Effects of leaf age on oviposition and on offspring fitness in the imported willow leaf beetle <u>Plagiodera versicolora</u>

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Running head: Leaf age choice and fitness effects

   Imported willow leaf beetles <u>Plagiodera versicolora</u> oviposit on willow leaves, and both larvae and adults feed on the leaves. In the field, eggs were found on leaves near the center of branchlets, and the number of eggs per cluster was independent of leaf area and position. However, in the laboratory, females chose young leaves over old leaves, for both oviposition and feeding and choice did not rely on information on relative position or size of leaves. Developing on young versus old leaves may provide both advantages and disadvantages. In the laboratory, larvae developed more quickly and attained greater adult weight when fed young versus old leaves, perhaps because of increased mandibular wear of larvae fed old leaves. However, in the field, survival of eggs was lower on young versus old leaves. In the laboratory, rates of cannibalism and survivorship to adulthood did not differ on young versus old leaves.

   Key words: <u>Plagiodera versicolora</u>, leaf age, fitness, oviposition choice, cannibalism, plant defenses

INTRODUCTION

Like many animals, most insects do not provide parental care after oviposition. Nevertheless, in some cases, females may be able to influence their offspring's fitness by choosing a suitable oviposition site (e.g., Rothschild and Schoonhoven, 1977; Pierce and Elgar, 1985). Characteristics of such a site would be assessed by the mother prior to oviposition. Among herbivores, one important oviposition site characteristic is leaf age. The value of a leaf to developing offspring may change with leaf age, e.g., because of changes in the chemical or physical properties of the leaf (references in Raupp and Denno, 1983). Here we examine the effect of leaf age on oviposition, feeding, and fitness in the imported willow leaf beetle <u>Plagiodera versicolora</u> (Laicharting) (Coleoptera: Chrysomelidae).

   <u>Plagiodera</u> <u>versicolora</u> is a small metallic blue beetle that feeds on the leaves of willow trees both as larvae and as adults (Hood,

1940). It has been in the United States since at least the early
1900s (Hood, 1940) and is now common in Illinois, where this study
was done (Breden and Wade, 1985). Females lay clusters of 2 to 48
eggs with an average clutch containing 15-19 eggs (Wade, 1994;
Crowe, 1995a). Upon hatching, the larvae of a cluster feed upon the
leaf in aggregate. They may move from the natal leaf individually,
but will reaggregate on a new leaf. They generally remain
aggregated for the first two instars and then become solitary.

   Here we examine what age of leaves females oviposit on, how this
affects their offspring's fitness, and how they may be assessing
leaf age. Young willow leaves usually contain more nitrogen and
moisture than older leaves and are not as tough (Raupp and Denno,
1983; Raupp, 1985; Denno et al., 1990). However, young leaves are
also smaller (see Results and Discussion) and closer to the ground.
Larvae on leaves closer to the ground may experience greater
predation and are more likely to be brushed off when branches drag
on the ground or against each other in the wind (Raupp and Denno,
1983).
   We examine whether the distribution and number of eggs in the
field are related to leaf position and leaf area. We examine
whether females preferentially oviposit and feed on young or old
leaves in the laboratory, both when leaf size is not controlled and
when it is.
   We also examine the effects of leaf age on offspring fitness.
The effects of leaf age on offspring size, development time, and
survivorship have been examined previously for P. versicolora in
Maryland (Raupp and Denno, 1983; see Discussion). Here we reexamine
those effects with Illinois P. versicolora to test the generality of
the results.
   In addition, we extend previous work by examining proximal
mechanisms by which leaf age may be affecting size, development
time, and survivorship. Specifically, we examine whether there is
greater wear on the mandibles of larvae fed old (versus young)
leaves. Feeding on old leaves increases mandibular wear in adults,
thus reducing feeding rate (Raupp, 1985). We also examine whether
being oviposited on a young versus old leaf affects an offspring's
risk of being cannibalized. During the first day after hatching, P.
versicolora larvae frequently cannibalize other eggs and larvae in
their cluster (Wade and Breden, 1986). After cannibalizing, the
larvae rock from side to side until one breaks through the leaf
surface; then all the larvae move to the break and begin feeding
(Wade, 1994). Cannibalism may be less on older leaves than on
younger leaves: less cannibalism means more larvae, and more larvae
may be needed to break through the tougher surface of older leaves.
Alternatively, cannibalism may be greater on older leaves: a larva
that cannibalizes becomes heavier (Breden and Wade, 1985), and being
heavy may be necessary to break through the tougher surface of older
leaves. Also, the lower nitrogen content of older leaves, means
that any nutritional advantage of cannibalism may be more important
on old leaves.

METHODS
   Field Studies. A field survey was done in 1993 on three Babylon
weeping willow trees (Salix babylonica) located at two different
sites in Freeport, Illinois. P. versicolora egg clusters were found
by searching leaves on branchlets that were within 2 m of the
ground.
   The number of eggs in each cluster, leaf position relative to the
apex of the branchlet (1 being the first expanded leaf at the apex),
and whether other clusters were located within 20 cm were recorded.
To determine the pre-feeding leaf size, the leaf was traced on
acetate paper; leaf area was measured using a digitizing tablet,

subtracting out damaged areas that were present before the eggs hatched.

We used linear regression to examine relationships among number of eggs in a cluster, leaf position, and leaf area. Regressions were done within sites because of site differences in mean number of eggs per cluster and in size of leaf on which eggs were laid.

A second field survey was done in July and August of 1995, on two of the trees used previously. Relative position of an egg cluster was calculated as the leaf position on which the cluster was located divided by the number of leaves on that branchlet. We tested whether the distribution of relative positions was skewed toward younger leaves (Sokal and Rohlf, 1981). Using linear regression, we also tested for relationships of number of eggs with leaf position, relative position, and number of leaves on the branchlet.

Survival in the egg stage on young versus old leaves was examined in a field experiment on Babylon weeping willow trees in DeKalb, IL. Branchlets were selected randomly from those that could be reached from the ground from one tree on 26 July 1995 and from a different but adjacent tree on 8 August 1995. For each branchlet, 16 eggs were placed in a cluster on the third leaf from the apex, and 16 eggs on the tenth leaf. The eggs were from a laboratory colony (see below). The number of eggs remaining was recorded 3, 6, 18, 24, and 30 h after placement. Percent remaining was compared between young and old leaves within each branchlet by paired test.

Laboratory Experiments. The P. versicolora used in the first laboratory experiment were collected from two S. babylonica in Freeport, IL. The P. versicolora used in subsequent laboratory experiments and in the field experiment (above) were from colonies established with beetles from several S. babylonica in DeKalb, Illinois. Adult beetles were fed S. babylonica ad libitum, either branchlets in water or leaves on moistened filter paper.

Laboratory experiments were performed in petri dishes containing moistened filter paper. Each dish was sealed with parafilm and kept at 23-26°C, 24 h light. Leaves were from several S. babylonica in DeKalb, IL. Young leaves were from position five or less from the apex of a branchlet, old leaves were from position ten or greater, unless otherwise specified.

The first laboratory experiment was designed to determine whether adult beetles chose young or old leaves for oviposition and feeding and also to determine whether feeding on young versus old leaves by offspring affected offspring size, development time, and survivorship. Each of 50 experimental adult beetles was placed in a separate dish with an old leaf and a young leaf. The leaves were from position 20 or less. Only undamaged leaves were used because P. versicolora larvae require a longer time to develop and obtain a lower adult weight when fed damaged leaves (Raupp and Denno, 1984). Leaves were taped to the top of the dish to prevent females from laying eggs only on the lid of the dish and to expose the underside of the leaf, which is where egg clusters are usually found in nature (Wade and Breden, 1986).

The number of eggs on each leaf and whether the adult beetle fed on the young and/or old leaf was recorded after 24 h and again after 48 h. Eggs laid on the dish, rather than on a leaf were excluded from analyses. Only beetles that laid eggs were included in analyses of egg number because nonlayers may have been virgin females or males.

Each leaf with eggs was placed in a separate dish. The emerging larvae were fed from the same type of leaf (young, old) as the eggs had been laid on. The larvae were transferred daily to a new leaf, before the previous leaf had been completely consumed. Manually transferring the larvae does not affect survival (M. Crowe

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unpublished data). The pupal stage was monitored daily; and as adults emerged, they were frozen. Total development time from day of oviposition to adult emergence was recorded. After emergence, three adults were randomly chosen from each cluster, frozen, and weighed. When less than three adults emerged, all adults were weighed.

Choices of leaf for feeding and for oviposition were analyzed by chi-square tests. Number of eggs laid, adult weight of offspring, offspring survival to the adult stage, and offspring development time were compared between old and young leaves. The mother was the sampling unit: mean weight and development time of offspring were computed for each mother prior to analysis; when there were data from both young and old leaves for the same mother, we randomly chose a leaf type. This was done to avoid the problem of offspring from the same mother not being independent samples. Relationships between the measures of offspring fitness and number of eggs laid were examined separately for young and old leaves.

The second experiment was designed to determine whether adult beetles chose young or old leaves for oviposition and feeding when leaf size was controlled. This experiment was similar to the first except that beetles were given rectangular pieces of leaves, instead of entire leaves. A young leaf (position 1-5) and an old leaf (position 10-15) from the same branchlet were aligned at the base and equal sized rectangles were cut, centered around the leaf midribs. Only one pair of leaves was used per branchlet, and only undamaged leaves were used.

Which leaf the beetle first fed on or walked onto (whichever came first) was recorded if a choice was made within one hour. After 24 h, we recorded which leaf the beetle was on; which leaves the beetle had fed on; and the number of eggs on each leaf. Forty beetles were tested. Leaf choices were analyzed by chi-square tests.

In the cannibalism experiment, approximately equal numbers of eggs from a single mother were placed on a young leaf (position 3-5) and an old leaf (position 11 or greater). There was no difference in the number of eggs placed on young versus old leaves ($t = 1.70$, $df = 14$, 2t $P = 0.11$; range: 6 - 22 eggs). The number of larvae was determined between 24 – 48 hours after hatching and compared between leaf ages.

In the mandible-wear experiment, we examined the effect of leaf age on wear of larval mandibles by providing larvae with either only young leaves or only old leaves. Each replicate consisted of two petri dishes, one for each host age. Each dish contained seven eggs ($n = 16$ replicates) or five just-hatched larvae ($n = 2$ replicates). Within a replicate, eggs and larvae were from the same mother. The larvae were fed ad libitum until they reached the wandering stage just prior to pupation. One larva was randomly chosen from each dish, frozen, and the left mandible was removed and measured at 16X using an ocular micrometer. Number of serrations on the mandible were counted. Length of the side with the longest serration, and depth of the longest serration were measured. Basal width of the mandible was also measured as a control for differences in size unrelated to wear.

Statistical comparisons were by t-tests, or if assumptions of normality were not met, Mann-Whitney U or sign tests. In order to increase power, we compared leaf ages by two sample tests when there was no correlation and by paired tests when there was a significant correlation (Zar, 1984, p. 152). Means are presented with standard errors and/or ranges. Two-tailed P values are indicated by "2t", one-tailed values by "1t". One-tailed tests were used when young leaves had the presumed advantage of greater nitrogen but not the presumed disadvantages associated with size, predation, and wind (see Introduction and Discussion); i.e., in tests of weight and

development duration in the first laboratory experiment, in the second laboratory experiment, and in the mandible-wear experiment.

RESULTS

Field Studies. In the 1993 field survey, twenty-eight egg clusters were located, eighteen at one site and ten at the other. About 70% of the clusters were on the undersides of leaves at both sites. Only two of the twenty-eight leaves had any pre-feeding damage. Three of the twenty-eight egg clusters (11%) were within 20 cm of another cluster.

Leaf area was greater farther from the apex of the branchlet at both sites (Fig. 1). Number of eggs in a cluster ranged from 5 to 27 and was not significantly related to leaf position at either site (R^2 = 0.0017, df = 16, 2t P = 0.87; R^2 = 0.011, df = 8, 2t P = 0.77). Number of eggs in a cluster also was not significantly related to leaf area at either site (R^2 = 0.00025, df = 16, 2t P = 0.95; R^2 = 0.096, df = 8, 2t P = 0.38).

In the 1995 field survey, there were 14 ± 1 eggs per cluster (range 3-24, n = 28). The 28 branchlets sampled had 28 ± 2 leaves per branchlet (range 4-60). The position of egg clusters ranged from 2-26 with a mean of 13 ± 1. Relative position of these clusters was normally distributed half-way up the branchlet (0.50 ± 0.04, 0.14-1.00) with no skew toward younger or older leaves (test for skewness: t = 1.25, df = 8, 2t P > 0.20). There were no relationships between number of eggs and either leaf position (R^2 = 0.03, df = 26, 2t P = 0.35) or relative position (R^2 = 0.0014, df = 26, 2t P = 0.85). However, number of eggs in a cluster decreased with number of leaves on the branchlet (Fig. 2).

In the field experiment to test egg survival, on the first experimental date there were no significant differences in number of eggs on old versus young leaves after 3 h and after 6 h (Table I). However, after 18, 24, and 30 h, more eggs remained on old than on young leaves. On the second date more eggs remained on old than on young leaves from 3 h on (Table I). Ants were observed on two of the branchlets on the first date. It rained between the sixth and eighteenth hours on the second date.

Laboratory Experiments. In the first laboratory experiment in which leaf size was not controlled, 27 beetles laid eggs. Twenty-one females oviposited on only one type of leaf, with more females choosing to oviposit on young leaves than on old leaves (16 versus 5, X^2 = 5.8, P < 0.05). Six of the 27 females oviposited on both young and old leaves. Females that laid eggs on both leaves laid just as many eggs per leaf as females that laid on only one leaf type (on young leaves: t = 0.53, df = 20, 2t P = 0.60; on old leaves: t = 0.05, df = 9, 2t P = 0.96). There was no significant difference in number of eggs laid on young leaves versus old leaves (mean (range): 14 (6 – 39) versus 13 (5 – 27); U = 59.5, n_1 = 19, n_2 = 8, 2t P = 0.38).

Of the 27 egg-laying mothers in the first experiment, 25 ate young leaf exclusively; one ate from both the young and the old leaves; and one did not eat. Among the 23 beetles that did not lay eggs, 16 ate young leaf exclusively; four ate from both the young and the old leaves; three did not eat.

Offspring were heavier and developed more quickly on young than on old leaves (6.6 mg ± 0.2 versus 6.0 ± 0.3, t = 1.69, df = 25, 1t P = 0.05; 16.0 days ± 0.3 versus 17.3 ± 0.7, t = 2.15, df = 25, 1t P = 0.02). Offspring survivorship did not differ with type of leaf on which the offspring fed (t = 1.18, df = 25, 2t P = 0.25).

There was no relationship between any of the measures of

offspring fitness and number of eggs laid on either young or old leaves. Larval survivorship was not related to the number of eggs laid on young leaves r = 0.14, n = 19, 2t P = 0.58) or on old leaves (r = -0.11, n = 8, 2t P = 0.30). Likewise, development duration was not related to the number of eggs laid on young leaves (r = -0.20, n = 19, 2t P = 0.41) or on old leaves (r = -0.20, n = 8, 2t P = 0.64). Adult weight of offspring was not related to the number of eggs laid for young leaves (r = 0.017, n = 19, 2t P = 0.95) or for old leaves (r = -0.25, n = 8, 2t P = 0.55).

   In the second laboratory experiment, in which leaf area was controlled, females showed similar preferences as when leaf area was not controlled. Within the first hour, approximately equal numbers of adult beetles walked onto or fed on young leaves first versus old leaves first (14 versus 11, X^2 = 0.4, P > 0.50). At the end of 24 h no females had oviposited on both leaves. More females oviposited on young leaves than on old leaves (12 versus 3, X^2 = 5.4, P < 0.03). In addition, females laid more eggs on young than on old leaves (18.6, 8-30 versus 10.3, 6-18; Mann-Whitney U = 5.0, 1t P = 0.03). Twenty-three beetles did not oviposit, and 2 oviposited only on the dish.

   At the end of 24 h, 3 of 40 beetles ate approximately equal amounts of both leaf types. The other 37 beetles showed a preference, with more beetles eating mostly young leaves than eating mostly old leaves (31 versus 6, X^2 = 5.4, P < 0.03). Those preferring young leaves usually also ate some of the old leaf: of the 31 and 6 preferring young and old respectively, 7 ate only young leaves and 4 ate only old leaves. After 24 h, more adult beetles were on young leaves than on old leaves (20 versus 5, X^2 = 9.0, P < 0.005).

   In the cannibalism experiment, there was no difference in the proportion of beetle immatures that survived on young versus old leaves (0.50 ± 0.06, range: 0.08 – 1.00 versus 0.46 ± 0.04, range: 0.20 – 0.77; t = 0.86, df = 14, 2t P = 0.40).

   In the mandible-wear experiment, larvae that ate old leaves had significantly shorter mandibles than did larvae that ate young leaves (Table II). In contrast, mandible width, serration depth and number of serrations did not differ with leaf age. Most (29 of 35) larvae had four serrations on their mandible; 4 had three; 2 had one.

                              DISCUSSION
   In the field, <u>P</u>. <u>versicolora</u> egg clusters tended to occur on leaves located midway up branchlets, rather than on the youngest or oldest leaves. Clutch size was unrelated to leaf position or leaf area. Similar field observations of egg and larval distributions in relation to leaf age have been used to suggest that females do not preferentially oviposit on younger leaves (Raupp and Denno, 1983). However, we found that when given a choice in the laboratory, female <u>P</u>. <u>versicolora</u> preferentially oviposited their egg clusters on younger leaves, regardless of whether or not we controlled for leaf size. In addition, when leaf size was controlled, the number of eggs laid on young leaves was greater than the number laid on old leaves.

   One explanation for the discrepancy between field and laboratory results is that eggs may disappear in the field between the time of oviposition and when they are counted: in particular, the greater loss of eggs on young leaves than on old leaves (see below) may mask any oviposition preference for young leaves. Alternatively, the discrepancy between field and laboratory results may be related to other differences between young and old leaves that are present in the field but not in the laboratory, e.g., temperature, light,

humidity, distance from the base of the branchlet. Such differences
might change the relative advantage of ovipositing on young leaves
versus old leaves and/or such differences might be cues that females
use in choosing the leaf on which to oviposit. Among herbivore
species, which age of leaves are preferred for oviposition and
feeding appears to be variable (references in Raupp and Denno, 1983;
Marino and Cornell, 1993; Skinner and Cohen, 1994; Wilson, 1994;
Bentz et al., 1995; Liu and Stansly, 1995); although chrysomelids
generally prefer younger leaves (references in Floate et al., 1993).

   Plagiodera _versicolora_'s preference for younger leaves does not
require information on relative position of leaves nor leaf size, as
is also the case in the chrysomelid _Haltica lythri_ for adult and
larval feeding (Phillips, 1976) and in the twospotted spider mite
for adult feeding and oviposition (Wilson, 1994). However, in our
study and these other studies, whether relative position also
influences leaf choice, i.e., when leaf quality is controlled or
reversed, remains to be determined. Ovipositing whiteflies, _Bemisia_
argentifolii, discriminate both with and without position cues (Liu
and Stansly, 1995). _Plagiodera_ _versicolora_ adults showed no
propensity to approach young leaves before old leaves. The sensory
mode used in leaf age preference remains to be determined.
Correlations between concentrations of certain chemicals and leaf
age suggest that insect herbivores may also use leaf chemicals to
discriminate among leaf ages (e.g., Skinner and Cohen, 1994; Bentz
et al., 1995), or they may use physical features of leaves. Leaf
age discrimination for feeding does not require visual cues in the
chrysomelid _Haltica lythri_ (Phillips, 1976) and appears to be by
leaf palpation in the chrysomelid _Paropsis atomaria_ (Larsson and
Ohmart, 1988).

   Our study suggests that an advantage to preferentially
ovipositing on younger leaves may be quicker development of
offspring. More rapid development may decrease time spent in the
first instar, which is when _P_. _versicolora_ larvae appear to be
particularly vulnerable to attack by coccinellid larvae (Raupp and
Denno, 1983). In addition, faster development will increase fitness
by reducing generation time, provided population size is increasing
(Lewontin, 1965; Stearns, 1992). Offspring also attained greater
adult weights when they fed on younger leaves. However, greater
adult weight may not lead to greater fitness in the field for _P_.
versicolora (Crowe, 1995a; unpublished data).

   The longer development and lower weight of larvae fed older
leaves may be related to the increased wear of their mandibles.
Increased wear of the mandibles was indicated by shorter mandible
length of larvae that had fed on old leaves versus young leaves.
Increased wear may cause larvae to have to feed for longer to eat
enough to reach adult size. Mandibular wear in the larval stage
would presumably be even greater if it were not for the replacement
of the mandibles between instars at molting. _Plagiodera_ _versicolora_
adults that feed on older leaves also exhibit increased mandibular
wear and subsequently lower leaf consumption rates (Raupp, 1985).

   The rapid development of _P_. _versicolora_ larvae on young leaves
might be expected to select not only for mothers that preferentially
oviposit on young leaves, but also for larvae that preferentially
seek out young leaves to feed on when they disperse from where they
were oviposited. Larvae do not show any preference in laboratory
choice experiments, regardless of larval age (Crowe, 1995b).
However, if mothers oviposit on young leaves, larvae will "choose"
young leaves simply by moving to nearby leaves.

   Although the quicker development on young leaves than on old
leaves suggests a selective advantage to ovipositing on young
leaves, there also appear to be disadvantages. Survival of eggs was
lower on younger leaves than on older leaves in the field. This

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survival effect may have been due to predation or to eggs being knocked off lower-hanging (younger) leaves by rain or by movement of adjacent branches in the wind (Raupp and Denno, 1983). Ants were observed on branchlets during one experimental date. Although ants have not been recorded as predators of P. versicolora eggs (Wade and Breden, 1986), ants do predate eggs of another chrysomelid, Chrysomela crotchi (Smereka, 1965).

In contrast to the effect of leaf age on survivorship of eggs in the field, leaf age did not affect survivorship from egg to adult in the laboratory. The effect of leaf age on survival to adulthood in the presence of predators remains to be determined.

Another potential disadvantage to ovipositing on young leaves is their small size. If the amount of usable nutrition a leaf provides is proportional to its size, smaller leaves may provide less usable nutrition. In which case, smaller leaves might require more interleaf movement by the larvae. Whether this is the case and the risks of such dispersal remain to be determined.

Effects of leaf age on P. versicolora from Illinois (this study) are generally consistent with effects on P. versicolora from Maryland (Raupp and Denno, 1983). Maryland eggs are also found near the middle of branchlets, and larvae tend to be on the same ages of leaves as eggs. As in our study, Maryland P. versicolora are larger and develop more quickly when the larvae feed on younger leaves, and survivorship of eggs is lower on younger leaves. Whereas we found no effect of leaf age on larval survivorship, Raupp and Denno (1983) found that survivorship of Maryland larvae decreased with leaf age in one experiment, although not significantly in another experiment.

The generally negative effects of leaf age on larval fitness in P. versicolora is consistent with results in most, although not all, other herbivorous insects (reviewed in Raupp and Denno, 1983; also Schroeder, 1986; Damman, 1987; Larsson and Ohmart, 1988; Quiring, 1992; Kouki, 1993; Hayashi et al., 1994; Stamp and Bowers, 1994; Wilson, 1994; Bentz et al., 1995). Our results suggest that effects of leaf age on larval fitness in P. versicolora may be mediated at least in part through effects of leaf toughness on mandibular wear but not through effects of leaf age on cannibalism. Further study is needed of the mechanisms by which leaf age influences fitness and maternal choice.

Adults in our laboratory experiments chose not only to oviposit preferentially on younger leaves, but also to feed on them. Adult P. versicolora are found on young leaves in the field, in fact, on younger leaves than are eggs (Raupp and Denno, 1983). Adults that feed on younger leaves have increased fecundity (Raupp and Denno, 1983). Feeding on younger leaves results in considerably less wear on their mandibles, which increases rate of leaf consumption, which increases egg production (Raupp, 1985). Feeding on younger leaves may also increase egg production because of the greater amounts of nitrogen in younger leaves. Effects of leaf age on adult longevity have not been examined.

We found no relationship between the number of eggs in a cluster and larval survivorship in the laboratory. In previous field studies of P. versicolora, larval survivorship either generally increases with group size (Breden and Wade, 1985) or increases as the number of larvae increases to sixteen, then begins to decline (Crowe, 1995a).

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REFERENCES

Bentz, J.A., Reeves, J., Barbosa, P., and Francis, B. (1995) Within plant variation in nitrogen and sugar content of poinsettia and its effects on the oviposition pattern, survival, and development of Bemisia argentifolii (Homoptera, Aleyrodidae). Environ. Entomol. 24: 271-277.

Breden, F. and Wade, M.J. (1985) The effect of group size and cannibalism rate on larval growth and survivorship in Plagiodera versicolora. Entomography 3: 455-463.

Crowe, M.L. (1995a) The effect of season and group size on survivorship and larval growth in Plagiodera versicolora. Ecol. Entomol. 20: 27-32.

Crowe, M.L. (1995b) Daytime mechanisms of reaggregation in imported willow leaf beetle, Plagiodera versicolora larvae (Coleoptera: Chrysomelidae). Anim. Behav. 50: 259-266.

Damman, H. (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology 68: 88-87.

Denno, R.F., Larsson, S., and Olmstead, K.L. (1990) Role of enemy-free space and plant quality in host-plant selection by willow beetles. Ecology 71: 124-137.

Floate, K.D., Kearsley, M.J.C. and Whitham, T.G. (1993) Elevated herbivory in plant hybrid zones: Chrysomela confluens, Populus and phenological sinks. Ecology 74: 2056-2065.

Hayashi, Y., Fjiyama, S. and Suekuni, J. (1994) Life cycle synchronization in Chrysomela aurichalcea (Coleoptera, Chrysomelidae) to its host Artmesia princeps -- effects of host-leaf age on survival. Appl. Entomol. Zool. 29: 149-155.

Hood, C.E. (1940) Life history and control of the willow leaf beetle. U. S. D. A. Circular 527: 1-9.

Kouki, J. (1993) Female's preference for oviposition site and larval performance in the water-lily beetle, Galerucella nymphaeae (Coleoptera: Chapmelida). Oecologia 93: 42-47.

Larsson, S. and Ohmart, C.P. (1988) Leaf age and larval performance of the leaf beetle Paropsis atomaria. Ecol. Entomol. 13: 19-24.

Lewontin, R.C. (1965) Selection for colonizing ability. In Baker, H.G., and Stebbins, G. L. (eds.), The Genetics of Colonizing Species, Academic Press, New York, pp. 77-91.

Liu, T. and Stansly, P.A. (1995) Oviposition by Bemisia argentifolii (Homoptera: Aleyrodidae) on tomato: effects of leaf factors and insecticide residues. J. Econ. Entomol. 88: 992-997.

Marino, P.C. and Cornell, H.V. (1993) Adult feeding and oviposition of Phytomyza ilicicola (Diptera: Agromyzidae) in response to leaf and tree phenology. Environ. Entomol. 22: 1294-1301.

Norusis, M.J. (1988) SPSS/PC+ Advanced Statistics V2.0. SPSS Inc., Chicago.

Phillips, W.M. (1976) Effects of leaf age on feeding 'preference' and egg laying in the chrysomelid beetle, Haltica lythri. Physiol. Entomol. 1: 223-226.

Pierce, N. E. and Elgar, M. A. (1985) The influence of ants on host plant selection by Jalmenus evagoras, a myrmecophilous lycaenid butterfly. Behav. Ecol. Sociobiol. 16: 209-222.

Quiring, D.T. (1992) Rapid change in suitability of white spruce for a specialist herbivore, Zeiraphera canadensis, as a function of leaf age. Can. J. Zool. 70: 2132-2138.

Raupp, M.J. (1985) Effects of leaf toughness on mandibular wear of the leaf beetle Plagiodera versicolora. Ecol. Entomol. 10: 73-79.

Raupp, M.J. and Denno, R.F. (1983) Leaf age as a predictor of herbivore distribution and abundance. In Denno, R. F. and McClure, M. S. (eds.), Variable Plants and Herbivores in Natural and Managed Systems, Academic Press, New York, pp. 91-124.

Raupp, M.J. and Denno, R.F. (1984) The suitability of damaged willow

leaves as food for the leaf beetle, _Plagiodera versicolora_. _Ecol. Entomol._ 9: 443-448.

Rothschild, M. and Schoonhoven, L. M. (1977) Assessment of egg load by _Pieris brassicae_ (Lepidoptera: Pieridae). _Nature_ 266: 352-355.

Schroeder, L.A. (1986) Changes in tree leaf quality and growth performance of Lepidopteran larvae. _Ecology_ 67: 1628-1636.

Skinner, R.H. and Cohen, A.C. (1994) Phosphorus nutrition and leaf age effects on sweetpotato whitefly (Homoptera, Aleyrodidae) host selection. _Environ. Entomol._ 23: 693-698.

Smereka, E.P. (1965) The life history and habits of _Chrysomela crotchi_ Brown (Coleoptera: Chrysomelidae) in Northwestern Ontario. _Can. Entomol._ 97: 541-549.

Sokal, R.R. and Rohlf, F.J. (1981) _Biometry_, 2nd ed. W.H. Freeman and Co., New York.

Stamp, N.E. and Bowers, M.D. (1994) Effect of temperature and leaf age on growth versus moulting time of a generalist caterpillar fed plaintain (_Plantago lanceolata_). _Ecol. Entomol._ 19: 199-206.

Stearns, S.C. (1992) _The Evolution of Life Histories_. Oxford University Press, Oxford.

Wade, M.J. (1994) The biology of the imported willow leaf beetle, _Plagiodera versicolora_ (Laicharting). In Jolivet, P. H., Cox, M. L., and Petitpierre, E. (eds.), _Novel Aspects of the Biology of Chrysomelidae_, Kluwer Academic Publishers, Netherlands, pp. 541-547.

Wade, M.J. and Breden, F. (1986) Life history of natural population of the imported willow leaf beetle, _Plagiodera versicolora_ (Coleoptera: Chrysomelidae). _Ann. Entomol. Soc. Am._ 79: 73-79.

Wilson, L.J. (1994) Plant quality effect on life-history parameters of the twospotted spider mite (Acari, Tetranychidae) on cotton. _J. Econ. Entomol._ 87; 1665-1673.

Zar, J.H. (1984) _Biostatistical Analysis_, 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

Table I. The Number of Eggs (out of 16) that Remained on
Young versus Old Leaves after 3 to 30 h[a]

Tree 1, date 1

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	Young Leaf		Old Leaf		
	Mean	Minimum	Mean	Minimum	Paired Comparison
3 h	15.5	10	16.0	16	Sign test, 1t P = 0.25
6 h	14.8	3	16.0	16	Sign test, 1t P = 0.13
18 h	14.5	3	16.0	16	Sign test, 1t P = 0.03
24 h	11.3	0	15.1	5	t = 2.7, 1t P = 0.01
30 h	7.8	0	13.8	0	t = 3.5, 1t P = 0.001

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Tree 2, date 2

_____

	Young Leaf		Old Leaf		
	Mean	Minimum	Mean	Minimum	Paired Comparison
3 h	12.2	0	15.3	16	t = 2.8, 1t P = 0.01
6 h	10.3	0	14.4	0	t = 2.3, 1t P = 0.02
18 h	7.2	0	13.3	0	t = 3.8, 1t P < 0.001
24 h	7.2	0	13.3	0	t = 3.8, 1t P < 0.001
30 h	6.2	0	13.8	0	t = 4.7, 1t P < 0.001

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[a]n = 20 clutches per leaf type per tree; maximum egg number was always 16.

Table II. Mandible Dimensions (mm) of Larvae that Fed on
Young (n = 18) versus Old (n = 17) Leaves

	Young Leaf Mean ± se (Range)	Old Leaf Mean ± se (Range)	
Length	2.82 ± 0.04 (2.60 – 3.14)	2.71 ± 0.04 (2.43 – 2.90)	t = 2.19 1t P = 0.02
Width	1.93 ± 0.02 (1.81 – 2.12)	1.95 ± 0.03 (1.73 – 2.20)	t = 0.56 1t P = 0.29
Serration Depth	0.24 ± 0.02 (0.08 – 0.39)	0.22 ± 0.02 (0.08 – 0.31)	t = 0.68 1t P = 0.25
# of Serrations	3.89 ± .08 (3 – 4)	3.53 ± .24 (1 – 4)	U = 132.0 1t P = 0.15

Fig. 1. Leaf area versus position of the branchlet from the apex (o = site one: r = 0.86, n = 18, 2t P < 0.001; area = 0.57 position + 1.48;   = site two: r = 0.75, n = 10, 2t P = 0.01; area = 0.39 position + 3.33).

Fig. 2. Number of eggs in a cluster versus number of leaves on the branchlet (R^2 = 0.17, df = 26, 2t P = 0.03, number of eggs = -0.19 number of leaves - 0.41).