

## Effect of Simulated Insect Herbivore Damage on Survival of Tree Leaves

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**ABSTRACT** Leaf abscission caused by herbivores is well documented, yet the relationship between abscission and amount of damage required to initiate abscission is poorly known. This relationship was investigated in a southern Appalachian forest by mechanically damaging (0, 25, 50, and 75% area removed) leaves from red maple, *Acer rubrum* L., flowering dogwood, *Cornus florida* L., tuliptree, *Liriodendron tulipifera* L., and chestnut oak, *Quercus prinus* L., and monitoring leaf survival. Leaf survival was negatively related to percentage leaf area removed in 1985 and 1986. Timing of leaf abscission was not significantly different among tree species in 1985. In 1986, there were, however, significant differences among species, which coincided with a severe drought. Damage by herbivorous insects after treatment was measured in 1986 and differed significantly among treatment levels in tuliptree only. Despite significant effects of treatment damage on leaf survival, abscission of damaged leaves occurred at the beginning of normal autumn senescence and leaf fall (except tuliptree in 1986). These results are interpreted with respect to insect-mediated litterfall and its potential influence on the activities of forest floor decomposer organisms.

**KEY WORDS** herbivory, leaf abscission, litterfall

INCREASING EVIDENCE SUGGESTS that leaf-eating insects may be important in the regulation of forest ecosystem processes even under conditions of chronic, nominal herbivory (Schowalter 1981, Lamb 1985). For example, transfers of materials from the forest canopy to the forest floor, as a result of herbivory, may promote decomposer activities. These materials include fecal pellets, nutrients leached from damaged leaves, and damaged leaves that fall prematurely. Presumably these materials are utilized relatively quickly by decomposer organisms, thus speeding the rate of nutrient cycling (Springett 1978, Kitchell et al. 1979, Seastedt & Crossley 1984). It is in this context that I treat the influence of simulated herbivory on seasonal leaf fall in a deciduous forest ecosystem.

Feeding damage caused by leaf-eating insects may result in premature leaf fall in at least three different ways: (1) by weakening the structural integrity of petioles (e.g., damage by petiole-boring larvae) so that leaves break free under slight mechanical force; (2) by completely severing petioles, causing attached leaf blades to fall; and (3) by triggering a plant physiological response that leads to detachment, or abscission, of damaged leaves. The first two ways in which

herbivores cause leaf fall were described previously (Risley 1986, Risley & Crossley 1988). The third reason for herbivore-caused leaf fall, damage-induced premature leaf abscission, will be addressed in this paper.

Despite numerous studies that describe the abscission of insect-damaged leaves (see references in Risley (1986) and Risley & Crossley (1988)), few have addressed the specific amount of damage necessary to cause abscission (but see Lowman 1982, Lam & Dudgeon 1985, Bultman & Faeth 1986). Addicott (1982) explained that sufficient quantities of the abscission-inhibiting plant hormone auxin exist in leaf midribs and blades so that partial consumption has "little effect" on premature leaf abscission. Indeed, some studies that addressed the survival of mechanically damaged leaves showed that those leaves were retained until the end of the growing season and, although damaged leaves fell earlier than other leaves, all leaves fell within the period of normal senescence and abscission (Lowman 1982, Pritchard & James 1984). On the other hand, damage thresholds may exist, above which damaged leaves will abscise relatively quickly (Lam & Dudgeon 1985, Grace 1986, Risley 1986).

In this paper, results are presented from a 2-yr study of tree leaves in which herbivorous insect damage was simulated by mechanical leaf area

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removal. Relationships between leaf survival and extent of damage, and herbivory after treatment are described for four tree species in a young, mixed-hardwood forest in the southern Appalachians.

### Materials and Methods

Field work was conducted at the Coweeta Hydrologic Laboratory, U. S. Forest Service, Otto, NC (35°N, 83°25'W). The watershed selected for this study (watershed 7, WS7) is 59 ha, south-facing, and was clear-cut and cable-logged in 1977 (Swank & Crossley 1988). At the time of this study, trees in this watershed formed a young, even-aged canopy that was accessible from the ground.

Individuals of chestnut oak, *Quercus prinus* L., flowering dogwood, *Cornus florida* L., red maple, *Acer rubrum* L., and tuliptree, *Liriodendron tulipifera* L., were selected at random along trails at middle elevations within the watershed. These tree species are dominant in lower-elevation watersheds at Coweeta (Day & Monk 1974). Five individuals per species were selected in 1985 and four individuals per species were selected in 1986. Individuals of each species were similar in size and apparent health and originated from different stumps. All trees were exposed to midday sun.

Branches were selected randomly in the middle to lower crown of each tree and had a southern exposure. Because the forest canopy was open, most leaves had some exposure to the sun. Leaves previously damaged by herbivores were not selected. Petioles of leaves were tagged with small, numbered self-adhesive paper labels. Petiole tagging or labeling does not appear to influence leaf abscission (Pritchard & James 1984, Bultman & Faeth 1986). On 19 July 1985, 24 leaves were tagged in each tree and on 3 June 1986, 40 leaves were tagged in each tree.

Treatment consisted of the mechanical removal of leaf area with stainless steel scissors and was applied randomly to tagged leaves on each tree. The result was an equal number of leaves with 0 (control), 25, 50, and 75% leaf area removed. Leaves in the 25 and 75% damage categories were cut transversely (i.e., at right angles to midribs), and the portion of the leaf distal to the cut was discarded. Leaves in the 50% damage category were cut longitudinally (i.e., parallel to midrib) so that midribs were retained. Resulting patterns of mechanical damage appeared similar to those caused by Lepidoptera larvae, the prevalent leaf-chewing herbivores in forest canopies at Coweeta (Crossley et al. 1988).

In 1985, tagged leaves were monitored every 10-12 d through November (12 dates) and in 1986, tagged leaves were monitored every 7 d through November (21 dates). On each date, the status of tagged leaves was recorded (i.e., at-

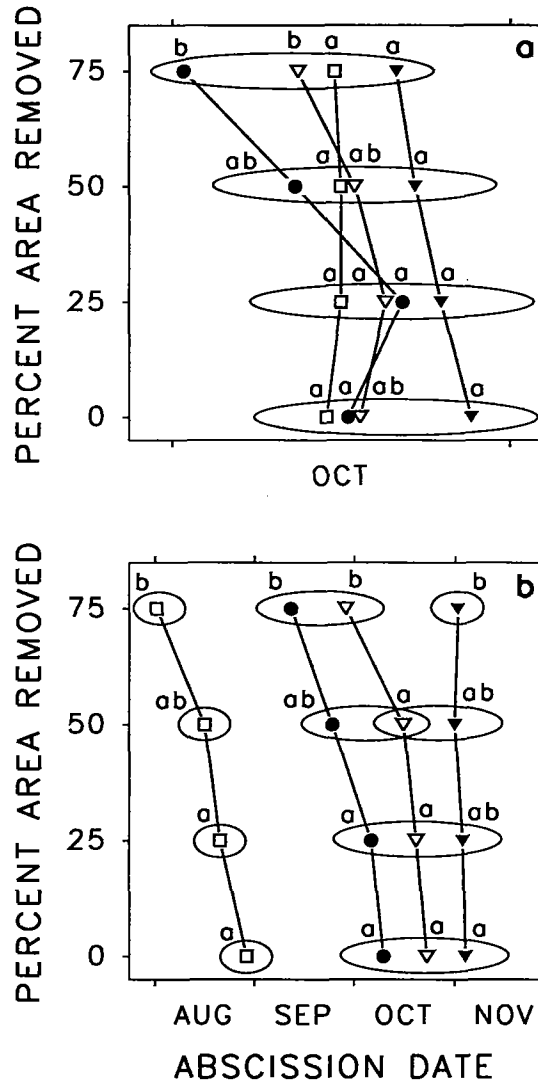
tached or fallen). Monitoring was continued until all tagged leaves had fallen. In 1986, fallen, tagged leaves were collected, pressed, dried, and photocopied. A Tektronix computer and graphics tablet were used to digitize photocopied leaf images. Posttreatment herbivory was measured as open holes, skeletonized areas, and mines. Sucking insects were uncommon, and stippling from feeding punctures was not measured. Leaf damage caused by decomposer organisms on the forest floor was recognizable and was not included in measurements.

Data were analyzed using a randomized block design (model III, two-factor ANOVA) without replication, where individual trees were treated as blocks (Zar 1984). Because individual leaves may not be true replicates (Neuvonen & Haukioja 1985, Athey & Connor 1989) and to avoid inappropriate error terms associated with pseudoreplication (Hurlbert 1984), means were calculated for life spans of leaves within each damage category in individual trees. Tukey's studentized range (HSD) multiple comparison tests were used to compare means among treatment categories (SAS Institute 1985). Significant differences are reported as  $P < 0.05$ . Posttreatment herbivory data were transformed before statistical analysis using the arcsine transformation described by Sokal & Rohlf (1969).

### Results

Simulated herbivore damage influenced leaf survival in the study trees. Percentage leaf area removed significantly effected leaf survival in dogwood (1985,  $F = 5.74$ ;  $df = 3, 12$ ;  $P = 0.0113$ ; 1986,  $F = 7.65$ ;  $df = 3, 9$ ;  $P = 0.0076$ ), red maple (1985,  $F = 3.63$ ;  $df = 3, 12$ ;  $P = 0.0450$ ; 1986,  $F = 10.34$ ;  $df = 3, 9$ ;  $P = 0.0028$ ), chestnut oak (1986,  $F = 5.14$ ;  $df = 3, 9$ ;  $P = 0.0242$ ), and tuliptree (1986,  $F = 10.05$ ;  $df = 3, 9$ ;  $P = 0.0031$ ) (Figs. 1 a and b). In 1985, survival of tagged leaves did not differ among treatment categories in chestnut oak ( $F = 2.48$ ;  $df = 3, 12$ ;  $P = 0.1112$ ) and tuliptree ( $F = 0.08$ ;  $df = 3, 9$ ;  $P = 0.9673$ ). In six of eight cases, multiple comparison tests (Tukey's HSD test;  $P = 0.05$ ) within tree species illustrate significant patterns of most heavily damaged leaves abscising earlier than control and lightly damaged leaves (Figs. 1 a and b).

Life spans of tagged leaves, within each treatment category, did not differ among tree species in 1985 (0% category,  $F = 1.22$ ;  $df = 3, 11$ ;  $P = 0.3495$ ; 25% category,  $F = 0.43$ ;  $df = 3, 11$ ;  $P = 0.7372$ ; 50% category,  $F = 1.09$ ;  $df = 3, 11$ ;  $P = 0.3934$ ; 75% category,  $F = 2.86$ ;  $df = 3, 11$ ;  $P = 0.0855$ ) (Fig. 1a). In contrast to 1985, life spans of tagged leaves differed significantly among tree species within all categories in 1986 (0% category,  $F = 17.91$ ;  $df = 3, 9$ ;  $P = 0.0004$ ; 25% category,  $F = 16.49$ ;  $df = 3, 9$ ;  $P = 0.0005$ ; 50% category,  $F = 19.08$ ;  $df = 3, 9$ ;  $P = 0.0003$ ;



**Fig. 1.** Comparison of the effects of simulated herbivore damage on the seasonal timing of leaf abscission in four tree species in the southern Appalachians. (A) Mean life span of leaves in 1985. (B) Mean life span of leaves in 1986. Reading each line vertically, symbols with the same letter are not significantly different according to Tukey's studentized range test ( $df = 12$ ;  $P < 0.05$  [SAS Institute [1985]]). Reading horizontally within treatment categories, symbols enclosed within the same ellipse are not significantly different according to Tukey's studentized range test ( $df = 11$ ;  $P < 0.05$  [SAS Institute [1985]]). Closed circle, flowering dogwood; open triangle, red maple; open square, tuliptree; closed triangle, chestnut oak.

75% category,  $F = 28.97$ ;  $df = 3, 9$ ;  $P = 0.0001$ ) (Fig. 1b). In 1986, tuliptree leaves within each treatment category abscised significantly earlier compared with the other species (Tukey's HSD test;  $P = 0.05$ ) (Fig. 1b). In 1986, dogwood leaves with 50% area removed had significantly shorter

**Table 1.** Within-species relationships between simulated herbivory and posttreatment herbivory in 1986

Species	Treatment categories, %			
	0	25	50	75
Dogwood	0.50a	0.57a	0.33a	0.21a
Red maple	0.80a	0.67a	0.31a	0.15a
Chestnut oak	2.4a	1.3a	1.4a	0.71a
Tuliptree	1.6b	0.73bc	3.1a	0.24c

Values are untransformed (arcsine square root transformation) mean percentage leaf area removed ( $n = 4$ ) obtained from Table K in Rohlf & Sokal (1969). Means with the same letter are not significantly different according to Tukey's studentized range test (error  $df = 9$ ;  $P = 0.05$  [SAS Institute 1985]).

life spans than chestnut oak leaves in the same category (Tukey's HSD test;  $P = 0.05$ ). In the 75% category, life spans of both dogwood and red maple were significantly shorter than those of chestnut oak (Tukey's HSD test;  $P = 0.05$ ).

Posttreatment leaf area removed by herbivorous insects was light in 1986: 90% of all tagged leaves had  $< 5\%$  additional leaf area removed. Posttreatment damage was not significantly related to treatment in dogwood ( $F = 0.58$ ;  $df = 3, 9$ ;  $P = 0.6430$ ), red maple ( $F = 1.62$ ;  $df = 3, 9$ ;  $P = 0.2529$ ), and chestnut oak ( $F = 2.30$ ;  $df = 3, 9$ ;  $P = 0.1459$ ) (Table 1). In tuliptree, posttreatment damage was significantly related to treatment ( $F = 25.22$ ;  $df = 3, 9$ ;  $P = 0.0001$ ), but not in a pattern consistent with the other tree species (i.e., decreasing posttreatment damage with increasing intensity of treatment) (Table 1).

In 1985, damaged and control leaves of the four tree species abscised during a relatively short period of time and blended with autumn leaf senescence and abscission (Fig. 1a). In contrast, timing of abscission of tagged leaves in 1986 extended across several months (Fig. 1b). For example, abscission of oak leaves occurred in early November, whereas tuliptree leaves abscised in August. Between-year differences were not compared statistically because of the disparity between start dates in 1985 and 1986.

Almost all tagged leaves (1,116 of 1,120 leaves) lost their green pigment and desiccated before abscission. The remaining four leaves (from red maple) fell green with abbreviated petioles that were characteristic of herbivore-caused greenfall (Risley & Crossley 1988). The petiole of one of the four leaves was severed by an unidentified caterpillar, and three fell as a result of petiole boring, probably by larvae of the maple petiole borer, *Caulocampus acericaulis* (MacGillivray) (Hymenoptera: Tenthredinidae).

**Discussion**

Results are consistent with the findings of Lowman (1982) and Pritchard & James (1984), where damaged leaves abscise earlier than undamaged leaves but abscission of damaged

leaves blends with normal foliar senescence and end-of-season abscission. Within the study trees, considerable damage to leaf blades was tolerated in both years. The departure of leaf life spans in the 75% treatment category from life spans in the other treatment categories may be, however, evidence for a threshold above which damage tolerance rapidly decreases until abscission occurs. It should be noted that, because this experiment used mechanical techniques to simulate damage caused by leaf-eating insects, it is not clear if results would have differed under conditions of actual herbivory. Although mechanical damage has been widely used to simulate herbivory by leaf-eating insects (Haukioja & Niemela 1977, Nielsen 1978, Lowman 1982, Lam & Dudgeon 1985, Wright et al. 1989) and produces "acceptable fidelity" to actual damage (Ostlie & Pedigo 1984), it is impossible to recreate the full suite of events that integrate to form relevant leaf-insect interactions, which include specialized behaviors (e.g., avoidance of vascular tissue) (Hagen & Chabot 1986) and chemical exchanges (e.g., cytokinins) (Engelbrecht et al. 1969).

Differences in leaf survival among tree species were most apparent in 1986. Explanation of these differences in an environmental context is confounded by earlier initiation of mechanical damage to tagged leaves in 1986 (19 July 1985 and 3 June 1986). Younger leaves may be more sensitive to injury than older leaves. Nevertheless, during 1986, there was an environmental extreme; the southeastern United States suffered one of its worst droughts in recorded weather history. At Coweeta, precipitation averages 182 cm/yr (50-yr average) on low-elevation watersheds but was deficient by as much as 74 cm during the height of the 1986 growing season. In 1986, there was an observed shortening of leaf life spans within a number of tree species in the Coweeta basin. For example, tuliptree foliage began to senesce and abscise in July (unpublished data). The extent to which the 1986 drought affected the life spans of tagged leaves is unknown, but this factor probably contributed to the atypically early abscission of tagged leaves in tuliptree (see Fig. 1b). It is also possible that the drought magnified the negative effect of treatment damage on leaf life spans in dogwood and red maple.

Because foliar herbivory by insects is continuous during the growing season at Coweeta (Crossley et al. 1988, Risley & Crossley 1988), and differential herbivory based on amount of previous damage to leaves has been documented (Schultz 1983, Smith 1983, Faeth 1986, Raupp & Sadof 1989), posttreatment herbivore damage to tagged leaves was considered a potentially important additional factor in leaf survival. In other words, posttreatment herbivory could have changed experimental patterns of leaf area removed; i.e., "relocated" leaves from one treat-

ment category to another. In 1986, post-treatment herbivore damage was light, was not sufficient to "move" leaves from one treatment category to another, and probably had little additional influence on abscission of tagged leaves.

In a related study, Risley & Crossley (1988) found that herbivore-caused green leaf fall (greenfall) occurred throughout the growing season. Greenfall was characterized by variable amounts of percentage leaf area removed and major damage to petioles or other primary vascular tissue. The influence of damage restricted to laminar portions of leaves on subsequent leaf survival was, however, unknown. In the current study, up to 75% leaf area removed from laminar portions of leaves was not an important factor in leaf abscission until late in the growing season. Because tagged leaves senesced and fell late in the growing season, some foliar nutrients (e.g., nitrogen) were probably translocated from damaged leaves to woody tissues (Kramer & Kozlowski 1979) before abscission. Thus, senesced leaves likely represent a relatively low-quality substrate for decomposers.

In conclusion, it appears that there are two components to herbivore-caused leaf fall. One component is the continuous input of greenfall during the growing season (Risley & Crossley 1988). The second component is the senescence and premature abscission of herbivore-damaged leaves at the end of the growing season (this study). These two processes overlap in autumn to provide continuous inputs of foliar litterfall to forest floor decomposer organisms from the beginning of the growing season to the onset of winter in a southern Appalachian deciduous forest.

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