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FEEDING PATTERNS AND ATTACHMENT ABILITY OF *ALTICA SUBPLICATA*
(COLEOPTERA: CHRYSOMELIDAE) ON SAND-DUNE WILLOWAron J. Gannon, Catherine E. Bach and Glenn K. Walker¹

ABSTRACT

To investigate feeding patterns of a specialist herbivore, *Altica subplicata*, larvae and adults were caged separately on host plants, *Salix cordata*, and leaf damage was estimated. Young, relatively more pubescent leaves near the tops of the shoots were consumed more than older leaves. Larvae clearly preferred the young, pubescent leaves and avoided the oldest leaves. Adults showed a stronger preference for the first five young leaves, but amount of consumption did not differ among the older leaves.

Attachment ability on smooth and pubescent leaves was examined as a possible factor influencing feeding patterns. Scanning electron microscopy of tarsal adhesive structures and leaf surfaces was conducted to investigate how *A. subplicata* attaches to its host. Adhesive setae on the tarsi of adults may be effective for attachment on the older, smooth leaves and their tarsal claws are likely used to cling to trichomes of pubescent leaves. Larvae have fleshy adhesive pads for attachment. Laboratory experiments on attachment of larvae and adults to smooth and pubescent leaves under various wind conditions showed that wind caused difficulty in attachment and movement, but leaf pubescence did not affect the number of beetles that fell off leaves. However, larvae fell off more quickly when placed on pubescent leaves. Thus, other factors such as nutritional quality and microclimate provided by trichomes may be responsible for the preference for pubescent leaves exhibited by *A. subplicata*.

Many specialist phytophagous insects exhibit very specific patterns of feeding behavior and distributions in response to food plant variability. Insects have been shown to prefer younger leaves that have higher nitrogen and water content than older leaves (Phillips 1976, Wilson 1986, Cassin 1989). Different leaf topographies such as wax blooms and pubescence, which vary with leaf age and plant phenotype, also influence insect distribution (Stork 1980a, Edwards 1982, Rowell-Rahier 1984, Lee et al. 1986, Kennedy 1986, Wilson 1986, Eigenbrode et al. 1991).

Attachment ability is an important component of insect specialization because insects that fall off a plant may feed less, risk desiccation and not be able to relocate the plant. These consequences are especially apparent for less mobile larvae. Cassin (1989) found that larvae of a willow flea beetle, *Altica subplicata* LeConte, placed on the ground were recaptured less often than larvae placed on plants in a mark-recapture experiment, suggesting adverse effects when larvae fall off plants.

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In many studies, the inability of herbivores to utilize leaves of certain textures is based on attachment. Lee et al. (1986) found that the potato leafhopper, *Empoasca fabae* Harris, was unable to orient in a proper feeding position or move about effectively on a pubescent variety of soybean. Studying oak aphids, Kennedy (1986) found that species with identical tarsal structures differed in attachment ability on smooth, rough, and pubescent leaves based on the positioning of tarsi. Glaucous (waxy) leaves also affect attachment and movement ability of insects, and hence, such leaves show resistance to damage (Stork 1980a, Edwards 1982, Eigenbrode et al. 1991). Stork (1980a, b, c) examined the morphology and adhesive mechanism of the tarsal setae of leaf-feeding adult Coleoptera. Based on scanning electron microscopy (SEM) and laboratory experiments, adhesive setae appear to attach by "molecular adhesion" and require a smooth substratum to gain sufficient contact for beetle attachment.

In this study we examined the feeding patterns of a willow flea beetle, *A. subplicata*, and the role of attachment ability in influencing these feeding patterns. Both larvae and adults feed on *Salix cordata* Michaux, the leaves of which are densely pubescent compared to other willow species. In *S. cordata*, pubescence appears to decrease with leaf age. Since larvae and adults tend to feed on young willows along the lakeshore where wind speeds are greatest, attachment may affect foraging ability. Our specific questions for this study were: (1) Does *A. subplicata* show feeding preferences for *S. cordata* leaves of various ages? (2) If so, do these feeding preferences differ between larvae and adults? (3) Do larvae and adults differ in the morphology of tarsal adhesive structures? (4) Does attachment capability of larval and adult *A. subplicata* differ on young, pubescent leaves vs. older, smooth leaves? (5) Does wind affect attachment duration?

MATERIALS AND METHODS

Feeding Preference Test. To determine if larvae and adults exhibit a feeding preference for young vs. old leaves of *S. cordata*, we selected 20 plants of approximately equal size along the lakeshore at Grass Bay Nature Conservancy Preserve on Lake Huron, Cheboygan Co., MI. For each pair of neighboring plants, we randomly assigned a treatment of either 10 larvae or 10 adults. Undamaged branches from each plant were covered with mesh bags containing adults or larvae on 19 July, 1993.

Damage estimates were recorded on the sixth day of the experiment for the two largest shoots in each mesh bag (except for three bags which had only one shoot). Leaves were numbered on each shoot within the mesh cages, 0 designating the young unexpanded leaves at the shoot apex and 1 being the first opened leaf, then numbers increased down the shoot. Thus, leaf number increased with leaf age. Damage was estimated visually by assigning to each leaf a damage category of 0 to 6 (0=0% leaf area removed, 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-99%, 6=100%). Damage categories were converted to mean percentages to calculate mean damage for each leaf number and two-way ANOVAs were performed to determine how extent of damage was affected by beetle stage, leaf age, and the interaction between beetle stage and leaf age.

SEM of Insect Tarsi and Leaf Surfaces. To examine the structures that *A. subplicata* uses for attachment, scanning electron micrographs were made of both adult and larval tarsi. Specimens collected from the study site were fixed in 3% glutaraldehyde in phosphate buffer and dehydrated to absolute acetone.

In order to clean off mucus, specimens were agitated in a sonicator, then cleaned with a fine artist's brush under a dissecting microscope.

Micrographs of *S. cordata* leaves were made to view the surface structures that might have influenced the attachment ability of *A. subplicata*, and also to quantify how trichome density varied with leaf age. Leaves were first fixed in buffered glutaraldehyde, post-fixed in 1% phosphate buffered osmium tetroxide and dehydrated in ethanol.

The leaves, seven adults and seven larvae were critical point dried, mounted on aluminum stubs with Duco cement and graphite paint, then sputter-coated with gold. The prepared specimens were viewed under an 1820I Amray scanning electron microscope at 10 Kv.

Leaf hair density was estimated for leaf numbers 1, 3, 5, 7, and 9 from 3 plants by placing a 6.4 mm grid over 102×127 mm micrographs of leaf surfaces at 100X magnification. The number of grid points that crossed leaf hairs was recorded.

Larval and Adult Attachment. The attachment ability of larvae and adults on smooth and hairy leaves was tested in the laboratory under three conditions: no wind, low, and high wind speeds. *Salix cordata* shoots collected from Grass Bay were inserted into cork stoppers in 250 ml Erlenmeyer flasks containing water. The shoots were placed 1.5m from a fan at high speed to simulate low wind (2.4m/s) and 0.8m from the fan for high wind (3.85m/s). These wind speeds are comparable to typical field conditions. Average wind speeds near the shore of Lake Michigan, measured with a digital anemometer, were 1.6 m/s and 3.7 m/s on two moderately windy days.

During mid-July to early August, 1993, 104 attachment trials were conducted with larvae (40 without wind, 40 with low wind, and 24 with high wind) and 82 trials were conducted with adults (32 without wind, 24 with low wind, and 26 with high wind). Shoots from 19 separate plants were used. For each trial one larva or adult was placed on a smooth or hairy leaf. Larvae tended to be more agitated after handling and were allowed to acclimate for one minute before being subjected to wind. During the high wind treatment, the fan was turned on medium speed for the first minute, then on high speed. The insects' location on the shoot at the time they fell off the leaf or after 10 minutes, and the time elapsed before falling were recorded.

To determine if time before falling off leaves and movement were affected by leaf type and wind condition, two-way ANOVAs were conducted separately for adults and larvae, testing for effects of leaf type, wind condition, and an interaction between leaf type and wind condition. Data on number of larvae falling off leaves and moving between leaf types were analyzed with chi-squared tests.

RESULTS

Feeding Preference Test. Larvae and adults showed a strong preference for young leaves, specifically leaves 0-5 (Fig. 1A, $F=40.5$, $df=(4,666)$, $p < 0.001$). The two stages differed in the amount of damage they caused, with larvae causing significantly more damage than adults (Fig. 1A, $F=9.3$, $df=(1,666)$, $p=0.002$). More importantly, larvae and adults differed significantly in how strongly they preferred the younger leaves because of the significant interaction between beetle stage and leaf category ($F=6.0$, $df=(4,666)$, $p < 0.001$). There was a greater proportional decrease in damage between the first and second leaf categories for adults than for larvae, thus adults exhibited a stronger preference for the youngest leaves (Fig. 1A). However, larvae

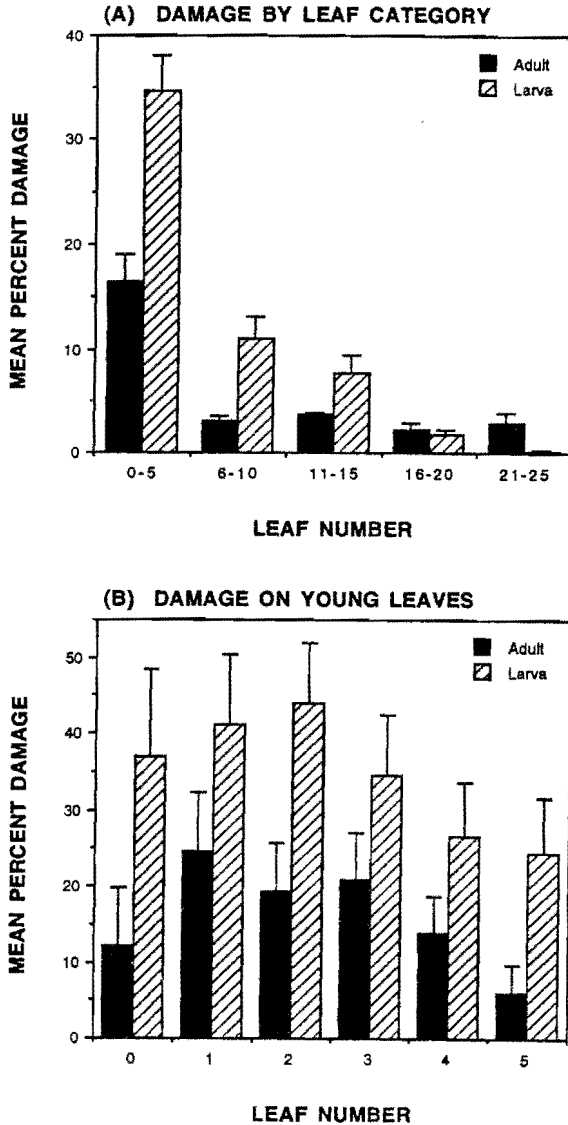


Figure 1. (A) Means and standard errors of percent damage (leaf tissue removed) by *A. subplicata* larvae and adults on five leaf categories ranging from youngest leaves (0-5) to oldest leaves (21-25). Sample sizes of each leaf category are: adults (102, 77, 68, 67, and 32, respectively); larvae (108, 85, 77, 42, and 18, respectively). (B) Means and standard errors of percent damage by larvae and adults on the five youngest leaves (0 designates unexpanded leaves at the shoot apex; 1 is the first expanded leaf). Sample sizes for each leaf number are: adults (13, 18, 18, 18, 18, and 17, respectively); larvae (13, 20, 20, 18, 19, and 18, respectively).



Figure 2. Electron micrograph of *A. subplicata* larval adhesive pad and tarsal claw. $\times 1,040$.

almost never fed on the oldest leaves, but adults caused similar amounts of damage to all leaf categories except the first category (Fig. 1A).

When the preference for young leaves (0-5) exhibited by both larvae and adults was analyzed separately for leaves 0-2 and leaves 3-5, mean damage was significantly greater on leaves 0-2 than on leaves 3-5 (Fig. 1B; $F=4.6$, $df=(1,206)$, $p=0.032$). Larvae again caused significantly greater damage than did adults ($F=18.4$, $df=(1,206)$, $p<0.001$), but differences between damage on the two categories of leaves were consistent for larvae and adults ($F=0.67$, $df=(1,206)$, $p=0.41$).

SEM of Insect Tarsi and Leaf Surfaces. The tarsi of larvae are distinctly different from those of adults. The larval attachment structure consists of a fleshy adhesive pad adjacent to a single claw (Fig. 2). Cleaning the specimens under a dissecting microscope revealed a clear and fragile pad which, under SEM, was seen to have an irregularly folded cuticle and sparse, simple tarsal setae.

The tarsus of the adult beetle is a complex structure and is composed of tarsomeres covered with thick clusters of adhesive setae (Fig. 3A). The setae of the third tarsomere have a double-pointed, spatulate adhesive plate, with setules on the dorsal side of the adhesive plate (Fig. 3B). The first and second tarsomeres have more simple, pointed setae (Fig. 3C). In addition, adults have two divergent, toothed claws beyond the final tarsomere (Figs. 3A).

Electron micrographs of different ages of *S. cordata* leaves show that the density of leaf hairs decreases with leaf age (Fig. 4). Counts of trichome densi-

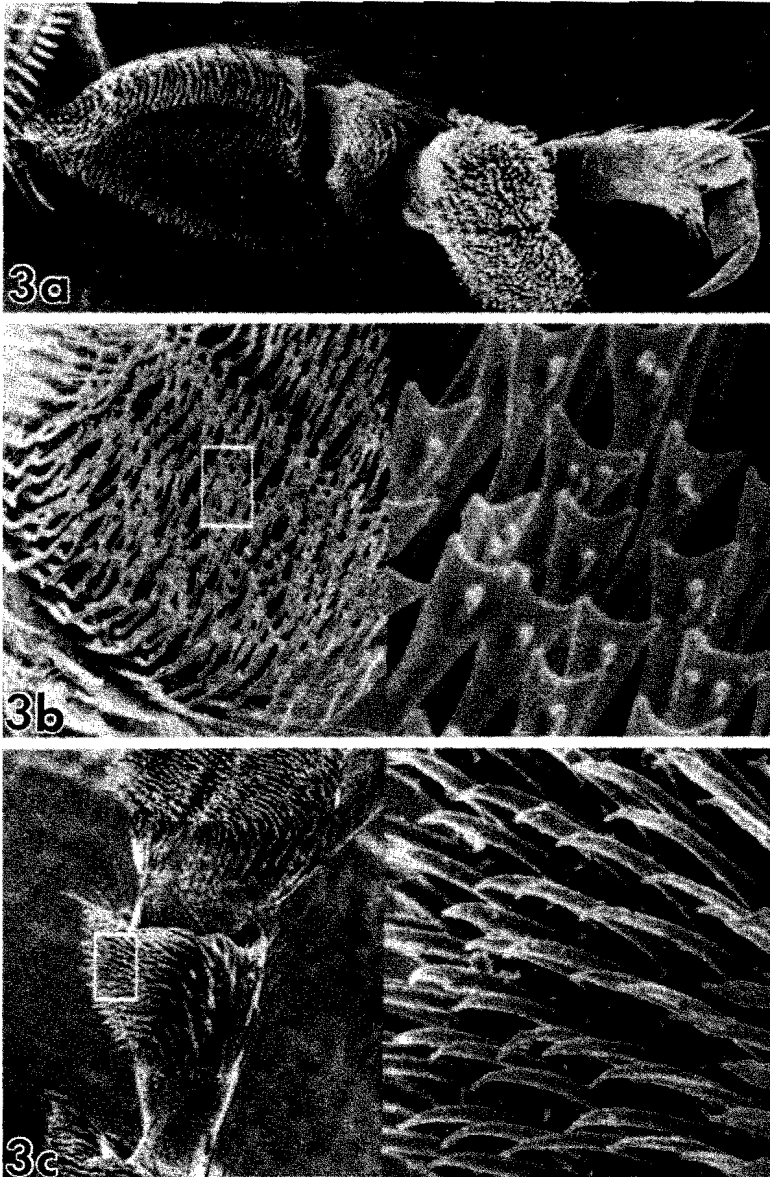
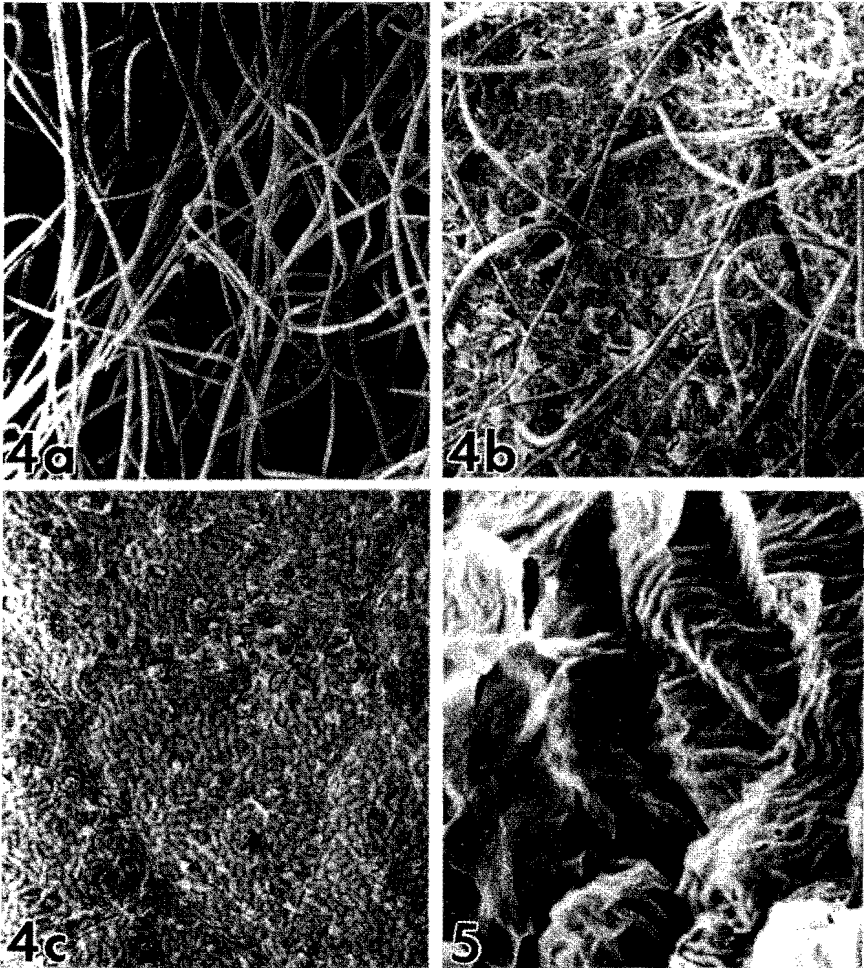


Figure 3. Adult *A. subplicata* adhesive structures: (A) adult tarsus from third leg, x114, (B) adhesive setae from third tarsomere with enlargement of adhesive plates with setules (x405; right figure, x3,270) and (C) first, second, and third tarsomeres with enlargement of simple, pointed setae from second tarsomere (x139; right figure, x1,370).



Figures 4 and 5. Fig. 4. Surfaces of *S. cordata* leaves: (A) First leaf, (B) fifth leaf, and (C) ninth leaf. Micrographs were taken of the center of each leaf next to the mid-vein. $\times 74$. Fig. 5. Surface of smooth *S. cordata* leaf. $\times 1,270$.

ties (number of grid intersections overlaying a trichome) on leaves of 3 plants showed a clear pattern of decreasing pubescence with leaf age (leaf 1, 145.7 ± 17.5 ; leaf 3, 100.0 ± 16.9 ; leaf 5, 82.7 ± 5.8 ; leaf 7, 62.7 ± 25.8 ; leaf 9, 23.0 ± 7.2). Average trichome densities on the youngest leaf were over 6 times greater than on the ninth leaf.

In order to view the texture of smooth *S. cordata* leaves, high magnification micrographs were made of the surface of older leaves. This revealed a highly reticulated, uneven surface (Fig. 5).

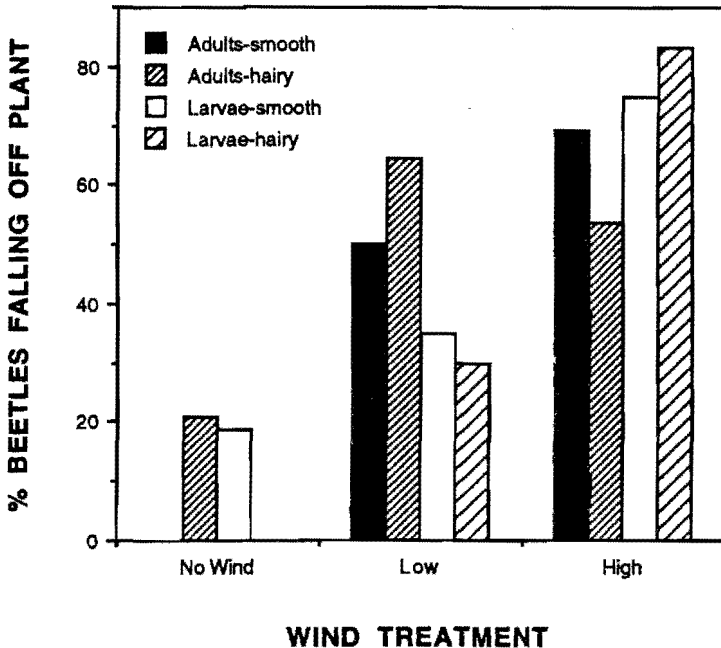


Figure 6. Percent *A. subplicata* larvae and adults that fell off leaves from pubescent (hairy) and smooth leaves under 3 wind treatments. Sample sizes for adults-smooth, adults-hairy, larvae-smooth, and larvae-hairy are: no wind (3, 29, 16, and 24, respectively); low wind (10, 14, 20, and 20, respectively); high wind (13, 13, 12, and 12, respectively).

Larval and Adult Attachment. Under all three wind intensities, leaf type (smooth and hairy) did not affect the number of larvae or adults that fell off leaves during the ten minute trials (chi-squared tests, $P > 0.05$ for all), although wind caused more insects to fall off leaves (Fig. 6), both for larvae (chi-squared=34.6, $df=2$, $P < 0.001$) and adults (chi-squared=12.1, $df=2$, $p < 0.005$). Wind intensity also affected the length of time adults and larvae remained on leaves before falling off (Table 1). Both adults and larvae remained on leaves longer under low wind than under high wind conditions (Fig. 7, Table 1), but the time beetles remained on leaves was only affected by leaf type for larvae (Table 1). Under low wind conditions larvae fell off hairy leaves more quickly than smooth leaves (Fig. 7, Table 1).

Wind speed also significantly affected the amount of movement for both larvae and adults (Table 1). Distance traveled along a shoot (determined by number of transitions between leaves) was greatest in the absence of wind (Fig. 8). Leaf type greatly affected the amount of movement for adults, and there was a significant interaction between leaf type and wind treatment (Table 1, Fig. 8). In the absence of wind adults tended to climb towards the top of the shoot when placed on smooth leaves (Fig. 8). Of 16 adults placed on smooth leaves in the no wind treatment, only three remained on smooth

Table 1. Results from 2-way ANOVAs of time before *Altica subplicata* adults and larvae fell off leaves for the attachment experiment. Only those insects that fell during the 10-minute trials were used for analysis.

	Effect								
	Leaf Type			Wind Condition			Interaction		
	F	df	P	F	df	P	F	df	P
Time before falling									
Adults	0.001	1,26		10.4	1,26	**	0.00	1,26	
Larvae	7.2	1,28	**	8.6	1,28	**	5.0	1,28	*
No. leaf transitions									
Adults	13.0	1,76	***	26.4	2,76	*	10.8	2,76	*
Larvae	0.44	1,98		8.7	2,98	*	0.62	2,98	

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

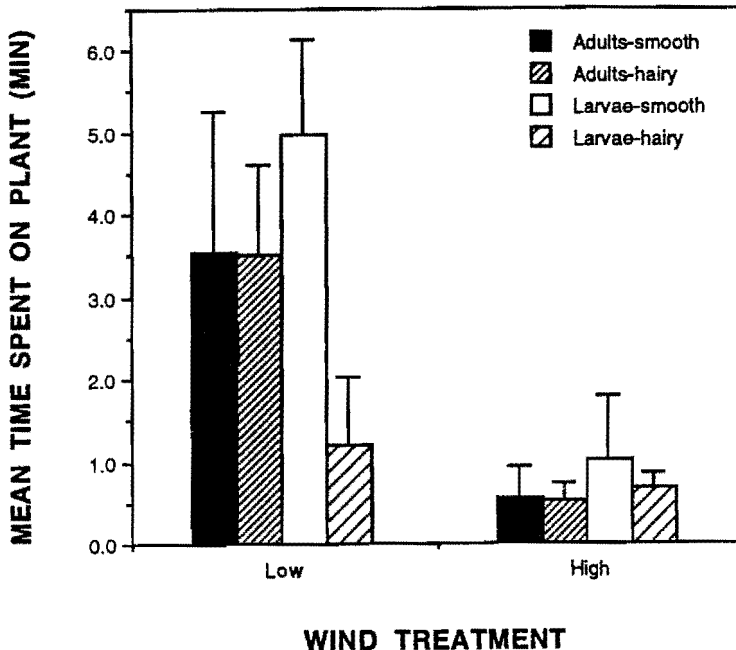


Figure 7. Means and standard errors of time (in minutes) that *A. subplicata* larvae and adults spent on leaves before falling from smooth or pubescent (hairy) leaves under 3 wind conditions. Sample sizes for adults-smooth, adults-hairy, larvae-smooth, and larvae-hairy are: low wind (5, 9, 7, and 6, respectively); high wind (9, 7, 9, and 10, respectively).

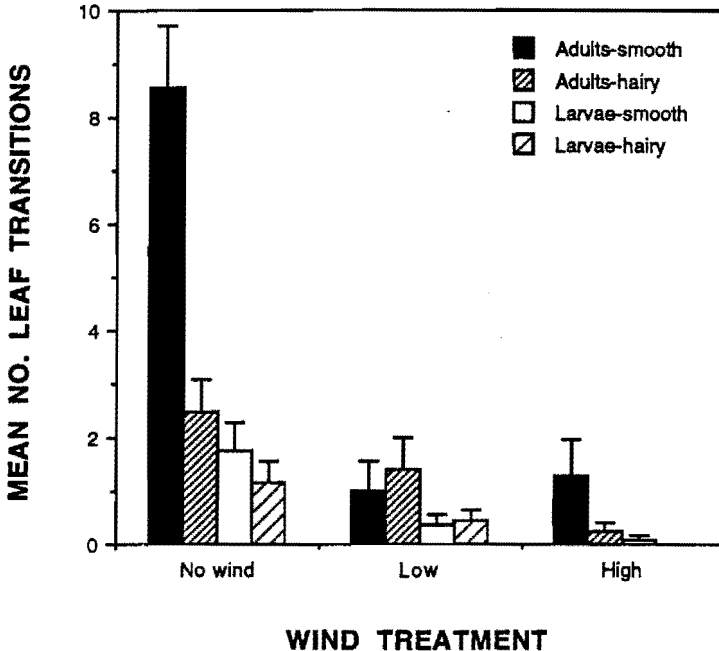


Figure 8. *Altica subplicata* larval and adult movement indicated by number of leaf transitions (absolute value of leaf number at end of trial - leaf number at start of trial) after initial placement on smooth or hairy leaves. Data presented are means and standard errors for adults and larvae placed on smooth or hairy leaves exposed to 3 wind treatments. Sample sizes for adults-smooth, adults-hairy, larvae-smooth, and larvae-hairy are: no wind (16, 16, 20, and 20, respectively); low wind (12, 12, 20, and 20, respectively); high wind (14, 12, 12, and 12, respectively).

leaves. The direction of movement indicates a strong preference for hairy leaves, because larvae and adults never moved from hairy to smooth leaves (Table 2). Wind greatly reduced the number of adults that moved from smooth to hairy leaves (chi-squared=21.0, $df=2$, $p < 0.001$) and larvae never changed leaf type during wind treatments (Table 2).

DISCUSSION

Results from the leaf preference test showed that larval and adult *A. subplicata* strongly prefer the youngest leaves from *S. cordata* shoots. Field observations also confirm a pattern of greater beetle densities and damage on the youngest leaves. Other studies attribute movement patterns toward younger leaves and preferences for young leaves to higher leaf nutritional quality (Phillips 1976, Wilson 1986). Cassin (1989) found higher nitrogen levels in young leaves than in older leaves of *S. cordata*. However, the younger

Table 2. Number of transitions between leaf types during 10-minute trials for *Altica subplicata* adults and larvae as a function of the leaf type on which insects were initially placed (smooth or hairy) and wind condition (no wind, low wind, or high wind). S refers to smooth, H refers to hairy, and "stay" means that insects did not change leaf type during the trial.

Leaf Type	Wind	Adult Movement			Larval Movement		
		S to H	H to S	Stay	S to H	H to S	Stay
Smooth	None	13	—	3	4	—	16
Smooth	Low	2	—	10	0	—	20
Smooth	High	1	—	13	0	—	12
Hairy	None	—	0	16	—	0	20
Hairy	Low	—	0	12	—	0	20
Hairy	High	—	0	12	—	0	12

leaves of *S. cordata* also have higher pubescence and trichomes often hinder feeding by imposing a barrier to the leaf surface and deterring attachment (Stork 1980c, Rowell-Rahier 1984, Wilson 1986). *Altica subplicata* does not consume *S. cordata* trichomes, which are devoid of nitrogen and low in water (Cassin 1989). In fact, in larval development tests in which larvae were fed smooth and hairy *S. cordata* leaves of the same age, Milanowski and Bach (1994) found that larval development was faster and pupae had greater weights when reared on plants with smoother leaves. Thus, it seems likely that the nutritional benefits gained by feeding on young, hairy *S. cordata* leaves must outweigh the costs of more difficult feeding.

Stork (1980a, b) and Edwards (1982) found that adhesive setae on tarsi of adult beetles aid in attachment on smooth surfaces but are not effective on pubescent leaves and glaucous leaves. Similarly, adult *A. subplicata* were probably able to feed on older, smooth *S. cordata* leaves in the preference test by attaching with their adhesive setae. Stork (1980b) concluded that molecular adhesion between the setae and the substratum is responsible for beetle attachment. Pubescent and glaucous leaves do not give the setae proper contact with the leaf surface and waxes also are trapped between the setae. However, the tarsal claws of beetles and other insects have been shown to be effective for clinging to rough surfaces such as pubescent leaves (Roth and Willis 1952, Stork 1980a, b, Kennedy 1986, Lees and Hardie 1988). Adult *A. subplicata* probably use their tarsal claws to hook on to the dense tangle of trichomes on young leaves (see Fig. 4A). In the field, this method of attachment may be more effective than adhesive setae on smooth *S. cordata* leaves, due to waxes and minute surface irregularities on the smooth leaves. However, the laboratory attachment experiment indicated that leaf topography did not affect attachment ability in adults.

The mechanism for attachment of coleopteran larvae is less well understood. The adhesive pad of larval *A. subplicata* may be functionally similar to the tarsal pulvilli of the potato leafhopper, *E. fabae* (Lee et al. 1986), and the aphid, *Megoura viciae* Buckton (Lees and Hardie 1988), and also the euplantulae and aroliar pads of cockroaches (Roth and Willis 1952). These studies show that adherence of pulvilli and euplantulae is most effective on smooth surfaces. In each case the adhesive organs have fluid secretions that provide an airtight seal around the adhesive organ which aids in suction. Lees and Hardie (1988) proposed that surface tension is the adhesive force. The folds in the adhesive pads of *A. subplicata* (see Fig. 2) may serve as a reservoir for an adhesive fluid.

Although the larval adhesive pads appear to be similar to fleshy tarsal structures of other insects, the proposed attachment mechanisms do not correlate with the strong preference of larval *A. subplicata* for hairy leaves.

Results from the attachment test show that larvae could attach equally well to smooth and hairy leaves, based on the number that fell off during the trials. However, larvae fell off hairy leaves more quickly which supports the conclusion that adhesive organs are more effective on smooth surfaces. The preference for young, hairy leaves may be explained by the pattern of larval feeding behavior. Larvae burrow into the trichomes to reach the leaf surface and feed, thus deriving benefit from the ability of trichomes to alter microclimate and provide a buffer to wind and temperature extremes (Cassin 1989). During the attachment experiment, larvae may not have had sufficient time to adjust and begin feeding before being exposed to wind.

Attachment ability can also be assessed in terms of movement patterns and amount of movement on the host plant. Wind reduced the amount of movement along the shoot for both larvae and adults; however, leaf type did not appear to affect ease of movement during wind conditions. The adults traveled more when placed on smooth leaves during the no wind trials, demonstrating their preference for young, hairy leaves at the tops of the shoots.

Although wind was a significant force in inhibiting attachment and restricting movement in the laboratory, the more complex flow patterns generated in the field may enable *A. subplicata* to attach and feed during gusty conditions. Cassin (1989) found that most larval and adult *A. subplicata* on *S. cordata* are found below a height of one meter. In addition to the warm microclimate created by the sand, wind speed is also much less near the ground (Bach 1993), providing a more protected environment for foraging.

In conclusion, attachment ability of *A. subplicata* is not a strong determinant of the observed feeding preferences on its host, *S. cordata*. Wind caused more difficulty for larval and adult attachment and movement, but neither adults nor larvae exhibited improved attachment ability on hairy leaves. The strong preference for the young, pubescent leaves shows that *A. subplicata* is adapted to utilize a food plant that is well armed with trichomes, potential feeding deterrents. This preference for young, hairy leaves most likely results from the improved nutritional quality and a more ideal microclimate (Cassin 1989), both of which would lead to faster development and greater survivorship.

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