from local, catastrophic events. For insects, the evolutionary development of functional wings greatly expanded their ability to disperse and dominate terrestrial habitats (*1*). Despite the absence of functional wings in immature insects and other arthropods, some still effectively disperse by wind. Examples include ballooning spiders and many first instar lepidoptera that use silk threads for dispersal. Others include small mites and scale insects (length $\leq$ 1 mm) whose presence in the aerial plankton is well documented (*2*, *3*).

We describe aerial dispersal behavior of the exotic ice plant scale, *Pulvinariella mesembryanthemi* (Homoptera: superfamily Coccoidea), an Old World coccid recently introduced into California (*4*), showing it to be an age-specific response to airstreams in which boundary-layer velocity gradients are used to become airborne.

Scale insects are economically important herbivores with worldwide distribution. Only the short-lived and fragile males possess wings, but they alone are unable to disperse and colonize new habitats. Instead, many scales disperse by wind during the first instar or crawler stage (*3*), and once they establish a feeding site on a host they display little tendency to move (*5*). Although aerial dispersal of scales is well documented, little is known of how crawlers enter the air column. Other investigators have suggested that crawlers are accidentally detached from their host plants (*6*), but our observations indicate that scales deliberately enter the air.

Pulvinariella mesembryanthemi reproduces parthenogenetically with each female producing up to 2400 crawlers. The progeny are minute (mean length, 0.41 mm, N = 50) and can live up to 8 days without feeding. We tested *P. mesembryanthemi* crawlers in a wind tunnel where dispersal behavior could be observed through a stereomicroscope (magnification, ×6 to ×50). To determine orientation of crawlers in an airstream, wind speeds at which dispersal occurs, and age at which crawlers disperse, individual crawlers were placed on a circular, horizontal arena (2 cm in diameter) on the stage of the microscope, and exposed to a stream of air (*7*).

Randomly chosen crawlers from 1 to 5 days old were tested first, and each was observed while the airstream across the arena was gradually increased from 0 to 4 m/sec. For each animal we recorded movement, orientation to the wind, and the speed at which dispersal behavior, if it occurred, began. While searching for a feeding site, crawlers walked about and periodically tapped the substrate with their antennae. Before dispersing crawlers lifted their antennae above the dorsum of the body and rotated laterally to face downwind; 92 percent (N = 88) of responsive crawlers oriented to within 10° of facing directly downwind. They then lifted the prothoracic legs and anterior of the body above the substrate, arched backward, and supported the body with the meso- and metathoracic legs (Fig. 1). Some crawlers lifted both the pro- and mesothoracic legs, supporting themselves only on the metathoracic legs. In this standing posture the longitudinal axis of the crawler body was 45° to 90° to the substrate, and this posture was held until they were blown from the arena. If the airstream was reduced or removed, crawlers remained standing and rotated for as long as 50 seconds. Individual crawlers exhibited dispersal behavior in airstreams from 1.8 to 4.0 m/sec (mean, 3.7 ± 0.4 m/sec; N = 20), but many were unaffected by currents as high as 4 m/sec and did not show systematic orientation to the wind.

We tested responses of crawlers of varying ages (*8*), reasoning that the youngest crawlers would not exhibit wind dispersal behavior because the probability of settling on a suitable host plant is low. Rather, they should initially search for feeding sites since, under natural conditions, crawlers hatch on plants that provide the requisites for successful development of their parent. The age at which unfed crawlers showed dispersal behavior (mean, 76 hours; N = 18) was greater than crawlers without dispersal behavior [mean, 40 hours; N = 40; $P < 0.005$; $t(56) = 4.59$]. Animals (N = 8) tested for several days became progressively responsive to airstreams.

Because of their small size, crawlers are rapidly embedded in the laminar

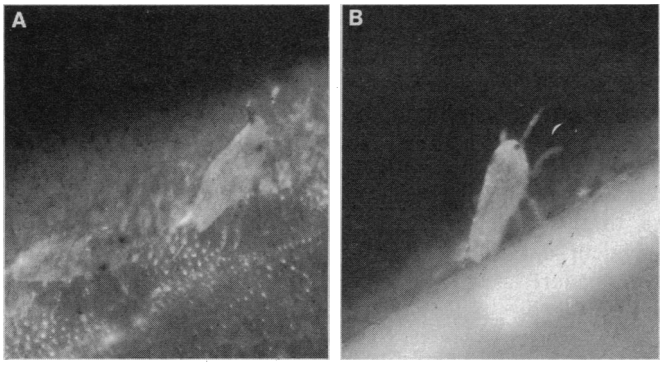

Fig. 1. Crawlers of *P. mesembryanthemi* on leaves of *Carpobrotus aequalateris*. (A) Walking (left) and standing (right) postures of crawlers are shown near leaf edge (×56). (B) Typical upright dispersal posture showing the position of antennae and prothoracic legs (×56).

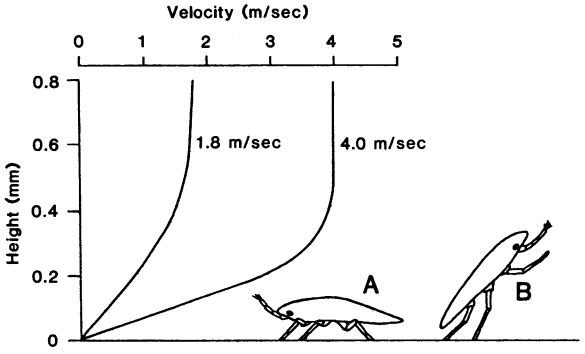

Fig. 2. Vertical velocity profiles for two free stream velocities 2.0 mm (five body lengths) from the leading edge of a flat plate and scaled illustrations of *P. mesembryanthemi* in (A) walking and (B) standing postures.

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boundary layer formed at the leading edge of the plant substrate. We estimated velocity profiles within this boundary layer by the Blasius solution (*9*) for free stream velocities of 1.8 and 4.0 m/sec (see Fig. 2). At the lowest free stream velocity for which dispersal was observed (1.80 m/sec) the velocity distribution is approximately linear over the standing height of the crawlers (0.34 mm). At positions further from the leading edge, the velocity profile over the standing height of the crawlers becomes more precisely linear as the boundary layer thickens. At the points in the boundary layer occupied by the crawlers, the vertical velocity gradient is largest, and changes in the vertical extent of the crawlers produce large increases in the range of velocities experienced. At a free stream velocity of 4.0 m/sec the crawlers extend well above the nearly linear region of the velocity profile. This situation would also occur at 1.8 m/sec if the crawlers were closer to the leading edge of the plant substrate.

Crawlers in the dispersal posture experience more drag than those in walking posture because of the greater fluid momentum higher in the boundary layer. We calculated Reynolds numbers for both the standing and walking postures from the average velocity over the height of the crawlers for the two positions (*10*). The Reynolds numbers for walking and standing crawlers are 6 and 15, respectively, for a free stream velocity of 1.80 m/sec. The drag coefficient (C_d) in this range of Reynolds numbers must be determined by observation and numerical simulation (*11*). For spheres in this Reynolds number range approximate results are available. White (*12*) gives an empirical relation for the variation of C_d with the Reynolds number; over the range 6 to 15 the total drag increases by a factor of about 3.5 for small spheres. We interpret this as a lower bound for the actual increase in drag force on the crawlers between the walking and standing postures because (i) the cross-sectional area of the crawlers is roughly doubled while standing, and (ii) the legs and antennae are extended while standing.

To become airborne a crawler apparently must generate enough drag to tear its tarsi from the substrate. During our experiments some crawlers dangled by a single tarsus and were unable to release. Crawlers are exposed to much lower drag forces while walking and are thus unlikely to be accidentally blown off the substrate as has been suggested (*6*). It is not clear why crawlers consistently adopt a standing posture with the dorsal side upwind. Possibly the drag coefficient is higher in this range of Reynolds number, or tarsal detachment from the substrate may be easier if the animal faces downwind.

Before dispersing, crawlers move up the plant (*13*). This moves the take-off point higher into the turbulent planetary boundary layer in which the plant is embedded and aids in the vertical entrainment of the crawlers into the air column. We have captured crawlers on sticky traps at heights of 50 m indicating that this vertical, turbulent entrainment can be very effective.

Once airborne, crawlers arch backward and extend their legs and antennae outward. We determined the terminal velocities of freshly killed and live crawlers and found that this posture decreases the average terminal velocity of live crawlers in comparison with dead ones from 32.7 to 26.2 cm/sec (*14*). This lower terminal velocity increases the probability that crawlers will be dispersed into the planetary boundary layer. The observed decrease in terminal velocities implies an increase in drag coefficient from 7.2 to 11.2 at Reynolds numbers of 7.0 and 5.6, respectively (*15*). For a sphere at Reynolds number 7.0, the C_d is 5.5, and at Reynolds number 5.6, the C_d is 6.5 (*12*). Thus, the dead crawlers fall more nearly like small spheres. Despite the vastly differing shapes between a descending live crawler and a small sphere, the drag coefficients differ by less than a factor of 2.

Boundary layers represent barriers which must be crossed by animals dispersing into fluids (*16*). For *P. mesembryanthemi* two velocity gradients must be crossed in aerial dispersal: (i) the laminar boundary layer at the plant substrate and (ii) the velocity gradient at the base of the planetary boundary layer.

The responses of crawlers to light and gravity serve to locate new leaf tissues (the preferred feeding sites) and situate the crawlers on the periphery of the plant, where aerial dispersal is most easily facilitated. Similar behavioral responses of other scales and mite species serve the same purpose (*17, 18*). Mites of three families (Tetranychidae, Phytoseiidae, and Eriophyidae) commonly disperse by wind, and where individual behavior has been observed (*2*) the animals display postures similar to *P. mesembryanthemi*. Eriophyid mites possess anal suckers to support their bodies above the substrate (*18*), while phytoseiids and tetranychids stand upright on their posterior legs (*2*). Crawlers of other coccids (for example, *Pulvinaria delottoi* and *Saissetia oleae*) have behavioral responses to wind streams identical to *P. mesembryanthemi*. Such postures may encourage aerial dispersal by capitalizing on air velocity gradients at the substrate-air interface and may represent a common dispersal strategy for many minute arthropods.

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References and Notes

1. H. V. Daly, J. T. Doyen, P. R. Ehrlich, *Introduction to Insect Biology and Diversity* (McGraw-Hill, New York, 1978).
2. L. R. Nault and W. E. Styer, *Ann. Entomol. Soc. Am.* **62**, 1446 (1969); D. T. Johnson and B. A. Croft, *ibid.* **69**, 1019 (1976); R. P. Field, thesis, University of California, Berkeley (1981); M. A. Hoy, personal communication.
3. H. J. Quayle, *J. Econ. Entomol.* **9**, 486 (1916); F. B. Rabkin and R. R. Lejeune, *Can. Entomol.* **86**, 570 (1954); J. L. Bean and P. A. Godwin, *Forensic Sci.* **1**, 164 (1955); M. S. McClure, *Environ. Entomol.* **6**, 539 (1977); G. R. Stephens and D. E. Aylor, *ibid.* **7**, 556 (1978); J. O. Washburn and G. W. Frankie, *ibid.* **10**, 724 (1981).
4. The rapid spread of this coccid throughout California has apparently been by aerial dispersal [see J. O. Washburn and G. W. Frankie in (*3*)].
5. D. J. Borror and D. M. DeLong, *An Introduction to the Study of Insects* (Holt, Rinehart, & Winston, New York, 1971); C. B. Hill, *Va. Agric. Exp. Stn. Bull. 119* (1952), p. 1; T. Oda, *Jpn. J. Entomol.* **13**, 14 (1963).
6. P. B. Cornwell, *Bull. Entomol. Res.* **51**, 175 (1960); T. R. E. Southwood, *Biol. Rev. Cambridge Philos. Soc.* **37**, 171 (1962).
7. A large cardboard cone terminating in a cardboard tube 30 cm long and 4 cm in diameter was attached to the front of a variable speed fan with a calibrated rheostat and used to direct a narrow stream of air across the arena. We measured wind speeds by placing a hot-wire anemometer (Alnor) 1.5 cm above the arena surface. The crawlers behaved similarly to those we observed on host plant leaves.
8. We removed 300 eggs from 50 ovisacs and placed them individually in gelatin capsules, which were examined every 8 hours to determine the interval of hatching. The onset of crawler activity was defined as initiation of leg movement.
9. H. Schlichting, *Boundary-Layer Theory* (McGraw-Hill, New York, 1968), p. 129.
10. In evaluating the Reynolds number (ul/ν), the length l was taken to be 0.32 mm, the average diameter of the elliptically shaped crawlers, ν to be 0.15 cm^2/sec, the kinematic viscosity of air at 20°C, and u the average velocity in the boundary layer.
11. G. K. Batchelor, *An Introduction to Fluid Dynamics* (Cambridge Univ. Press, Cambridge, 1977).
12. F. M. White, *Viscous Fluid Flow* (McGraw-Hill, New York, 1974), p. 209.
13. Ice plant scale crawlers are positively phototactic and negatively geotactic.
14. Crawlers were dropped through a glass cylinder illuminated from above, and the time to fall a measured distance was recorded. Crawlers were killed with cyanide and tested within 5 minutes to minimize weight loss from desiccation; 100 crawlers of each class were tested.
15. Reynolds numbers of 7.0 and 5.6 are based on the measured terminal velocities.
16. S. Vogel, *Life in Moving Fluids* (Willard Grant Press, Boston, 1981).
17. C. C. Hall, Jr., *Univ. Kans. Sci. Bull.* **47**, 601 (1967); D. J. Greathead, *Bull. Entomol. Res.* **61**, 547 (1972).
18. L. R. Nault and W. E. Styer, *Ann. Entomol. Soc. Am.* **62**, 1446 (1969).
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