**ORIGINAL ARTICLE**

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# Relative importance of weather and density dependence on the dispersal and on-plant activity of the predator *Orius minutus*

**Abstract** The present study evaluated the relative effects of abiotic (weather: temperature, wind speed, and rain) and biotic (intra- and intertrophic density dependence: densities of conspecifics, prey per predator individual and leaves on plants) factors on the dispersal and on-plant activity (foraging and oviposition) of the predatory bug, *Orius minutus*, under seminatural field conditions. Experiments were conducted at plots, each comprising 25 potted azuki bean plants, placed symmetrically in concentric circles, in 1998 and 1999. At the central pot within each plot, 5 marked females of *O. minutus* (with a male in 1998) were released, and their location and activity were recorded hourly up to 24 h. A total of 78 individuals were released. Stepwise multiple logistic regression was used to select among weather, density dependence, and time variables. Hourly dispersal probability of individuals was positively correlated with temperature and negatively with time since release and with prey density per individual *O. minutus*. Hourly probability of individuals being active was positively correlated with temperature and negatively with number of leaves of visited plants and conspecific density per leaf. Between-year difference was observed in the probability of individuals being active, which was higher in 1998 than in 1999, probably generated by hunger and higher age. By contrast, diffusion rate was estimated to be lower in 1998, suggesting a trade-off between foraging/oviposition and dispersal by flight. The results indicate that dispersal is affected by temperature and intra-/intertrophic-level density dependence within and between trophic levels, as are foraging/oviposition. The importance of incorporating both abiotic and biotic factors should be stressed when modeling predator–prey metapopulation dynamics on a greenhouse scale.

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## Introduction

Understanding the relative roles of abiotic, exogenous factors (weather) and biotic, endogenous factors (density dependence) on population dynamics is a central theme in ecology. In a metapopulation scheme, the extent to which these two driving forces govern dispersal of organisms would be critical for the behavior of the whole system. Insects are the major group of organisms that have functional wings to fly for dispersal. Although the flight of insects is affected by the weather, through aerodynamics (Wootton 1992; Brodsky 1994) and metabolism, density dependence in dispersal within and between predator and prey induces and regulates time lags in subpopulation responses (Travis et al. 1999; Travis and French 2000; Keeling et al. 2000; French and Travis 2001). The relative influence of these two factors on dispersal has barely been evaluated in the common scheme but is inevitable in predicting the dispersal of insects by flight, especially those of minute size, as ambient abiotic conditions have enormous effect for small insects because of the large surface to volume ratio, the greater amount of energy required (Tucker 1975), and because air is as viscous as is water for larger organisms (Brodsky 1994).

The species in *Orius* (Hemiptera: Anthocoridae) are beneficial predators that can control greenhouse and garden pests (Lattin 1999). *O. minutus* (L.) is a promising natural enemy of thrips and other pests (Kohno and Kashio 1998), with its fecundity and adult longevity, and its combined effects on intrinsic growth rate are superior to those of the closely related *Orius sauteri* (Poppius) (Honda et al. 1998), a species as common as *O. minutus* in Japan (Nakata 1995; Nagai and Yano 1999). The predatory bug is distributed in the Palearctic region ranging from western Europe to China (Pericart 1972, 1996), and throughout Japan, together with several other *Orius* species (Yasunaga 1997;

Ohno and Takemoto 1997). Its distribution as a nonindigenous species has been extended to North America (Tonks 1953; Lattin et al. 1989). *Orius* spp. occur naturally on various crops including *Vigna* spp. (Bottenberg et al. 1998) and other wild and crop legume plants (Yasunaga 1997; Bottenberg et al. 1998; Lam and Pedigo 1998; Pfannenstiel and Yeargan 1998). Movement of *O. minutus* is commonly accomplished by short, low-level flights, as compared to other anthocorids and hemipterans (Southwood 1960; McPherson and Weber 1981; Lattin 1999). Females engage less in flight activity than do males in this species, which is a diurnal flier (Southwood 1960).

Studies under constant environmental conditions and constant population density in a greenhouse have demonstrated the importance of abiotic and biotic conditions on flight activity of the predator *Orius* (Shipp and Zhang 1999; Zhang and Shipp 1998). We propose that the natural dispersal process could be better evaluated in the open field than in closed systems, if careful statistics are employed, to evaluate the response of insects to realistic concurrent changes in weather and biotic interactions and the relative importance of the two factors. Prediction of the dispersal pattern of released natural enemies is inevitable as a guideline for release programs.

Our aim was to study the relative importance of weather components and density dependence within and between trophic levels on the short-range dispersal and foraging/oviposition behavior of *O. minutus,* a natural enemy of *Thrips palmi* Karny (Thysanoptera: Thripidae), in the open field.

## Materials and methods

### Study site and the prey

All experiments were conducted on the Hakozaki campus (33°37′ N, 130°25′ E) of Kyushu University, Fukuoka, Japan. *Thrips palmi*, which uses many vegetable crops including the azuki bean *Vigna angularis* (Willd.) (Fabaceae) as host plants (Umeya et al. 1988), was used as the prey source for *O. minutus* in the experiments. The larvae of *T. palmi* do not have wings for flight.

### The effect of weather and density dependence

Size of plots, time interval of observation, and duration of experiments were determined based on the preceding information: *O. minutus* females are reluctant to fly compared to conspecific males, and the species is considered to move most commonly by short flights at a low height (1–3 m) (Southwood 1960; McPherson and Weber 1981). Residence times of a closely related *O. sauteri* on leaves without prey *T. palmi* and on those with the prey are about 2 h in both sexes, and 8 h in female and 2 h in male, respectively (Nakashima 1998), which approximates the time required for the assessment of patch quality and decision making of whether to leave a patch. We determined time intervals
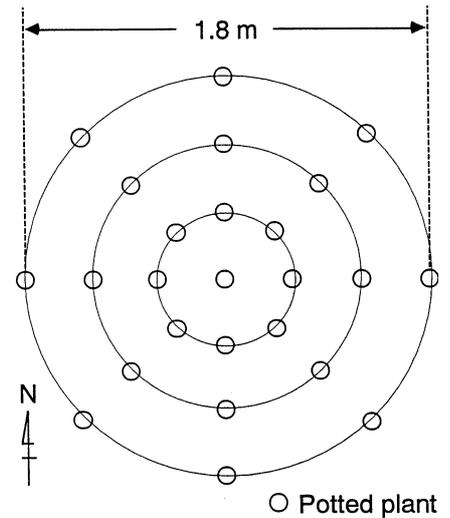


**Fig. 1.** Diagram of spatial arrangement of potted plants (azuki bean). Distance between potted plants is 30 cm on each radius. Two such experimental plots are located 3 m apart from each other

during the day to be 1 h and total observation periods to be >8 h, so that our observations would be frequent and long enough to allow *O. minutus* to assess a potted plant and disperse.

The summer variety of *V. angularis* was grown under the laboratory conditions of 25° ± 1°C, 70% ± 17% RH, and LD 16 h : 8 h. Twenty-five potted azuki bean plants were placed randomly in symmetrical positions, 30 cm apart from each other, in a pattern of three concentric circles, with a maximum radius of 90 cm in each of two replicated plots (Fig. 1). The numbers of leaves on all the potted plants were counted before the experiments. Two such experimental plots were located 3 m apart from each other. A total of 70 females and 8 males were released in early to mid-June 1998 and in late May through early August 1999. Preparation of the prey and the predators, presence of a male predator, release time, and duration of experiments were different between years.

### Release experiment in 1999

Individual *O. minutus* collected from flowering clover (*Trifolium repens*) (Fabaceae) fields in early to mid-May 1999 were reared in the laboratory at 25°C and LD 16:8 h, on a daily supply of 20 larvae of *T. palmi* on a leaf disk (2 × 2 cm²) of kidney beans (*Phaseolus vulgaris* L.) (Fabaceae). Females were allowed to mate for 2 h before being released. Five mated females (1–9 days old) marked by one of four different colors of fluorescent dust (AX-15-N, A-17-N, A-21, and A-594-5; Ryukyu Sankei, Toyomigusuku, Japan) for each replicate plot on the same release date were released at 0800 on May 30 (to only one plot), July 9, and August 6, or at 1100 on June 6 (to only one plot), 1999. A total of 30 female *O. minutus* were released in 1999. The bottle containing the *O. minutus* to be released was placed so that its mouth was attached to a potted *V. angularis*; thus, the

predators could choose their way upward to the leaves or downward to the soil surface. The location and behavior of the released female predators were then observed and recorded every hour subsequently until dark (1930 or 2000). Behavioral status was recorded as "active" if an observed individual was moving or walking on plants, presumably engaged in either searching for prey or oviposition sites, feeding on prey, or depositing eggs. Otherwise, individuals that stayed motionless were evaluated as "inactive". All plant parts including axils where the insects tend to hide and the soil surface within and around pots were carefully examined without touching the plants to observe the density and activity of insects. The reduction in number or disappearance of a marked *O. minutus* individual on a plant and on soil surface and the direct observation of take-off behavior were interpreted as dispersal. Whenever other insects such as aphids, spiders, or unmarked *Orius* spp. were found invading the plant, they were removed by an aspirator. All the plants were checked to count the final density of thrips and to collect released individuals of *O. minutus* after the experiments.

*Release experiment in 1998*

The release experiments were performed likewise, except under partly different conditions as follows: *O. minutus* were collected by sweeping flowering heads of clover and *Coreopsis drummondii* (Asteraceae) from 1300 to 1600 before each release. The azuki bean plants were inoculated with the larvae and adults of *T. palmi* from nearby potted *P. vulgaris* (Fabaceae) plants under the aforementioned laboratory condition. Six marked adults, five females and one male, of the wild-caught *O. minutus* were released at the central potted plant, and the location and behavior of the released individuals were then observed and recorded for up to 24h. The experiments were sequentially repeated four times at each experimental plot, starting at 1700 on June 6, 1900 on June 7, 1600 on June 11, and 1400 on June 16, 1998. A total of 48 individuals (40 females and 8 males) were released in 1998.

*Weather variables*

Ambient temperature and relative humidity were monitored during the observations by an automatic temperature-humidity recorder (3-3128; Isuzu, Tokyo, Japan), whereas wind direction and speed were monitored by a windmill anemometer with a wind vane (Micro Anemo KC101R; Makino, Tokyo, Japan) that were placed 1m above the ground, within 5m of the experimental plots. Global solar radiation was also measured by a pyranometer (PCM-01; Solarmini, Kipp & Zonen, Saskatoon, Canada) set 3m above the ground. Vapor pressure deficit (VPD) was estimated based on its relationship with temperature and relative humidity (Shipp and Zhang 1999).

Rates of change in weather factors at time interval $t$ were calculated by subtracting the values at time $t - 1$ (h) from those at time $t$. To test the bimodality of activity reported in *Orius tantillus* (Sigsgaard and Esbjerg 1997), absolute time

difference from either 1200 or 1300, along with direct values and rates of change in weather factors, densities of conspecifics and prey, and year in which experiments were performed, were incorporated in a multiple logistic regression model (see Statistical analyses).

*Quantification of foraging and oviposition*

To quantify predation activity and oviposition by *O. minutus*, all the potted plants, each with two leaves, were inoculated with ten larvae of thrips each as part of the release experiments on May 30 and July 9, 1999. Another ten potted plants with ten larvae of thrips each were set up as a control 5m away from the experimental plots. The potted plants were collected at the end of the experiments and placed indoors (22°–30°C) to enable an estimation of egg deposition by counting the number of developing immature *O. minutus,* 8d after their release. The Kruskal–Wallis test and a nonparametric multiple comparison test with a control were used to detect the reduction in prey by *O. minutus*, by comparing the experimental plant to the control (Zar 1996).

Diffusion coefficient

Diffusion coefficient $D$ (m²/h) was estimated by the observed number of released individuals within distance $d$ of the release point:

$$D = \text{MSD}/4t \tag{1}$$

where MSD (m²) is the mean squared displacement of released individuals at time $t$ (Okubo 1980):

$$\text{MSD} = \sum n_d d^2 / \sum n_d, \qquad n_d \leq n_0 \tag{2}$$

where $n$ is the number of observed individuals at distance $d$ (m) at time $t$ (h) and $n_0$ is the number of released individuals. In our case, the number of potted plants, i.e., observation points, changes inversely over distance $d$ (see Fig. 1). We corrected $n_d$ according to $d$:

$$n_d' = (d/0.3)n_d \tag{3}$$

Statistical analyses

Stepwise multiple logistic regressions with a backward procedure were used to select which of weather factor(s), per-leaf density of conspecifics, prey density either per predator or per leaf, whether visited plant is a release or nonrelease pot, time since release, and year of release experiments can be incorporated as explanatory variable(s) for active/inactive and dispersed/staying states of individuals. To eliminate multicollinearity among variables in the model, Pearson's correlation coefficients and Bonferroni probabilities were used to detect and eliminate correlations among weather variables in advance. Probabilities for adding and removing variables from the model were set at 0.05. Fits of selected models were evaluated by $G$ test as improvement

**Table 1.** Matrix of Pearson's correlations between pairs of variables used in logistic regression analyses ($n = 45$)

| | Direct values | | | | | Change rates | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | **Temp.** | Humid. | VPD | SR | **WV** | **Temp.** | Humid. | VPD | SR |
| **Direct values** | | | | | | | | | |
| Humid. | −0.877** | | | | | | | | |
| VPD | 0.898** | −0.994** | | | | | | | |
| SR | 0.667** | −0.689** | 0.746** | | | | | | |
| **WV** | 0.524* | −0.265 | 0.297 | 0.137 | | | | | |
| **Change rates** | | | | | | | | | |
| **Temp.** | 0.047 | 0.009 | 0.028 | 0.086 | 0.282 | | | | |
| Humid. | 0.233 | −0.120 | 0.113 | 0.129 | 0.048 | −0.538* | | | |
| VPD | −0.262 | 0.178 | −0.162 | −0.106 | 0.010 | 0.677** | −0.966** | | |
| SR | 0.322 | −0.163 | 0.200 | 0.399 | 0.279 | 0.382 | 0.014 | 0.102 | |
| **WV** | −0.093 | 0.021 | −0.023 | −0.202 | 0.533* | 0.396 | −0.331 | 0.387 | −0.113 |

Weather factors in bold letters indicate those used in logistic regression model as default
Temp., temperature; Humid., humidity; VPD, vapor pressure deficit; SR, solar radiation; WV, wind velocity
Bonferroni probabilities are shown by *$P < 0.01$, **$P < 0.001$

**Table 2.** Results of stepwise multiple regression on probabilities of emigrations from plants and of active individuals on plants

| | Coefficient | $P$ |
| --- | --- | --- |
| Dependent variable: *probability of individuals being dispersed* | | |
| Selected independent variables: | | |
| Constant | −5.53 | 0.0001 |
| Temperature | 0.196 | 0.0009 |
| Time since release | −0.0890 | 0.002 |
| Prey density per *Orius minutus* individual | −0.0446 | 0.045 |
| $n = 252$, $G = 21.0$, $df = 3$, $P = 0.0001$, $\rho^2 = 0.0796$ | | |
| Dependent variable: *probability of individuals being active* | | |
| Selected independent variables: | | |
| Constant | −6.15 | 0.0006 |
| Temperature | 0.253 | 0.0003 |
| Number of leaves | −0.325 | 0.001 |
| Year | 2.00 | 0.006 |
| Density of conspecifics per leaf | −0.974 | 0.048 |
| $n = 252$, $G = 24.8$, $df = 4$, $P < 0.0001$, $\rho^2 = 0.108$ | | |

Selected variables are listed with $G$, $\chi^2$ $P$ values, and McFadden's $\rho^2$

from constant-only models. SYSTAT ver. 9.0.1 was used for statistical analyses (SPSS 1999).

## Results

There were highly significant correlations of hourly temperature with hourly humidity, VPD, and solar radiation, as well as correlations of rate of change in temperature with that in humidity and VPD (Table 1). We therefore disregarded humidity, VPD, and solar radiation in our analysis.

A stepwise logistic regression showed that hourly probability of individuals being dispersed was positively correlated with temperature and negatively with the time since release and the density of prey per *O. minutus* individual (Table 2). Hourly probability of individuals being active was correlated positively with temperature and negatively with the number of leaves of plants visited by *O. minutus* and the density of conspecifics per leaf and was higher in

1998 than in 1999 (Table 2). No significant effects of wind, rain, time deviation either from noon or from 1300, density of conspecifics per leaf on dispersal, and within-plant activity were detected. Incorporation of per-leaf density of prey, instead of per-predator density of prey, did not alter the result and resulted in exclusion of the prey variable by stepwise procedure.

During the first release in 1999, the number of thrips per plant was reduced to $5.33 \pm 1.23$ (mean $\pm$ SE) ($n = 6$) in plants that were visited by the released *O. minutus* within experimental plots, as compared to the control plants ($9.80 \pm 0.13$, $n = 10$) ($H = 10.80$, $P < 0.005$; $Q' = 3.28$, $k = 3$, $P < 0.005$). There was no significant difference between unvisited plants ($9.10 \pm 0.35$, $n = 10$) and the control ($Q' = 1.21$, $k = 3$, $P > 0.2$). The average rate of predation per individual *O. minutus* on visiting plants was $2.48 \pm 1.55$/h and the average rate of oviposition was $0.393 \pm 0.155$/h. All the collected *O. minutus* individuals at the end of release trials were females. No dead body of *O. minutus* was observed during any of the release experiments.
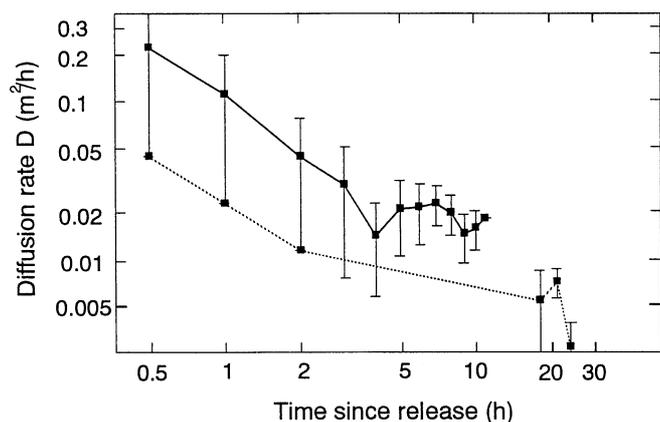
**Fig. 2.** Estimated diffusion rates (*D*) (mean ± SE) over time in 1998 (*dotted line*) and in 1999 (*solid line*)

The mean ± SD (range) of weather conditions was 25.3 ± 3.2° (range, 19.4–31.2°)C, 63.5 ± 13.0 (43.9–95.5)% RH, 1.26 ± 0.60 (0.124–2.532) for VPD, and 0.682 ± 0.340 (0.0840–1.472) m/s for wind speed. The mean ± SD (range) of density was 0.686 ± 0.563 (0.05–2.5) for conspecifics per leaf, 8.02 ± 10.6 (0–55) for prey per *O. minutus* individual, and 7.38 ± 4.56 (2–20) leaves per plant.

The estimated diffusion coefficients were 0.0450 m²/h in 1998 and 0.315 m²/h in 1999 at 0.5 h after release. The estimated values declined over time, and the decline was linear during initial 3 h in log-log scale (Fig. 2). Recapture rates in each release, as calculated by (number of observed individuals at time *t*)/(number of released individuals at time 0), were not different between years ($U_{6,6} = 23.0$, $P > 0.2$) and 0.542 ± 0.092 (mean ± SE, $n = 12$) at $t = 2$ (h). The final recapture rate at $t = 11$ in 1999 (0.280 ± 0.185, $n = 5$) was not different from the recapture rate at $t = 18$ in 1998 (0.389 ± 0.111, $n = 6$) ($U_{5,6} = 19.0$, $P > 0.2$). The final recapture rate in 1998 was 0.333 ± 0.063 ($n = 8$) at $t = 24$.

## Discussion

Both abiotic and biotic factors were detected as controlling flight and foraging activity of the predator *O. minutus*. The predator initiates flight according to conspecifics and prey availability per predator. Although most experiments and models on dispersal of insect predator (or parasitoid) have neglected density dependence of dispersal on either prey or predator density or both (Comins et al. 1992; see Travis and French 2000; French and Travis 2001 for recent development), the aforementioned result showed that the predator dispersed according not to prey density itself but to prey density available for an individual predator. This finding parallels the experimental evidence that females of the closely related species, *O. sauteri*, stay a shorter time and move out to prey patches when released to prey-absent patches (Nakashima 1998). Such ratio-dependent dispersal has never been reported, and this type of dispersal can easily lead to ideal free distribution (Fretwell and Lucas

1970). Predators of this property would quickly emigrate from a low-efficiency patch and control a pest population effectively as a natural enemy, on a relevant spatial scale such as that of a greenhouse.

The diffusion rate in 1999 was seven times higher than that in 1998. The higher dispersal is considered due to the factors that were not incorporated in the model; it is possible that gut saturation and factors associated with lower age in 1999 than in 1998 may have contributed to the difference (see Materials and methods). It has been reported, in the parasitoid *Nasonia*, that females showed higher locomotor activity immediately after mating than virgins, but the difference disappeared the next day and later on (King et al. 2000). The short time after mating in 1999 may also have triggered more flights in the predator.

Estimated diffusion rates decreased over time constantly for the first 3 h, probably because of restricted spatial range for sampling migrants and a consequent decline in recapture rate (see Fig. 2). Interestingly, the rate of decline was initially substantial, followed by a moderated decline phase that was similar in the 2 years, suggesting a common rule. The result of logistic regression analysis suggests that *O. minutus* individuals that find patches with high prey density are reluctant to fly out from the patches (see Table 2). Therefore, *O. minutus* initially flies out relatively randomly but as they discover a prey patch, their activity may shift from dispersal to foraging activity. The other possibility is behavioral variation among individuals; those dispersing are observed earlier during experiments but are lost later by flying out of the experimental plots and those with high foraging activity remain on plants within the experimental plots.

Intriguingly, the activity of the predator was affected by plant size, or patch size. The effect of plant patch size on herbivorous insects (Doak 2000) and on parasitoids (Wang et al. 1997) is known but, as far as we know, not on predators of herbivores. Such ratio dependence in dispersal, which can be termed intertrophic density dependence, should modify predator–prey metapopulation dynamics. Negative correlation between on-plant activity and plant size can be either trophic or nontrophic: it results from trophic interaction if *O. minutus* feed on plant sap more, considering plant-feeding is a common behavior in the genus (Lattin 1999). The size of plants in this case may serve as availability of suitable plant parts for sap-feeding. Alternatively, the negative correlation may be attributed to moderation of the microclimate (e.g., temperature) within plants, in which case plants serve as habitat, nontrophically. To determine the mechanism for this correlation, further experiments would be required.

We observed a between-year difference in the probability of individuals being active, which was higher in 1998 than in 1999. The difference is just the opposite of that in flight activity, suggesting a trade-off between the two activities. The difference can be explained by hunger and factors associated with higher age because field-caught individuals, which may not have been fully fed on prey compared to laboratory-reared individuals, were released in the former. *O. sauteri*, a closely related species, engages more in ovipo-

sition after deprivation of prey (Nakashima 1998). If prey was present, foraging activity would also be accelerated by hunger. Higher ages are predicted to accelerate oviposition (Iwasa et al. 1984; Mangel 1987).

Higher temperature associated with lower humidity and higher solar radiation is correlated with higher on-plant foraging/oviposition activities. This finding is not surprising because the positive effects of temperature on insect activities and flight are common knowledge (e.g., in Hemiptera: Southwood 1960; Lehane et al. 1992; Lachance and Cloutier 1997; Zhang and Shipp 1998; for windborne flight, Gatehouse 1997; in flies, Shipp et al. 1987; and in parasitoids, Forsse et al. 1992). The same is implied by the increased flight activity caused by high VPD for *O. insidiosus* (Zhang and Shipp 1998) and water loss in a hemipteran bug (Velasco and Millan 1998). On the contrary, the effects of rain and wind were relatively unimportant in the present field conditions, although adverse effects of rain and wind on flight activity have been recently confirmed experimentally in insects, especially parasitoids (Fink and Volkl 1995; Weisser et al. 1997; Schworer and Volkl 2001; Gu and Dorn 2001). The apparent contrast in their results to ours is probably attributable to quantitative rather than qualitative difference in the adverse weather effects.

The relative contributions of weather components and intra-/intertrophic-level density dependence to the small-scale dispersal of insects that the present study detected suggests that a metapopulation model for predator–prey population dynamics in a greenhouse or in a garden plot should incorporate both temperature and density dependence within and between trophic levels. How the dispersal rule and density dependence on this scale would be extended to those on the larger scale (e.g., Tuda 1993; Tuda and Shimada 1993) will be a subject for future studies, in which abiotic factors, e.g., incidence of strong wind turbulence, could play a more significant role in governing dispersal.

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