Characterizing Toxicity of *Pelargonium* spp. and Two Other Reputedly Toxic Plant Species to Japanese beetles (Coleoptera: Scarabaeidae)

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**ABSTRACT** The Japanese beetle (*Popillia japonica* Newman), a polyphagous scarab, feeds on certain palatable plants that are toxic, or reputedly toxic. Paralysis of the beetle after consumption of flowers of zonal geranium (*Pelargonium × hortorum* L. H. Bailey) has been documented, but factors affecting expression and range of this phenomenon are poorly known. Published anecdotes regarding toxicity of two other hosts, larkspur (*Delphinium* sp.) and bottlebrush buckeye (*Aesculus parviflora* Walt.), have not been empirically tested. For zonal geraniums, we compared toxicity with *P. japonica* of flowers versus leaves, sun-grown and shaded plants, and different-colored flowers. The progression of paralysis and recovery, as well as survival of paralyzed beetles under laboratory and field conditions, also were evaluated. Beetles became paralyzed after feeding on flowers of zonal geranium, but not by consuming leaves, suggesting the active compound is unique to flowers. Shaded or sun-grown flowers, and red-, white-, or salmon-colored flowers, were equally active. Beetles generally became paralyzed within 3 h of the onset of feeding. Most of them recovered when held in the laboratory, but paralyzed beetles placed in the field for 3 h did not recover. Flowers of *Pelargonium inquinins* (L.) L’Heritier, and *Pelargonium zonale* (L.) L’Heritier, which are the parental species of *P. × hortorum*, as well as ivy geranium (*Pelargonium peltatum* [L.] L’Heritier), another member of the type section *Ciconium*, all were active. *Pelargonium × scarborovia*, which belongs to the type section *Pelargonium*, was the only geranium species that did not cause paralysis. Although the active compounds have not been identified, our results suggest that light-activated flavonoids or anacardic acids probably are not responsible for geranium-induced paralysis. Contrary to published anecdotes, neither flowers nor foliage or larkspur and bottlebrush buckeye were toxic to Japanese beetles.

**KEY WORDS** *Popillia japonica*, *Pelargonium*, *Delphinium elatum*, *Aesculus parviflora*
documenting the putative toxic effect of bottlebrush buckeye on *P. japonica*.

The best-documented case of plant toxicity to Japanese beetles is the paralysis and mortality that follow consumption of flowers of zonal geraniums. This phenomenon, first documented by Davis (1920), has been validated by two subsequent investigations (Ballou 1929, Potter and Held 1999). Paralysis begins in the hind legs and progresses anteriorly until all legs are paralyzed. The beetle appears dead except for slight movements when disturbed. Affected beetles may recover or die. Beetles that had become paralyzed after feeding on detached flowers of Orbit Red zonal geranium did not exhibit food aversion learning (Potter and Held 1999). However, suggested that flavonoids may be responsible for paralysis (Potter and Held 1999). They continued to choose geranium flowers over linden (*Tilia cordata* L.), a highly suitable host, even after several successive bouts of paralysis and recovery.

Factors such as flower color, feeding site (flowers versus foliage), and light exposure reportedly may influence geranium's toxic effect on *P. japonica*. An apparently nonreplicated field test by Ballou (1929) showed slightly higher mortality of beetles caged on a red-flowered geranium than on a pink-flowered one. A similar test suggested higher mortality of beetles in a cage containing geraniums placed in full sunlight, as opposed to a similar cage kept in shade. High light intensity may be associated with increased secondary metabolism in plants (Schoonhoven et al. 1998). For example, plants grown in full sunlight may have higher levels of flavonoids, pigment compounds that protect the cell nucleus by absorbing damaging UV light (Taiz and Zeiger 1991). Based on the observations of Ballou (1929) and the bioactivity of flavonoids, it was suggested that a flavonoid may be responsible for paralysis (Potter and Held 1999). However, *P. japonica* feeds more vigorously on plants growing in sunlight (Fleming 1972) and has a higher thoracic temperature when in the full sun (Kreuger and Potter 2001). Considering these potentially confounding effects, it is unclear whether Ballou’s (1929) observation of higher beetle mortality on geraniums in full sun was caused by increased toxicity of the plants themselves or elevated beetle metabolism. Clarifying this point may provide insight about the phytochemical basis for the phenomenon.

Insect resistance of zonal geranium is not unique to Japanese beetles. Glandular trichomes on leaves, stems, and sepals are responsible for mediating resistance to mites and aphids (Hesk et al. 1992). Sticky exudates from these trichomes offer a physical defense, and their primary constituents, anacardic acids, are inherently toxic (Hesk et al. 1992). Zonal geranium is a hybrid of two species, *Pelargonium zonale* (L.) L’Héritier and *Pelargonium inquinins* (L.) L’Héritier (Miller 1996). Sticky exudates produced by the tall, glandular trichomes on *P. inquinins* contain anacardic acid, whereas *P. zonale* lacks glandular trichomes and is therefore susceptible to mites (Grazzini et al. 1997). Whether anacardic acids of geranium are involved in the paralysis of Japanese beetles has not been studied. Toxic components identified from geranium or other plants might have value as botanical insecticides or antifeedants. The current study further characterized the narcotic effects of *Pelargonium* spp. on *P. japonica*. We tested the toxicity of flowers and foliage from zonal geraniums and related species, *P. peltatum* (L.) L’Héritier and *P. × scarborowia* Sweet, as well as the capacity of the biological parents of *P. × hortorum* to induce paralysis. Using *P. × hortorum*, we investigated the toxicity of plants grown in the sun or under shade, variation in toxicity among different colored flowers, and factors affecting recovery from paralysis. Finally, the claims that flowers and foliage of *A. parvisflora* and *Delphinium elatum* L. are toxic were evaluated.

**Materials and Methods**

Beetles were collected using standard Japanese beetle traps baited with food-type lures (phenethyl propanoate, eugenol, and geraniol; 3:7:3 ratio; Tréée, Garwood, NJ). The sexes were separated using foretibial characters (Fleming 1972), and only active, apparently healthy females were used in tests. Unless otherwise noted, beetles were held without food for 4 h before each assay. Newly collected insects were used for each trial. All tests were conducted during the first half of the Japanese beetle seasonal flight (late June to mid-July) to reduce possible confounding effects of beetle age.

**General Procedures.** Leaves and flowers, free of apparent disease symptoms and insect damage, were collected into sealable plastic bags and transported to the lab in a cooler. For experiments testing flowers, a single flower was removed from the inflorescence and pinned through the center of the corolla. In some experiments, foliage of littleleaf linden (*Tilia cordata* L.), a palatable, suitable host (Fleming 1972), was used as a control for the beetles’ condition, i.e., proclivity to feed. Linden foliage was collected from six trees of relatively uniform height (7–8 m) and trunk diameter (22–26 cm at 1 m height). Because zonal geranium flowers induce distinctive paralysis when fed upon (Ballou 1929, Potter and Held 1999), they were included as a positive control for paralysis in most experiments. These flowers were collected from plots of Orbit Red geraniums planted in full sunlight.

Test arenas were 240-nl cups (Solo, Baltimore, MD) with a layer of wax and moistened filter paper in the bottom. Cups were sealed with a piece of clear plastic film secured by a rubber band. Unless otherwise noted, experiments were conducted on the lab bench (22–24°C) under fluorescent lighting. Beetles were allowed to feed for 24 h, or less if they became paralyzed. If a beetle became paralyzed, it was removed from the container and placed on its back under an inverted 30-ml plastic cup. A beetle was considered to have recovered if it was able to right itself under the cup (e.g., Potter and Held 1999).

Consumption of petal or leaf material was quantified by tracing missing areas onto clear acetate sheets. Traced areas were blackened with a marker, then
measured with an electronic area meter. Measured areas were converted to a fresh weight equivalent using a constant calculated from measuring the area-weight relationship of additional plant material. Beetles that did not feed were excluded, such that mean consumption represents an average of only those beetles that fed.

**Sunlight Effect on Geranium-Induced Paralysis.** In May 2000, four plots (1.5 x 1.2 m) were tilled in a sunny lawn, and each was planted with 16 Orbit Red zonal geraniums. At planting, all flower buds and blooms were removed to ensure that flowers used in experiments were grown under the experimental conditions. Half of each plot was randomly selected to receive either full sunlight or shading. Sun-grown plants were chosen. Those 20 females and 20 females from the unfed group received a topical application (1 μl) of the 1% PBO solution applied to the dorsal thoracic surface with a pipette. During that period, beetles that were not treated with PBO were kept on their respective feeding regimes. One hour after PBO treatment, all beetles were transferred to the arenas with a pinned zonal geranium flower and allowed to feed for 5 h. Paralysis and recovery were recorded for 24 h. The amount of petal tissue consumed, measured as before, was compared using analysis of variance (ANOVA) for main effects of PBO treatment and diet treatment, and their interaction, followed by Tukey’s honestly significant difference (HSD) to separate the means (P < 0.05).

Recovery from paralysis was compared under laboratory and outdoor conditions to clarify the fate of beetles that consume geranium in the field. Three 1-liter plastic cups were prepared with detached inflorescences of sun-exposed Orbit Red zonal geranium plants. Twenty female beetles were allowed to feed on those flowers and become paralyzed. A second set of three cups was prepared with foliage from crabapple (Malus sp.) with 10 females per cup. After feeding for 2 h, four beetles from each cup with crabapple foliage (12 total) were removed and weighed. Only beetles that were actively feeding were used. After weighing, beetles were placed into individual 33-ml plastic cups covered with fine mesh. Likewise, two sets of four paralyzed beetles (eight total paralyzed females) from each cup with geranium flowers were removed, weighed, and placed into cups.

Cups containing either foliage-fed or paralyzed beetles were placed into an environmental chamber (Percival, Boone, IA) with constant fluorescent lighting at 32°C to match the measured mid-afternoon temperature (31.7–33.3°C) that day. The remaining set of 12 paralyzed beetles was taken outdoors to the geranium beds from which the flowers had been harvested. Within the four separate plantings of geraniums, three individual plants were chosen to receive a paralyzed beetle. Each beetle was placed on its back (the typical paralyzed position), in full sunlight on an upper leaf of each plant. Its location was marked with a numbered paper label attached to the petiole of that leaf with an insect pin. Beetles were left on the leaves for 3 h (1200–1500 h) and then collected with their number label into 33-ml cups, brought into the labo-
The genus *hybrid* occurs with other species within the genus. *P. zonale* occurs naturally (Bailey 1976, Miller 1996). Zonal geraniums, their parentalspecies, inquinins.

Pelargonium (Miller 1996, Grazzini et al. 1997). The type section covery for 18 h. Similarly, 15 control beetles were before. All paralyzed beetles were monitored for re-

amount of petalmaterialconsumedwasdeterminedas to feed for 6 h, or until they became paralyzed. The 

was replicated 10 times. Paralysis and recovery were evaluated for 36 h. The amount of feeding also was 

was replicated 18 times. The final trial evaluated *P. × scarbororia* to deter- 

whether paralysis activity was unique to the 

type section *Ciconium*. Flowers of that species were collected from three plants growing in full sunlight. Foliage of linden and flowers of Orbit Red zonal ger- 

anium were also included for comparison. Experi-

mental setup and conditions were as before. Each treatment was replicated 18 times.

Testing Reputed Toxicity of Bottlebrush Buckeye and Larkspur. Flowers and leaves of bottlebrush buckeye were obtained from five multistemmed plants of similar size (1.2–1.6 m tall, 1.5–2 m spread). Growe at the University of Kentucky Arboretum (Lexington, KY). Single beetles were confined with one buckeye leaflet, three buckeye flowers, or one linden leaf for 24 h. Foliage was placed, unpinned, into the cups. Flowers were grouped in a triangular formation ≈1 cm apart. Test arenas were held in an environmental chamber under fluorescent lighting 14:10 (L:D) at 25°C. Each treatment was replicated 20 times, and the occurrence of paralysis or other visible malaise was monitored hourly for the first 6 h, then periodically thereafter. Consumption was noted, but not quanti-

fied in this trial. The experiment was repeated using the same treatments, except that leaf discs (22 mm diameter) of linden and buckeye were used to facilitate measurement of consumption. Leaf discs were mounted on insect pins sandwiched between 2 × 2-mm bits of craft foam to prevent them from tearing away during feeding (Held et al. 2001). Three indi-

vidual buckeye flowers were pinned and grouped, as previously described. A single female beetle was intro-

duced into each cup and allowed to feed for 12 h. Each treatment was replicated 20 times. The amount consumed (mg) was compared by ANOVA, followed by Tukey’s HSD test, as before. The second experiment tested putative toxicity of larkspur. Flowers and leaves were collected from three white-flowered *D. elatum* Magic Fountain Series plants grown in 3.8-liter pots. The first trial compared flowers of larkspur or zonal geranium (Orbit Red), each replicated 16 times. Individual flowers were pinned through the center of the corolla. Consump-
tion and the incidence of paralysis were recorded as before.

A second trial was conducted with larkspur flowers, larkspur foliage, linden foliage, and zonal geranium flowers (Orbit Red). For the foliar treatments, whole leaves of each species, petioles removed, were placed into the test arenas. Flowers were pinned through the corolla, as previously described. Each flower and foliage treatment was replicated 20 times, with consumption and paralysis determined as before. The amount of larkspur foliage and petals consumed also was compared by a two-sample $t$-test.

### Results

#### Sunlight Effect on Geranium-Induced Paralysis

All 40 beetles that fed on geranium flowers became paralyzed, regardless of whether the plants were grown in sunlight or shade. For beetles fed sun-grown flowers, 17 recovered, 1 died, and 2 remained paralyzed after 24 h. For beetles fed shade-grown flowers, 14 beetles recovered, 1 died, and 5 still were paralyzed after 24 h. Most (80%) of the beetles provided with geranium foliage fed regardless of the light regime under which the plants were grown. Only 2 of these 32 became paralyzed. Both of these had fed on shade-grown foliage, and they had recovered within 1 h.

#### Factors Affecting Recovery from Geranium-Induced Paralysis

In this test, 38 of the 40 beetles tested (95%) became paralyzed after feeding on geranium flowers (Fig. 1). Beetles consumed, on average, 72% of one petal before becoming paralyzed. This amount was variable, with some taking only small bites and others consuming nearly two whole petals before being incapacitated. Mean ($\pm SE$) time to paralysis after introduction into the test arena was $2 \pm 0.2$ h, but ranged from 1 to 4 h (Fig. 1). There was no significant linear relationship between amount consumed by the beetles and the time to paralysis (regression coefficient $= 0.0065$, Student's $t = 0.57, P = 0.57$). Only 55% (21) of the beetles that became paralyzed recovered, whereas the other 45% (17) died (Fig. 1). Beetles that died after feeding had not consumed more petal tissue than beetles that recovered (19.5 versus 23.2 mm$^2$, respectively; $t = -0.7, df = 36, P = 0.47$). Time required for recovery of beetles after paralysis ranged from 4 to 26 h.

Beetles that were treated with PBO consumed less zonal geranium petals than those that were not treated ($F = 30.3; df = 1, 19; P < 0.01$), regardless of whether or not they had recently fed (Table 1). The main effect for diet treatment ($F = 0.00; df = 1, 19; P = 0.98$) and the diet by PBO interaction ($F = 0.9; df = 1, 19; P = 0.36$) was not significant for amount consumed. Among PBO-treated beetles, those that also had been starved had relatively low incidence of feeding (13 of 20, or 65%) and subsequent paralysis (8 of 15, or 61.5%) compared with the other groups. Incidence of paralysis with each of the treatments was at least 85%. The percentage of beetles that recovered from paralysis was high (range, 85.7–100%) regardless of PBO treatment or diet treatment (Table 1).

Paralyzed beetles that were placed outdoors on geranium plants for 3 h lost significantly more weight than either paralyzed or normal beetles kept in the environmental chamber (Fig. 2). Those beetles lost 14–35% of their total body weight (average 27.7 ± 2%), and all of them died within 48 h of being brought back into the laboratory. In contrast, paralyzed beetles kept in the environmental chamber lost only 2–5.1% of their total body weight and 75% of them recovered. Those paralyzed beetles lost significantly less weight.

### Table 1. Effect of pretreatment with piperonyl butoxide (PBO), with or without food deprivation, on geranium-induced paralysis and recovery of Japanese beetles

<table>
<thead>
<tr>
<th>Synergist treatment</th>
<th>Diet treatment</th>
<th>Mean amount consumed (mg ± SE)</th>
<th>No. of beetles that</th>
<th>Percentage recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Fed</td>
<td>Became paralyzed</td>
</tr>
<tr>
<td>PBO treated</td>
<td>Unfed</td>
<td>$2.1 \pm 0.2$</td>
<td>13</td>
<td>8</td>
</tr>
<tr>
<td>PBO treated</td>
<td>Fed</td>
<td>$1.5 \pm 0.3$</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Nontreated</td>
<td>Unfed</td>
<td>$2.9 \pm 0.3$</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>Nontreated</td>
<td>Fed</td>
<td>$3.2 \pm 0.3$</td>
<td>20</td>
<td>17</td>
</tr>
</tbody>
</table>

Regardless of PBO or diet treatment, recovery of beetles from paralysis from geranium was high.
than normal, nonfeeding counterparts, which lost, on average, 6.3 mg or 4.8% of their total body weight (Fig. 2).

Effect of Zonal Geranium Flower Color on Paralysis and Recovery. Flowers of all colors induced paralysis. Numbers of beetles that became paralyzed, out of the number that fed, were 5 of 7, 9 of 10, and 9 of 9 for white-, salmon-, and red-colored flowers, respectively. Beetles consumed significantly more ($F = 8.9$; df = 2, 10; $P < 0.01$) of the white-colored petal tissue than of either salmon- or red-colored petals (13.9 ± 2.8 versus 9.2 ± 1.4 and 10.7 ± 1.6, respectively). All of the beetles that fed on white-colored flowers became paralyzed within 5 h, whereas 8 h passed before all of those consuming red or salmon petals were paralyzed. There was no mortality among paralyzed beetles. All the beetles fed white or salmon flowers, and all but one that consumed red flowers, recovered after being paralyzed. Most beetles recovered within 5 h after paralysis.

Is Toxicity of Zonal Geranium Unique Among Pelargonium Species? Paralysis resulted from feeding on either petals or sepals of the parental species, P. zonale and P. inquinins, and P. × hortorum (Table 2, trial 1). For P. inquinins, 10 beetles became paralyzed, one of which fed only on sepals. For P. zonale, however, only one beetle fed on the petals, the rest of the paralyzed ones having fed on sepals. All of the control beetles that were held without food were able to right themselves at the end of the experiment.

Most beetles that fed on the flowers of either P. × hortorum or P. peltatum became paralyzed (Table 2, trials 2 and 3). Those paralyzed beetles that had not recovered by the end of the experiment (36 h) responded by twitching their appendages when touched. Numbers of beetles that fed on foliage were 16 of 20, 17 of 20, and 14 of 20, for linden, red-, or white-flowered ivy geranium, respectively. Mean (±SE) consumption was 51.5 ± 9.1, 76.6 ± 14.4, and 74.7 ± 16.4 mg, respectively. No beetles became paralyzed after feeding on foliage of linden or either cultivar of P. peltatum.

Most of the beetles fed on the flowers of P. × scarborovia, consuming a weight equivalent of 1–5 petals, but there was no paralysis with either that species or linden, which was included as a standard (Table 2, trial 4). All beetles that fed on either treatment were able to right themselves at the end of the experiment. As expected, all beetles fed flowers from P. × hortorum became paralyzed.

Testing Reputed Toxicity of Bottlebrush Buckeye and Larkspur. Beetles fed upon both flowers and foliage of bottlebrush buckeye ($≥$85%, or 17 of 20 fed in each group), but this resulted in no apparent ill effects or death. In the second trial, beetles provided with linden foliage or buckeye flowers consumed significantly more than those given buckeye foliage (15.6, 19.8, and 6.3 mg, respectively; $F = 9.7$; df = 2, 32; $P < 0.01$). Beetles feeding on the flowers primarily ate petals. Filaments, too, were occasionally consumed. The amount of petal material consumed ranged from 5.1 to 66.4 mg, the latter being the approximate mass of two flowers. There was somewhat less feeding on the buckeye leaf discs (range, 1.8–12.7 mg); the latter corresponds to 22.4% of the disc.

Most beetles ate the flowers of larkspur, 13 of 16 and 14 of 20, for trials 1 and 2, respectively, but fewer beetles (8 of 20) consumed larkspur foliage, which was included in trial 2. None of the beetles that consumed larkspur suffered any apparent ill effects or death.

### Table 2. Consumption and relative toxicity of other Pelargonium spp. to Japanese beetles

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Flower color</th>
<th>Mean amount consumed (mg ± SEM)</th>
<th>No. of beetles that Fed</th>
<th>Became Paralyzed</th>
<th>Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. inquinins</td>
<td>R</td>
<td>3.9 ± 1.2</td>
<td>11</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>P. zonale</td>
<td>L</td>
<td>0.5 ± 0.0</td>
<td>14</td>
<td>11</td>
<td>8</td>
</tr>
<tr>
<td>P. × hortorum</td>
<td>R</td>
<td>1.1 ± 0.1</td>
<td>14</td>
<td>13</td>
<td>11</td>
</tr>
</tbody>
</table>

| Flowers of all colors induced paralysis. Numbers of beetles that became paralyzed, out of the number that fed, were 5 of 7, 9 of 10, and 9 of 9 for white-, salmon-, and red-colored flowers, respectively. Beetles consumed significantly more ($F = 8.9$; df = 2, 10; $P < 0.01$) of the white-colored petal tissue than of either salmon- or red-colored petals (13.9 ± 2.8 versus 9.2 ± 1.4 and 10.7 ± 1.6, respectively). All of the beetles that fed on white-colored flowers became paralyzed within 5 h, whereas 8 h passed before all of those consuming red or salmon petals were paralyzed. There was no mortality among paralyzed beetles. All the beetles fed white or salmon flowers, and all but one that consumed red flowers, recovered after being paralyzed. Most beetles recovered within 5 h after paralysis.
Beetles fed mainly on the petals, but some also nibbled the flower spur. In trial 1, beetles consumed 2.0 ± 0.6 and 0.6 ± 0.1 mg of larkspur and geranium petals, respectively. In trial 2, they consumed more larkspur foliage than petals (7.4 ± 3.1 versus 1.6 ± 0.3 mg, respectively; \( t = 2.5, df = 20, P = 0.02 \)). In that trial, all beetles that consumed geranium flowers (18 of 20) became paralyzed. As expected, linden foliage had no toxic effect.

**Discussion**

Organic gardening books and magazines (e.g., Yepsen 1984, Cunningham 1998) as well as observations published in the early scientific literature (e.g., Landreth 1932, Hawley and Metzger 1940, Fleming 1972) suggest that certain plants are toxic to Japanese beetles. Earlier tests failed to support putative toxicity of castor bean and Carolina silverbell (Metzger 1933, Hawley and Metzger 1940). Despite published statements that they are toxic (Fleming 1972, Yepsen 1984), we found no evidence of paralysis or other ill effects from feeding on foliage or flowers of either bottlebrush buckeye or larkspur.

For *Pelargonium × hortorum*, however, paralysis of *P. japonica* has been confirmed (Ballou 1929, Potter and Held 1999). Our study with foliage and flowers from that species suggests that the active component is flower specific. This was reinforced by the trials with ivy geraniums, *P. peltatum*, in which paralysis resulted from feeding on flowers, but not the foliage. Beetles readily fed, and became paralyzed, on all flower colors of *P. × hortorum* and *P. peltatum*, including white. This concurs with early observations (Ballou 1929) that both red and pink flowers of *P. × hortorum* induce paralysis. The toxic compound is most likely not a flower pigment because paralysis was induced by white-flowered cultivars of both zonal and ivy geranium.

The assay conducted with flowers of *P. × scarborovia* suggests that not all *Pelargonium* spp. cause paralysis of Japanese beetles. Hybrid zonal geraniums and other species in which such activity was confirmed (Table 2) all belong to the type section *Cicinonium* (Miller 1996). *Pelargonium × scarborovia*, a hybrid of *P. crisimum*, belongs to type section *Pelargonium*, which contains the most primitive species of the genus (van der Walt 1985, Miller 1996). A future study, similar to that of Grazzini et al. (1997), which linked taxonomy of *Pelargonium* and anacardic acid activity, may reveal that this chemical defense is a relatively new antiherbivore adaptation within this genus.

Ballou (1929) observed that Japanese beetles suffer greater paralysis and mortality when feeding on sun-exposed geraniums than on shaded ones. This was the basis for our earlier speculation (Potter and Held 1999) that flavonoids, known to accumulate in plant cells under high light intensity (Taiz and Zeiger 1991), might be responsible for paralysis. The current study, however, showed that detached flowers from shaded and sun-grown plants caused comparable paralysis in the laboratory, a pattern seemingly not consistent with the flavonoid hypothesis. Anacardic acids mediate the resistance of zonal geranium to both mites and aphids (Hesk et al. 1992); however, anacardic acids are most likely not responsible for paralysis of *P. japonica* because beetles that feed on the foliage of zonal geranium are not affected. Furthermore, paralysis was induced by both *P. inquinins* and *P. zonale*.

Japanese beetles that have been paralyzed by geraniums either recover or die. In the laboratory, some beetles recovered in as little as 2–3 h, whereas others did not recover until the following day. The high rate of recovery in the lab may be an artifact because predation or desiccation most likely increases mortality of geranium-intoxicated beetles in the field (Potter and Held 1999). We observed, for example, that paralyzed beetles invariably were preyed upon when placed near the nest entrance of *Formica schaufussi* Meyer, a large aggressive ant species found in turfgrass and landscapes (López and Potter 2000), whereas normal beetles took flight when attacked by the ants (D. Held, unpublished data). We showed that 3-h exposure of paralyzed beetles on the foliage of zonal geranium plants in full sunlight resulted in substantial weight loss and eventual death. Japanese beetles have some capacity to thermoregulate, decreasing thoracic temperatures through evaporative cooling (Oertli and Oertli 1990) or behavior (Kreuger and Potter 2001). When a beetle is paralyzed, its body may warm uncontrollably, increasing water loss. Such stress most likely accounts for Ballou’s (1929) observation of higher mortality of beetles confined on sun-exposed geraniums.

There can be substantial variation in paralysis and mortality, even under laboratory conditions. In the test examining time to paralysis and recovery, for example, mortality was 45%, whereas it was much lower in the bloom color test conducted just 1 mo later. The flowers for both tests were collected from the same plantings. Potter and Held (1999) reported \( \approx 60\% \) mortality of female beetles provisioned solely with geranium flowers for 2 wk. Rate of paralysis or recovery was not directly proportional to the amount of flower tissue consumed, nor was recent feeding history a factor in whether or not beetles became paralyzed or recovered. Variation in the concentration of active components in the flowers may mediate whether beetles will recover or die. Within particular plant tissues (e.g., flower petals), concentration of secondary compounds can vary with tissue age, fertility, or plant stress (Taiz and Zeiger 1991).

Geranium is the only plant reputed to be toxic to Japanese beetles for which activity has been confirmed. This study further characterizes the toxicity of *Pelargonium* spp., especially the zonal geraniums, to *P. japonica*. Although the intoxicant in these flowers has not been identified, this work discounts the role of anacardic acids, and probably flavonoids, in paralysis. Efforts aimed at identifying the active component can now be focused on floral-specific biochemistry.
Acknowledgments

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