

Patch colonization by *Trirhabda canadensis* (Coleoptera: Chrysomelidae): effects of plant species composition and wind

P.A. Morrow¹, D.W. Tonkyn², and R.J. Goldberg³

Department of Ecology, Evolution and Behavior, University of Minnesota, 318 Church St. S.E., Minneapolis, MN 55455, USA

Summary. The goldenrod leaf beetle, *Trirhabda canadensis*, is known to respond to odors of host and non-host species in the laboratory. Here we report movements of *T. canadensis* in the field in response to volatile odors from monocultures and polycultures of host plants. Overall, beetles preferentially colonized plots with a higher density of host plants and lower diversity of allelochemicals, but under some wind conditions there were marked exceptions. At high windspeeds, they colonized whichever plot(s) was upwind. At low windspeeds, beetles colonized preferred plots even when they were not upwind. The data suggest that odor dispersion varies in a complex way with windspeed: at low windspeeds beetles received information from a wide arc of vegetation and made choices while at high windspeeds information was available only from upwind plot(s).

Key words: *Solidago altissima* – *Trirhabda canadensis* – Host plant odors – Insect host colonization – Host finding – Odor dispersion

The distribution of plants is highly variable on a local scale; plants occur in patches of varying size, density and diversity. It is widely thought that many herbivorous insects use plant volatile chemicals as an aid in host finding (de Wilde 1976). Insect response to host odors varies with concentration and is influenced by non-host vegetation near the host (reviews in Andow 1986; Kareiva 1983; May and Ahmed 1983; Stanton 1983). Non-hosts may affect host finding a) indirectly, by decreasing host plant density and thus concentration of host volatiles, or b) directly, by altering host quality through competitive interactions, making hosts less attractive (Bach 1980; Kareiva 1983), or changing the way that host volatiles are perceived by the insect (Thiery and Visser 1986). The extent of these effects on

host finding can depend on the identity of the non-host species (Atsatt and O'Dowd 1976; Lower 1972; Saxena and Prabha 1977; Tahvanainen and Root 1972; Thorsteinson 1960; Visser and Nielson 1977). The diversity of odorous cues, and of herbivore responses to these cues, are thought to contribute to the generally uneven distribution of insects among host plant patches. There are, however, few field studies that demonstrate use of odors in long distance location of host patches (Hawkes 1974; Miller and Strickler 1984).

In this paper we present data from field experiments on the influence of neighboring plants, host plant density, wind direction, and windspeed on colonization of host plant patches by adult *Trirhabda canadensis* Kirby (Chrysomelidae: Coleoptera), a specialized herbivore that feeds on three clonal species of goldenrod, *Solidago* L., at our field sites. In the laboratory, *Trirhabda* respond to plant volatiles. Dickens and Boldt (1985) recorded antennal receptor responses of *T. bacharides* adults to volatiles of 26 plant species. The strongest responses were elicited by the host species and non-host species that were in the same family but did not co-occur with the host plant. Puttick et al. (1988) found in olfactometer tests that *T. canadensis* has complex odor preferences. Beetles preferred higher concentrations over lower concentrations of pure host odor, but only up to a threshold; above this, increasing concentration of host volatiles did not influence beetle choice. Combinations of a non-host with host volatiles generally did not affect beetle preference, but combinations of host odors with odors from two or more non-host species were less attractive than pure host odors. Thiery and Visser (1986) also found complex responses to odors in Colorado potato beetles, *Leptinotarsa decemlineata* Say., walking in a wind tunnel. Upwind movement was elicited by odors of potato but not by wind alone or by odors of two non-host species. When odors of these two neutral species were blended with host odors, each neutralized the attractiveness of host odors.

In the laboratory *T. canadensis* responds to plant volatiles and, when given choices, demonstrates preference. We asked whether preferences for groups of host and non-host species observed in the laboratory are exercised in the field. We did this by releasing marked beetles under different wind conditions and recapturing them from four types of experimental plots in which hosts were interplanted with different non-host species.

Offprint requests to: P.A. Morrow (above address)

¹ and Department of Plant Biology, University of Minnesota, St. Paul, MN 55108, USA

Present addresses: ² Department of Biology, Clemson University, Clemson, SC 29634, USA

³ Environmental Defense Fund, 257 Park Avenue South, New York, NY 10010, USA

Table 1. Plant species and their taxonomic affiliations in the species, genus, family and orders plots. S, A, B and C refer to the positions of such species in the experimental design illustrated in Fig. 1a. Subtribe classification of the Asteraceae follows Heywood et al. (1977)^a

Species plots

S,A,B,C, *Solidago altissima*^b

Genus plots

S *Solidago altissima* L.
A *Solidago nemoralis* Ait.
B *Solidago missouriensis* Nutt.
C *Solidago rigida* L.

Family plots

S *Solidago altissima* L. (Astereae, Solidaginaceae)
A *Helianthus laetiflorus* Pers. (Helianthaceae, Helianthinae)
B *Liatris aspersa* (Michx.) Greene (Eupatoriaceae, Adcnostylinaceae)
C *Aster ericoides* L. (Astereae, Asterinae)

Orders plots

S *Solidago altissima* L. (Asterales, Asteraceae)
A *Asclepias tuberosa* L. (Gentianales, Asclepiadaceae)
B *Lepedeza capitata* Mickx. (Fabales, Fabaceae)
C *Monarda fistulosa* L. (Lamiales, Lamiaceae)

^a Voucher specimens of all species are in the University of Minnesota, Department of Plant Sciences herbarium. Vouchers of the *Solidago* species are also in the L.H. Bailey Hortorium, Cornell University

^b *S. altissima* ($N=54$) was distinguished from *S. canadensis* ($N=18$) by a count of chromosomes (Melville and Morton 1982). *S. altissima* is considered *S. canadensis* var. *scabra* by Cronquist (1980) and Werner et al. (1980)

Field site

Field work was conducted in July of 1984 and 1985 in experimental plots and fields at the University of Minnesota's Cedar Creek Natural History Area (CCNHA), a 2185 ha reserve 50 km north of Minneapolis, Minnesota. CCNHA is on the prairie forest border; the original vegetation was a mixture of fire-maintained oak savannah, prairie, upland deciduous forest and lowland marshes and swamps (Cushing 1963). Soils are 20–40 m deep outwash sediments of wellsorted fine and medium sands (Grigal et al. 1974) that are well drained and extremely low in nitrogen (Tilman 1984). Old fields support a sparse cover of herbs and grasses about 0.5 m tall.

We worked in experimental plots of native prairie plants in which one species was common to all plots and other species were unique to particular plots. For herbivores using the plant species common to all plots, this design allowed us to ask whether different groups of plant species influenced the probability that a plot would be colonized by *T. canadensis*. The ten plant species used in the plots (Table 1) are herbaceous perennials native to North American tallgrass prairie and are also those used in the olfactometer studies by Puttick et al. (1988).

Four types of experimental plots were used: a monoculture of *Solidago altissima* and three polycultures in which *S. altissima* was interplanted with three other species in the genus *Solidago*, three species from different tribes or subtribes of the same family (Asteraceae), or three species from different orders (Gentianales, Fabales, Lamiales).

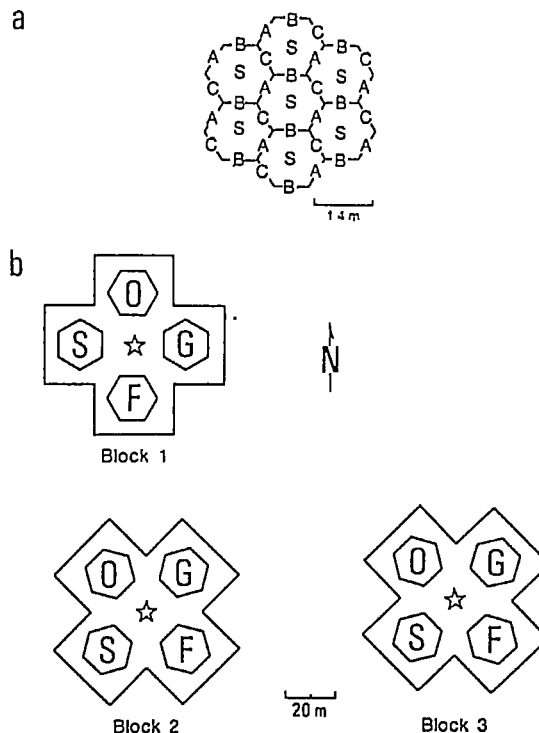


Fig. 1. a Detail of planting design for species in Table 1. A, B and C are neighboring species of *S. altissima*, S. Experimental plots were designed so that the outer row of plants in the polycultures does not contain *S. altissima*. b Layout of the four plot types in a block and orientation of replicate blocks in the field. The stars in the center of the blocks are release points for colonization experiments. Vegetation inside each block, excluding the hexagonal plots, is mowed. S, G, F and O are species, genus, family and orders plots, respectively

They are referred to as the species, genus, family, and orders plots respectively (Table 1). Within each of these increasingly diverse taxonomic groupings, we selected the most distantly related species from those species which are at CCNHA and have roughly similar growth forms. We controlled for growth form because many insects use shape as a long distance orientation cue, although they can only distinguish between plant species at close range (Stanton 1983).

Taxonomic distance between species reflects the degree of phytochemical similarity between plants (Ehrlich and Raven 1964; May and Ahmad 1983). The families represented in the orders plots are characterized by cardiac glycosides (Asclepiadaceae), alkaloids (Fabaceae), and monoterpenes (Lamiaceae) (Hegnauer 1964; Scora 1967). In the family plots, *Helianthus* and *Liatris* contain small quantities of sequi-, tri- and diterpenoids, *Aster* has just diterpenoids and *Liatris* and *Aster* produce simple phenolics (Heywood et al. 1977; M. Villani, unpublished data). The four *Solidago* species produce large amounts of steroids and lipids and contain simple phenolics and mixtures of kaurenoid and labdane diterpenoids (Cooper-Driver et al. 1987; Le Quesne et al. 1986); *S. rigida* and *S. missouriensis* have particularly large concentrations of diterpenoids, steroids and simple phenolics (Le Quesne et al. 1985). Thus, these experimental plots represented a continuum of phytochemical diversity from very diverse (orders plots) to very similar (species plots).

The plots were laid out in a hexagonal array (Fig. 1a). In the three polycultures, each individual was surrounded by six individuals – two of each of the other three species. Each plant was 0.7 m from each neighbor; plots were 21 m across. Each of the 12 plots had 721 plants. The plots were mulched with straw and each was surrounded by a sparse sward of mowed grass. A block consisted of one species, genus, family and orders plot; there were 3 replicates blocks (Fig. 1b).

The plots were established in a field abandoned in 1957 and burned two out of every four years since 1965. Seeds for all species in the plots were obtained from this or nearby fields. Seeds for the obligately outcrossed *S. altissima* (Melville and Morton 1982 and footnote in Table 1) came from a single clone with only one potential pollen donor in the vicinity, so all *S. altissima* in the plots are probably full sibs.

The plots were weeded so that soil between the experimental plants was bare or sparsely covered with straw mulch. In 1984, vigorous plant growth, especially of the rhizomatous *S. altissima*, made it impossible to census insects visually or to move through the plots without disturbing insects. We therefore trimmed all plants to a similar size, equivalent to an *S. altissima* with 3 ramets. Trimming was completed by mid-June, about 3 weeks before adult *T. canadensis* emerged and 5 weeks before the first experiment was done in the plots. In September 1984, the plots were burned and each plant was surrounded with a 10 cm diameter, 25 cm long plastic pipe sunk flush with the soil surface. All plants regenerated the following year; their growth was restricted by the small volume of soil in the tube and by low rainfall, so trimming was unnecessary in 1985.

Experimental insect

Trirhabda canadensis Kirby (Coleoptera: Chrysomelidae) is widespread in the northern United States and southern Canada where it feeds on *S. altissima* and *S. missouriensis* (Hogue 1970). In addition to using these goldenrods at CCNHA, *T. canadensis* populations also use *S. gigantea*. These three species are rhizomatous and form large, often isolated, clones in undisturbed prairie (personal observation). *S. altissima* was present in all plots and *S. missouriensis* was in the genus plots described above. Thus, for *T. canadensis*, the plots provide a gradient of decreasing host plant density in addition to a gradient of increasing phytochemical diversity. All individuals in the species plots were hosts (2.52 hosts/m²), two of the four species in the genus plots were hosts (1.23 hosts/m²), and one of four species was a host in the family and orders plots (0.64 hosts/m²).

T. canadensis egg masses overwinter in soil and in folds of dried leaves at the base of goldenrod plants (Balduf 1929). Larvae hatch in May, feed on and later pupate beneath host goldenrods (Messina 1982a). Adults emerge in late-June to early July and feed and mate repeatedly on goldenrods throughout the remainder of the growing season (personal observation). Messina (1982b) reported that the goldenrod leaf beetles *T. virgata* and *T. borealis* exhibited a pre-ovipositional dispersal period for about two weeks following the teneral phase, and were sedentary thereafter. For several weeks after emergence, *T. canadensis* are able to fly long distances but we have rarely seen them fly unless host plants are unavailable where they emerge; females

other than three weeks are generally gravid and disperse by walking (personal observation). We used beetles more than three weeks old in the experiments reported below. *Trirhabda* reach very high population densities in individual host clones and leave in large numbers over a short time when they have defoliated the clone (personal observation). Walking beetles cover 5.5 m/h on average with a top rate of 12.9 m/h (Puttick et al. 1988).

Field collected beetles used in the experiments described below were color coded with two spots of Testor's model paint on their elytra to identify data and place of release and, when determined, sex. They were allowed to feed during the time required to sex, mark and count them. Voucher specimens are housed in the Cornell University Insect Collection under lot number 1174.

Methods

Colonization experiments

To assess colonization we released marked beetles in the center of a block of plots (stars in Fig. 1b), and recaptured them as they entered the plots. In eleven experiments, we released either 150 marked beetles of each sex or between 144 and 200 unsexed beetles. Since no host plants were available at the release point, beetles had to move a minimum of 12.7 m to feed and oviposit.

The day before each experiment, we removed *T. canadensis* from the plots in which experiments were to be run. Marked beetles were released early on still mornings, while it was cool and the beetles inactive (0600 and 0900 h in 1984 and 1985, respectively). They dispersed as ambient temperature increased.

In 1984, colonization was assessed by censusing all plants 24 h after beetles were released. In 1985, released beetles were collected from all plants in the plots each time the plots were censused. On 5 July 1985, beetles were censused at 1200 h and 1600 h and on 15 July only at 1500 h. For the remaining 1985 releases we collected on three or more occasions between the time beetles first arrived at the plots and 1700 h on the day of release.

Data were modeled with multinomial logistic regression (Meyer 1981; Maddala 1983).

Wind measurements

Wind is measured at a small number of locations in central Minnesota. We used data from Becker, 54 km west of CCNHA, for our analyses (Seeley and Spoden 1984, 1985). Wind data available from Becker were 24 h vector wind direction (degrees), mean and vector windspeeds (m/s). Vector windspeed is the overall speed of the air when both speed and direction are taken into account and is considered the trajectory speed for airborne materials or organisms (Seeley and Spoden 1985). Wind constancy (vector windspeed/mean windspeed) provides a measure of the steadiness of wind during the 24 h period. Constancy varies from 0 to 1, where 1 indicates a wind blowing from one direction throughout the day and low values indicate highly variable winds with a circular or opposing distribution of wind directions (Baker 1983). On days of high constancy, mean and vector windspeeds are highly correlated. Days on which we ran experiments were clear, and winds had high constancies on 7 of the 8 days. Wind directions varied from 164°

Table 2. Colonizing beetles recaptured in each plot in a block of experimental plots. S, G, F, O are species, genus, family and orders plots, respectively. Wind direction is in tens of degrees where 36° is north; mean windspeed is in m/s; wind constancy varies from 0–1 with high values indicating increasingly steady winds and low values highly variable winds (see text). Upwind plot(s) for each experiment are in bold type. Orientation of the three blocks is shown in Fig. 1b. Wind data are from Becker except for 7/26/85 where wind direction was measured at CCNHA (see appendix)

Date	Beetles released	% recaps.	Block	No. recaps. in				Wind		
				S	G	F	O	direction	speed	constancy
7/11/84	300	12	1	21	7	4	4	29	1.7	0.89
7/18/84	300	45	3	96	25	6	7	22	1.8	0.69
7/22/84	300	43	3	94	6	23	6	19	3.7	0.82
7/05/85	144	60	1	21	35	7	23	33	2.9	0.72
7/15/85	149	23	2	12	5	1	16	31	2.4	0.84
7/23/85	150	46	2	46	19	2	2	16	4.0	0.73
7/25/85	200	26	2	50	40	8	17	32	1.8	0.75
7/25/85	200	46	3	13	29	8	41	32	1.8	0.75
7/26/85	200	44	1	39	26	13	9	32	1.3	0.55
7/26/85	200	43	2	38	26	11	11	32	1.3	0.55
7/26/85	200	39	3	28	22	10	18	32	1.3	0.55

(SSE) through 360° (N) and mean windspeeds varied from nearly calm (1.3 m/s) to strong (4.0 m/s) (Table 2).

We were able to use wind data from another site because, away from the Great Lakes, passage of frontal systems in the upper midwest are characterized by very uniform wind direction and windspeed fields (M. Spoden, personal communication and Appendix).

Results

Overall, 458 beetles colonized species plots, 240 colonized genus plots, 94 colonized family plots, and 154 colonized orders plots. An ANOVA on the number of beetles colonizing each plot showed that plot type significantly affected beetle colonization (Table 3, $F=10.15$; (3,30) df.; $P=0.0001$; square-root transformed data). The linear contrast (Snedecor and Cochran 1967) for the plot means (ordered species, genus, family and orders) was significant ($P\sim 0$); thus, statistically, the number of beetles colonizing plots declined as host density decreased and the diversity of phytochemicals increased.

This sequence of preferences (species > genus > family > orders) prevailed for most of the experiments. But there were several marked exceptions: wind direction and windspeed varied between experiments and appeared to affect beetle movement (Table 2). To understand how wind interacts with plot to influence beetle movement, we modeled the probability that a beetle will go to a particular plot under different wind regimes.

The *Trirhabda* colonization data were modeled with logistic regression (Fienberg 1980), the categorical analogue to standard multiple regression techniques. The response variable in logistic regression is binomial (probability of success = P , of failure = $1-P$); a linear regression model is developed for $\log(P/1-P)$. The response variable for our experiments, however, was multinomial since the beetles chose between the species, genus, family, and orders plots. Such multinomial responses can be modeled with a series of binomial logistic regressions (Meyer 1981; Maddala 1983) where P in each regression equals the probability of a beetle reaching a particular plot. S is the probability that a beetle goes to the species plot and G , F , and O

Table 3. ANOVA for the numbers of beetles colonizing each plot type

Source	df	MS	F	P
Experiment	10	2.78		
Plot	3	23.49	10.15	0.0001
Error	30	2.31		
Total	43			

are analogous probabilities for the other three plots. We modeled $\log S/G$, $\log G/F$, $\log F/O$, and $\log O/S$, with an iterative procedure programmed with the statistical package GLIM (Baker and Nelder 1978). (The ultimate probabilities do not depend on how the plots are paired.) We first modeled $\log S/G$ with the species and genus plot data. Then, using the fitted values for the genus plots from this regression, and the data for the family plots, we calculated the regression for $\log G/F$. This procedure was continued, cycling through the 4 regressions repeatedly, until the solution converged. After the first cycle only fitted values from the previous regression, rather than data, were used.

We repeated the entire fitting scheme a number of times, adding explanatory wind variables to the regression in a stepwise fashion. A variable was included in the regression if it explained a statistically significant amount of the deviance (McCullagh and Nelder 1983). We had a total of 33 degrees of freedom for the eleven experiments – three degrees of freedom for each experiment.

Wind direction was expressed with respect to the species plot, since the plots in a block are always oriented in the same way with respect to each other (Fig. 1b). Thus wind direction = (angle of the species plot with respect to north) – (angle of the wind direction with respect to north). When direction is 0 degrees the species plot is upwind; when direction = 180 degrees the species plot is downwind. Since direction is a circular variable, we worked with cosine (direction) plus sine (direction).

The predictive variables wind direction and mean windspeed were first added stepwise to the model; both significantly reduced the deviance (Table 4, $P < 1 \times 10^{-8}$). Then the variables (mean windspeed) \times (wind direction), wind

Table 4. Analysis of deviance for multinomial logistic regression used to model colonization probabilities (see text)

Variable	ΔG^2	df	<i>P</i>
Wind direction	110.3	6	$<1.0 \times 10^{-8}$
Wind speed	31.8	3	$<1.0 \times 10^{-8}$
Speed \times direction	27.6	6	$<1.2 \times 10^{-4}$

constancy, and vector windspeed were each added to the model. The interaction term was significant (Table 4, $P < 1.2 \times 10^{-4}$). Wind constancy did not reduce deviance significantly, probably because winds were generally steady throughout the region on experimental days. Vector windspeed also was not significant, probably because mean and vector windspeeds are highly correlated on days with constant winds. Our final model was

$$\log P/(1-P) = \text{block} + \text{wspd} + \cos + \sin + (\text{wspd} \times \cos) + (\text{wspd} \times \sin)$$

where block is block 1, 2 or 3 and wspd is mean windspeed.

Because the iterative fitting procedure cycled through the four regressions, the model was the same for all the paired comparisons of plots (e.g. log S/G, log G/F), although the parameter estimates (equivalent to slopes) varied depending upon which pair of plots were compared. By simultaneously solving three of the regression equations we calculated the probability that a beetle goes to a particular plot as a function of wind direction and speed.

The probabilities of colonizing each plot under different wind conditions are presented graphically for each plot type (Fig. 2) as the position of the plot varies from upwind to downwind and windspeed varies from nearly calm to strong. The range of windspeeds, 1–4 m/s, is approximately the range over which our experiments were run.

The probability that an orders plot will be colonized is high if windspeed is high and the plot is upwind of the beetles' release point, but declines rapidly as wind direction

shifts or windspeed drops. A similar pattern of colonization occurs in genus plots except the rate at which probability of colonization declines is lower in genus than orders plots. Moreover, a genus plot always has a moderate probability (0.2–0.25) of being colonized at low windspeeds, regardless of wind direction. This is not the case for orders plots, for which the probability of colonization at low windspeeds is always less than 0.1. Like orders and genus plots, species plots have the highest probability of being colonized when they are upwind and windspeed is high (Fig. 2). But colonization of species plots differs in two ways: 1) probability of colonization decreases little as windspeed declines, and 2) at low windspeeds, the probability of colonizing a species plot that is cross- or downwind of the release point increases. At very low windspeeds, species plots have a fairly high and constant probability of being colonized irrespective of wind direction ($P \sim 0.5$ – 0.75).

Family plots have a low probability of being colonized under any conditions. This may reflect that no experiments were run on days when family plots were directly upwind or that family plots are unattractive to beetles under any circumstances.

Discussion

Considerable anecdotal evidence suggests that herbivorous insects use host plant volatiles to facilitate host finding. There are however few well documented examples of host finding in the field from distances greater than 1 m (Miller and Strickler 1984; but see Hawkes 1974). There are several reasons why this may be so.

First, the ability of insects to use host odors is influenced by both concentration and the presence of non-host odors that interfere with host finding (Altieri and Letourneau 1982; Cromartie 1981; Kareiva 1983; May and Ahmad 1983; Ralph 1977; Risch et al. 1983; Tahvanainen and Root 1972; Thiery and Visser 1986). As in nature, these factors were confounded in our plots. We found that, overall, more beetles colonized the species than the genus plots,

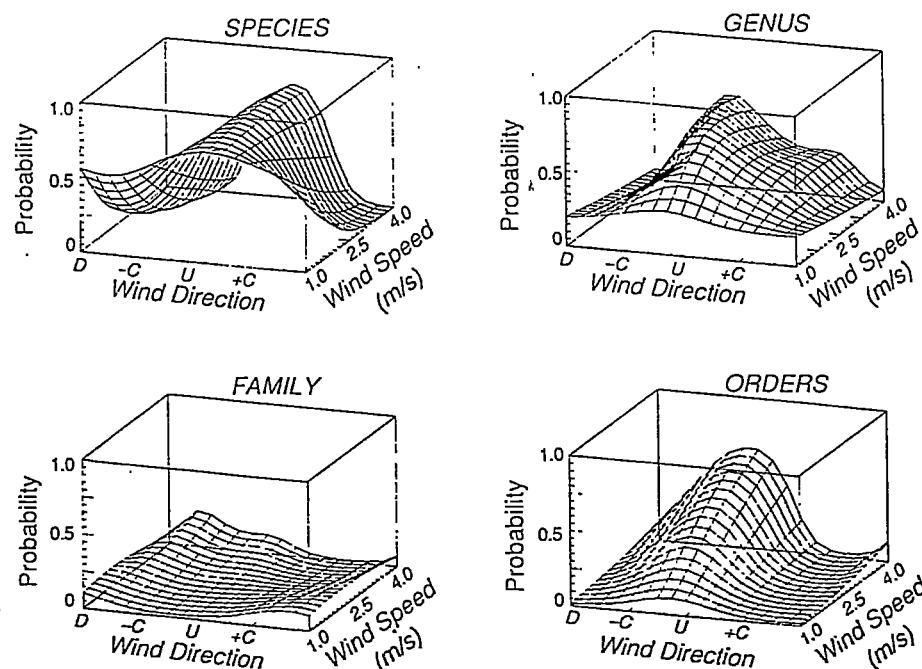


Fig. 2. The probability that a beetle will colonize different plots in a block under different wind conditions. Wind direction indicates the orientation of each plot with respect to the wind and the beetle release point (see text). U = plot upwind of release point, D = downwind, +C, -C = cross-wind of the release point (90° clock- and counterclockwise, respectively, from the upwind direction)

and more beetles colonized the genus than the family and orders plots. Since host density decreases in the order species>genus>family = orders, beetles may prefer higher over lower concentrations of host volatiles, as they do at lower concentrations of volatiles in the laboratory (Puttick et al. 1988). However, this order of preferences is also consistent with non-host odors interfering with host-finding. Choice in the field is probably not based entirely on host density, since Puttick et al. (1988) found that beetles preferred a given concentration of pure host odor over the same concentration blended with odors of non-host species characteristic of each type of plot.

The second reason why long distance host-finding is little documented is that air flow in the field is very complex. Insects in the laboratory may repeatedly demonstrate preferences. But, out of doors they may not always receive information in ways that allow them to exercise preference. It has generally been assumed that the concentration of volatiles declines with increasing distance from the source and that insects move upwind inside the resultant plume (Bell 1984; Stanton 1983). Most methods of calculating the distribution of plumes predict mean concentrations (Elkinton and Cardé 1984; Murlis 1986; Stanton 1983).

But insects do not experience averages outside of wind tunnels (Kennedy 1986). Instead, plumes are disrupted and convoluted by turbulent eddies (Kramer 1986; Murlis 1986) which cause them to undulate and to break into different sized pockets of air which vary in volatile concentration from undiluted to odorless (Aylor 1976; Murlis 1986). So a stationary insect or one moving upwind in a straight line would encounter a series of bursts of odor separated by odorless air pockets (Murlis 1986). It is not clear how these tortured odor plumes are used for orientation by flying (Cardé 1986; Kennedy 1986; but see David et al. 1983) or walking insects (Borden et al. 1986; May and Ahmad 1983; Visser 1976) or how plumes generated from an insect's scent gland differ from those created by a group of plants (Cardé 1986).

Our data suggest that in the field *T. canadensis* use volatiles in host finding and that both wind and vegetation composition influence movement. Beetles chose between plots on calm days and colonized upwind plots on windy days. This behavior suggests that beetles released in the center of a block of plots (Fig. 1b) on windy days received odors just from the upwind plot(s) but on still days, odors also reached them from cross-wind plots.

This might occur because the size and movement of turbulent eddies that disrupt odor plumes varies with wind-speed. Eddies are generated in two ways; by heat and by friction (Campbell 1976; Legg and Bainbridge 1978; Pedgley 1982). Thermal turbulence is created when air is heated at the surface, becomes buoyant and rises. Mechanical turbulence is created by friction between air and surface. Thermal eddies are dominant under calm conditions and are larger and fluctuate more slowly than eddies produced by the mechanical turbulence dominant at higher windspeeds (Campbell 1976). At lower average windspeeds, large slow moving eddies might bring cross-wind odors to a beetle. At higher average windspeeds, small quickly moving eddies might only bring upwind volatiles to a beetle. Analogously, turbulence associated with low velocity winds is thought to account for the greater lateral spread of spores observed with lower than higher velocity winds (Wolfenbarger 1975).

Dispersing beetles frequently climb stems, ca. 0.5 m tall

at CCNHA, where they appear to sample the air stream for several minutes to several hours before descending the stem and walking on (Puttick et al. 1988). If beetles sample the air stream for host volatiles, they do so near the ground where the influence of temperature gradients, wind drag, topography and local obstacles are much greater than at 3 m (Campbell 1979; Chamberlain 1975), the height of weather sensors at Becker. Given the coarseness of averaged wind data and that wind measurements were not made in the experimental plots, the terms in the model (Table 4) have remarkably high significance values. This is encouraging since accurate characterization of air movement near the ground is technically difficult and expensive to measure (Aylor et al. 1976; Burrage 1978).

Beetles chose species over genus plots, and genus over family and orders plots at low windspeeds, when they may have received chemical signals from a wider array of plots than at high windspeeds. Whatever the balance of factors – plant density, plant diversity, or others – contributing to preference, the field data strongly suggest several conclusions. *T. canadensis* use volatiles to guide them to distant host plants; they will accept a mix of host and non-host odors in the absence of choice; a model of downwind dispersion of plant volatiles to which insects react by walking upwind is too simple to explain their movements. A slightly more complex model, in which beetle preference and the influence of windspeed on odor dispersion influence the probability of plant colonization, explains our movement data much better.

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Appendix

Three stations within 79 km of CCNHA record wind direction and speed. Average wind direction for days on which we did experimental releases of beetles are given for these stations in Table 5. Also shown are estimates of wind direction made from a wind vane located between experimental blocks 1 and 2 at CCNHA (Fig. 1b). Wind directions at the stations are remarkably close in spite of the lack of measurement uniformity at the sites (station details in Table 5). Only on 26 July 1985, a calm day with inconstant winds (Tables 2, 5), did wind direction vary much between stations.

Average windspeeds for the three stations appear much more variable than wind directions (Table 5). This is probably largely because sensor height is different at each station. Nearer the ground windspeed is lower and more strongly influenced by local surface features. For each station, the rank of the windspeed, from lowest to highest, is shown in parentheses. The within station rankings are virtually the same (Spearman rank correlations, $r_s = 0.95$, $P \ll 0.01$, Sokal and Rohlf 1981) indicating that winds were fairly uniform across the region on experimental days and that relative values – calm, moderate or strong – can be extrapolated to CCNHA with some confidence.

With one exception, we used Becker data for our analyses.

Table 5. Wind directions (tens of degrees) and windspeeds (m/s) measured at stations within 79 km of CCNHA. Numbers in parentheses are within station ranking of windspeed from lowest to highest, see text. Height is height of sensor placement above ground; distance is km between station and CCNHA; direction is direction in degrees from CCNHA to station (18° is south)

Station	Wind direction (10's of degrees)				Windspeed (m/s)		
	CC ^a	BEK ^b	STC ^c	MSP ^d	BEK	STC	MSP
height	2	3	6	10	3	6	10
distance	-	54	79	63	54	79	63
direction	-	27	28	18	27	28	18
Date							
7-11-84	-	29	29	28	1.7 (2)	3.3 (3)	9.0 (3)
7-18-84	-	22	21	22	1.8 (3)	1.2 (2)	6.9 (2)
7-22-84	-	19	18	19	3.7 (7)	5.2 (7)	14.2 (7)
7-05-85	-	33	34	34	2.9 (6)	5.0 (5.5)	13.1 (6)
7-15-85	-	31	31	31	2.4 (5)	5.0 (5.5)	11.8 (5)
7-23-85	18	16	18	18	4.0 (8)	6.4 (8)	15.2 (8)
7-25-85	31	32	31	31	1.8 (4)	3.6 (4)	11.2 (4)
7-26-85	32	36	36	30	1.3 (1)	0.7 (1)	6.5 (1)

^a CC=University of Minnesota, Cedar Creek Natural History Area, Bethel, MN. In 1985, wind direction was estimated by eye from a wind vane located at a height of 2 m, every 15 minutes, 0900-1700 h. Beginning in 1987, wind measurements are as described for BEK

^b BEK=University of Minnesota, Sand Plain Experimental Farm, Becker, MN, Continuous electronic measurements summarized as mean windspeed, vector windspeed and vector wind direction, midnight to midnight. Data source: University of Minnesota Cooperative Agricultural Weather Advisory Program

^c STC=St. Cloud Municipal Airport, St. Cloud, MN. Average of three 3-hour averages of electronically measured windspeed and wind direction taken at 0900, 1200, 1500. Data source: Local Climatological Data Monthly Summary, National Oceanic and Atmospheric Administration (NOAA)

^d MSP=Minneapolis/St. Paul International Airport, Minneapolis, MN. Electronic measurements with averages based on 21 or more hourly observations summarized as resultant wind direction and resultant windspeed, midnight to midnight. Data source: NOAA

This station is nearest CCNHA and has wind sensors nearest the ground. Also, it has a weather station like one established at CCNHA in 1987, two years after our experiments were completed. Wind patterns in July 1987 (Seeley and Spoden 1987) were very similar at the two sites (vector wind direction, $r_s=0.88$, $P \ll 0.01$, and windspeed, $r_s=0.73$, $P \ll 0.01$). Below 2 m/s, windspeeds are very similar but on windy days, Becker windspeeds tend to be higher than at CCNHA, the difference increasing with windspeed. For the 26 July 1985 wind direction, we used the average value measured at CCNHA rather than Becker; this very calm day was the only day on which wind direction was not constant across the region (Table 5).

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