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Aerodynamic Aspects of Dispersal Take-off Behavior Among the Phytoseiid Mites, *Phytoseiulus persimilis,* *Neoseiulus fallacis* and *N. californicus*

포식성 이리응애류, *Phytoseiulus persimilis,* *Neoseiulus fallacis*와 *N. californicus*의 공중이동 이륙행동에 관한 공기역학적 연구

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Abstract – Some wingless species have evolved take-off behaviors that enable them to become airborne. We examined aerodynamic attributes of dispersal relative to the body size and standing vs. walking postures for three phytoseiids that were suspected to have different take-off behaviors and dispersal abilities, *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus fallacis* (Garman) and *N. californicus* (McGregor). The average vertical profile of Pp in the walking position was significantly higher than those of Nf and Nc when in walking position. The body height of Nf in the standing posture was significantly greater than the body height of Pp when in the walking position. Cross-section areas also showed similar patterns of difference. Nf in the standing posture would have more than twice the drag force than in walking posture because of more fluid momentum in the wind boundary layer. However, Pp in the walking position would have similar drag to Nf in the standing posture because of a higher vertical profile and larger size. Thus we add the scientific evidence of presence and absence of take-off behavior of some phytoseiid mites and evolutionary aspects of aerial dispersal are further discussed.

Key Words – Drag force, Force of attachment, Boundary layer, Phytoseiidae, Biological control

초 록 – 날개가 없는 몇몇 절지동물들은 공중이동을 하기 위한 수단으로써 이륙행동 보이는 종들이 있다. 본고는 포식성 이리응애류중에서 이륙행동을 보이는 종(*Neoseiulus fallacis* (Garman))과 이륙행동은 보이지 않으나, 공중이동률이 높은 종(*Phytoseiulus persimilis* Athias-Henriot), 이륙행동이 없고 공중이동률이 중간치인 종(*N. californicus* (McGregor)) 간에 공기역학적 측면에서 어떠한 메커니즘이 작용하는 지에 관한 연구이다. 위 종들의 도보이동 자세와 공주이동 이륙행동 자세의 몸체의 수직적 위치, 몸체의 크기, 다리의 길이 등의 자료를 가지고 공기역학적 파라미터를 계산한 결과, *P. persimilis*는 도보이동 자세에서도 *N. fallacis*가 이륙행동을 보여야만 얻을 수 있는 양의 항력을 얻을 수 있음이 밝혀졌다. 이러한 관점에서 포식성 이리응애류의 이륙행동 진화에 대한 고찰하였다.

검색어 – 항력, 생물적 방제, 행동진화, 경계층

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Dispersal is an adaptive process that permits individual organisms to escape unfavorable conditions and colonize new habitats (Price, 1984). Winged arthropods disperse actively by flight, whereas some wingless species have evolved take-off behaviors that enable them to become airborne. Described take-off behaviors (Brandenburg and Kennedy, 1982; Washburn and Washburn, 1983; Margolies and Kennedy, 1985; Weyman, 1993) include one type that involves standing erect and facing downwind. This behavior occurs among scale insects (Stephens and Alyer, 1987; Washburn and Washburn 1983), spider mites (Smithly and Kennedy, 1985), and some phytoseiid mites (e.g., *Neoseiulus fallacis* (Garman) (Johnson and Croft, 1976) and *Galendromus occidentalis* (Nesbitt) (Hoy, 1982).

Recently, some have questioned whether an aerial take-off behavior is an essential component of dispersal because some highly dispersive phytoseiids do not show such behaviors (Sabelis and Afman, 1994). Even with added information on biotic/abiotic conditions that affect dispersal, factors that mechanically constrain take-off have not been studied to any extent. Especially fluid mechanics (aerodynamics) that affect take-off of a mite from a surface boundary layer are important: Wind blowing parallel to a surface decreases as height decreases, creating less wind at the boundary layer. Thickness of the laminar boundary layer increases, as distance from the leading edge increases to where flow becomes unstable and forms a turbulent layer. Organisms under the boundary layer experience different wind speeds and momentum depending on their size and behavior. Take-off of a mite occurs when drag overcomes force of attachment to a surface.

We hypothesized that species with high vertical profiles may not require other behaviors to gain momentum for take off, but species with lower vertical profiles may have evolved behaviors such as standing erect for these purposes. We examined the aerodynamic attributes of dispersal for three phytoseiids that were suspected to have different take-off behaviors and dispersal abilities, *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus fallacis* (Garman) and *N. californicus* (McGregor) (hereafter referred to as Pp, Nf and Nc). We measured profiles, weights and cross-sectional areas and calculated fluid dynamics.

Materials and Method

Measurements: vertical height and cross-sectional area:

As noted, three species were selected for study because of possibly different dispersal mechanisms: *P. persimilis* has a high tendency to disperse ambulatorially and aerially, but it does not show any known take-off behavior (Sabelis and Afman, 1994; Jung and Croft in press). *N. fallacis* also has a high tendency to aerially disperse and frequently shows a take-off behavior (standing posture) in air currents (Johnson and Croft, 1976, 1981), but its ambulatory dispersal is more confined than that of *N. californicus* when with prey (Pratt et al., 1998). *N. californicus* has lesser tendency to disperse aerially than *N. fallacis* (Pratt et al., 1998) and as yet, no take-off behavior has been seen for this species.

Using stop motion pictures taken by a CV camera (CV-730 series) mounted on a binocular microscope (20X), we measured vertical height and cross-section area of each species in the walking posture (n = 10 each) and *N. fallacis* in a standing posture (n = 1; it was difficult to observe Nf standing upright on a 0.5 mm dia. rod for mechanical pencil). Starved adult females (24 hr) were used because they are the stage that most frequently disperses aerially (Johnson and Croft, 1976; Sabelis and Afman, 1994, Jung and Croft in press). Aspects of vertical height measured were leg height: distance from surface to bottom of abdomen; body height: sum of leg height and thickness of abdomen for mite in walking posture; and sum of leg height and longitudinal length of idiosoma for an individual in standing posture. In calculating cross-section area, we assumed that mites always faced directly away from the wind (Johnson and Croft, 1976).

Boundary layer and drag force

Assuming laminar flow on a smooth surface, wind speed profile was estimated at 10 and 30 mm away from the leading edge by the Blasius approximation (Curle, 1962; pp.20) for a free stream velocity of 4 m/s. At this wind speed, frequent aerial dispersal and specific dispersal behaviors have been seen (Johnson and Croft, 1973; Sabelis and Afman, 1984). Thickness of boundary layer (δ) relative to increasing distance from the

leading edge was estimated (Monteith and Unsworth, 1997) where, x is the distance from the leading edge, and Re is the Reynolds number at x. Within the boundary layer, drag force (Fm) was calculated using Reynolds number (Re) and drag coefficient (Cd) parameters from the above measurements. Reynolds numbers (Re, Curle, 1962) were estimated for walking (Pp, Nf, Nc) and standing (Nf). The drag coefficient (Cd) over this Re ($1 < Re < 400$) range was determined assuming a spheroid shape (Monteith and Unsworth 1997), where, V is a wind speed corresponding to height of mite (H), and υ is kinematic viscosity of dry air ($20°C$). Drag forces (Fm) on a smooth surface was calculated (Monteith and Unsworth, 1997), where, A is cross-sectional area of mites, ρ is the density of the air ($1.204\,kgm^{-3}$), and V is the corresponding wind speed at the apex height of each posture.

$$\delta = x \times 1.72 \times Re_x^{-0.5}$$
$$Re = (V \times H)/\upsilon$$
$$Cd = (24/Re)(1 + 0.17 \times Re^{0.66})$$
$$Fm = Cd \times 0.5 \times \rho \times V^2 \times A$$

Results

The average vertical profile of Pp in the walking position was significantly higher than the average verticle profile of Nf and Nc in walking position (Table 1, ANOVA, df = 2,29, F = 31.24 and 40.64, P<0.001 for leg height and body height, respectively). The apex of the body height of Nf in the standing posture was significantly greater than the apex of the body height of Pp in the walking position (Table 1, t-test, P<0.001).

Cross-sectional areas of bodies for each mite also showed these same patterns of difference (Table 1).

Wind speed decreases as distance from surface decreases from a vertical point that defines boundary layer thickness (Fig. 1). Boundary layer thickness increases as the distance from the leading edge increases until a critical point where air movement becomes turbulent. So, wind velocity gradient relative to height become greater as the distance from the leading edge decreases (Fig. 1).

Table 1 shows the Reynolds number, drag coefficient and drag forces of Pp, Nf and Nc when in walking and standing postures. Nf in the standing posture would have more than twice the drag force than in walking posture because of more fluid momentum in the boundary layer. However, Pp in the walking position would have similar drag to Nf in the standing posture because of a higher vertical profile and a larger size.

Discussion

Aerial take-off occurs when drag on a mite is sufficient to overcome force of attachment to a substrate. Assuming that attachment force was equal among species (which may not be so), our calculations suggest that a species with a more vertical profile (e.g. Pp), may not require a standing behavior to achieve enough momentum to become airborne, but those with a less vertical profile (e.g. Nf), may benefit from standing, and become highly dispersive. With Nc, its limited vertical profile and lack of upright posture may account for its more limited aerial dispersal ability relative to Nf (Croft *et al.*, 1997; Pratt *et al.*, 1998) and presuma-

Table 1. Vertical profiles; $H1$: height of leg, $H2$: height of body, distance from the surface to the dorsum, A: cross-section area of predatory mites in walking vs. standing posture, and aerodynamic parameters; V: wind speed at the corresponding height, Re: Reynolds number, Cd: drag coefficient and Fm: drag force

Species[a]	Posture	$H1$ mm	$H2$ mm	A[c] mm²	V m/s	Re	Cd	Fm 10^{-8} N
Pp	Walking	0.138 a[b]	0.38 a	0.137	1.300	32	2	278.9
Nf	Standing	0.121*[c]	0.45 **[d]	0.144	1.410	40.9	1.74	300.1
Nf	Walking	0.101 b	0.27 b	0.086	0.920	16.1	3.07	135.2
Nc	Walking	0.093 b	0.26 b	0.088	0.88	14.9	3.23	133.3

[a]: Pp indicates *Phytoseiulus persimilis*, Nf does *Neoseiulus fallacies*, and Nc does *Neoseiulus californicus*.

[b]: means with different letter within a column represent significant difference (ANOVA, df = 2, 29, ea. P<0.001)

[c]: Difference of H1 between standing and walking posture in Nf (t-test, P<0.05)

[d]: Difference of H2 between standing and walking posture in Nf, and standing Nf vs. walking Pp (t-test, ea. P<0.05)

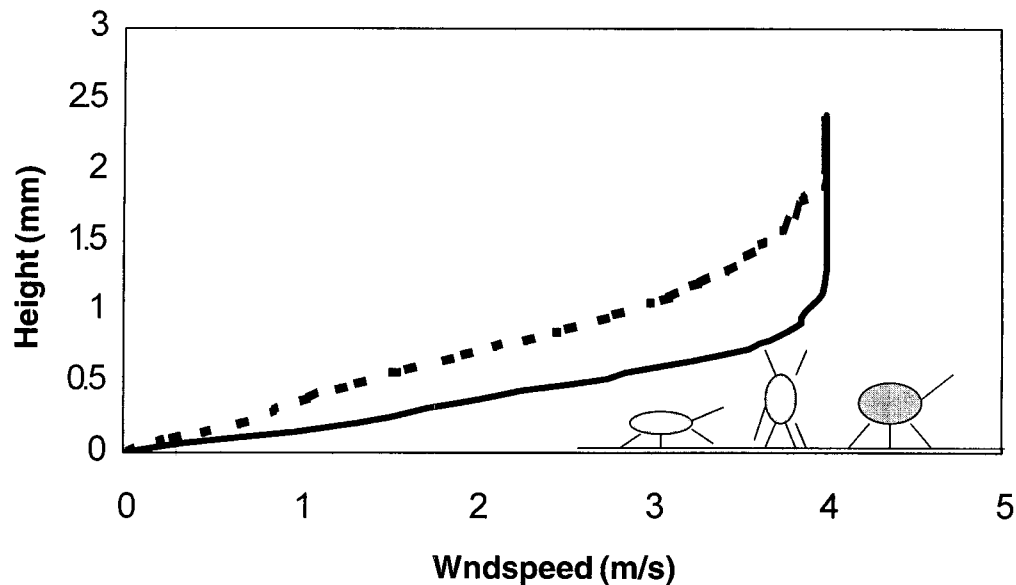[e]: Partial data from Croft *et al.*. 1999

Fig. 1. Vertical velocity profiles for a free stream wind speed (4 m/s) at 10 (broken line) and 30 mm (continuous line) away from the leading edge on a flat surface and scaled illustration of 3 phytoseiid mites in walking and standing posture (from the left, Nf (*Neoseiulus fallacies*) and Nc (*Neoseiulus californicus*) in walking posture, Nf in standing posture and Pp (*Phytoseiulus persimilis*) in walking posture).

bly to Pp.

The quantitative relationships and results of this study may not exactly reflect conditions as they occur in nature. Drag and attachment force may depend on mite's condition with respect to wind, surface topography and position on a plant. Also air currents in nature are more complex and violent than the laminar flow of the laboratory. However, qualitative aspects of our results would not be invalidated with more realistic parameter estimates.

Drag is positively correlated with mite size and wind speed at height H. Boundary layer would be thicker on a hairy than smooth leaf, thus providing more space of reduced wind, and less take-off. A thicker boundary layer would occur on under- vs. upper-sides of leaves since, in most plants, undersides have more trichomes, hairs, ribs, veins and domatia (Walter and O'Dowd 1992a, b). Grace and Wilson (1976) demonstrated using a *Populus* leaf held parallel to laminar airflow, that winds of the upper surface were similar to a theoretical boundary structure model, but at the lower surface, distorted wind profiles produced a thicker boundary layer and shelter. So individuals on an underside of a leaf would have less momentum than on the upper. Many generalist predators that have lower dispersal rates (Dunley and Croft, 1990; Jung and Croft in press) are

more often associated with domatia on leaf undersides than are specialists that have higher dispersal rates (Walter and O'Dowd, 1992a, b). Movement of a mite to a leaf upper-side also may increase aerial take-off. Higher frequency of Nf (a specialist) on the upper-sides of leaves than Nc (more generalist) (Jung and Croft in press), suggests that this mechanism alone could confer a differential dispersal rate to these two very closely related species. The horizontal position of mites on a leaf can influence take-off. If near a leading leaf edge, a mite will experience more wind and dispersal than when further inward from a leaf edge. High frequency of edge walking in Nf (Berry and Holtzer, 1990) could lead to increased aerial take-off as well.

Force of attachment may depend on physical powers of grasping, levels of physiological starvation and/or any active behavioral component of take-off. The force required for 50% aerial take-off of Pp on an upper-side of apple leaf was estimated at 4×10^{-8}N, based on Sabelis and Afman (1994). When compared to force required to detach spores of *Helminthosporium maydis* from infected maize leaves (ca. 1×10^{-7}N, Aylor, 1975), Pp becomes airborne at much lower wind speeds than the passively dispersing spore. Active control over take -off has been established in several phytoseiid species (Sabelis and Aftman, 1994; Jung and Croft in press).

The standing behavior of Nf (Johnson and Croft, 1976) may either lessen grasp or increase drag or both. Dispersal rates increased as starvation increased for some phytoseiids (Johnson and Croft, 1976; Sabelis and Afman, 1994; Jung and Croft, 2001).

Our results may indicate the possible adaptive value of standing for aerial take-off for Nf; Pp when walking has as much drag as standing Nf. However, the evolutionary value of standing cannot be inferred by mechanistic analyses. More detailed behavioral analyses of take-off are needed. Also, it is unresolved just why standing is so common in many wingless arthropods when an organism could readily move to the upwind edge of the leaf where boundary layer is small (Sabelis and Afman, 1994).

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