

**THE INFLUENCE OF HERBIVORES ON SEASONAL LEAF-FALL:
PREMATURE LEAF ABSCISSION AND PETIOLE CLIPPING**

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Abstract: A review of the literature on insect-plant interactions documents mechanisms by which herbivores regulate the transfer of materials from host plants to litter and soil decomposer communities. Emphasis is placed on the acceleration of seasonal leaf-fall through premature abscission of insect-damaged leaves and petiole clipping by caterpillars. Green leaves falling (greenfall) during the growing season are evidence for the occurrence of both phenomena. Greenfall was 1.3% of total foliar production (1901 kg/ha/yr) for dominant tree species on a site at the Coweeta Hydrologic Laboratory, North Carolina. Significantly ($P < 0.05$) higher percent leaf area removed in greenfall compared with *in situ* leaves is further evidence that herbivores accelerated leaf-fall. The addition of greenfall to insect fecal pellet production strengthens the role of herbivores as regulators of nutrient cycling in forest ecosystems.

Key Words: Herbivory, leaf abscission, petiole clipping, forest insects.

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Leaf-eating insects, or folivores, are ubiquitous in forest ecosystems and constitute a small but important fraction of the living biomass. The chronic influence of folivores on primary producers is nominal except under conditions of outbreak. However, the potential for rapid, exponential increases in folivore populations, and observations of substantial unutilized food resources have sparked a number of studies designed to explain this paradox. Factors influencing herbivory are exceedingly complex, thus an explanation which appears satisfactory for a particular combination of folivore and host may not be applicable to another, different combination. Host plant quality, including intraplant genetic variability (Whitham et al. 1984), is important in shaping physiological and behavioral responses of attacking folivores. Secondary consumers also exert selective pressure which results in specialized forms of predator avoidance behavior.

Premature leaf abscission is an area of insect-plant interactions which has received little attention. Economically important agricultural systems, especially cotton, have provided evidence for insect-induced bud abscission (Crawley 1983). Trees will abscise fruit and nuts in response to folivore feeding damage (Proctor et al. 1982; Sork and Boucher 1977). Plant foliage has received less attention although the phenomenon of insect-induced premature leaf abscission further supports the role of herbivores in ecosystems. Studies of herbivory at the ecosystem level are based on growing acceptance that herbivores regulate the activities of primary producers by short-circuiting pathways of important nutrients (Mattson and Addy 1975; Schowalter 1981; Seastedt and Crossley 1984; Wolaver 1983). Premature leaf abscission provides nutrient-rich inputs to decomposer communities and

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dampens seasonal oscillations in nutrient availability. Furthermore, failure to account for losses of insect-damaged leaves from host plants may result in underestimates of actual herbivory.

In this review emphasis is placed on the literature describing plant responses to folivore damage and folivore responses to its milieu. Recent studies will serve as a backdrop to previously unemphasized acceleration of seasonal leaf-fall caused by feeding activities of canopy folivores. Supporting evidence from a study conducted in the southern Appalachians documents consistent and measurable host-plant losses of insect-damaged leaves during the growing season.

PLANT RESPONSES TO FOLIVORE DAMAGE

Through the work of Feeny (1970) and subsequent investigators, seasonal variability in leaf quality was recognized and attention drawn to the relationships of leaf compounds (e.g., tannins) to rates of herbivory. More recent investigations have focused on changes occurring in concentrations of tannins and other foliar allelochemicals in response to varying degrees of defoliation. Some authors have suggested that plants respond to defoliation by increasing production of digestion-inhibiting compounds (Edwards and Wratten 1983; Green and Ryan 1972; Ryan and Green 1974). Ingestion of these compounds results in longer developmental periods and lower pupal weights in primary consumers (Hart et al. 1983; Haukioja 1979, 1980; Haukioja and Niemela 1977; Neuvonen and Haukioja 1984; Raupp and Denno 1984; Schultz and Baldwin 1982; Tuomi et al. 1984; Valentine et al. 1983; Wallner and Walton 1979; Wratten et al. 1984). A particularly interesting series of studies led to the discovery that a tree may not only defend itself, but may communicate a warning to neighboring trees (Baldwin and Schultz 1983; Schultz 1983). However, some authors have described instances where pupal weights of herbivores (Crawley and Nachapong 1984) or caterpillar growth rates (Myers and Williams 1984) were not different between defoliated and undefoliated host plants. Furthermore, Crawley and Nachapong (1984) found that ovipositing females of the cinnabar moth, *Tyria jacobaeae* (Linnaeus) (Lepidoptera: Arctiidae) showed no significant ($P > 0.1$) preference for undamaged ragwort (*Senecio jacobaea* Linnaeus) (Asteraceae) plants compared with those defoliated previously.

By shifts in nutrient and carbon allocation strategies, plants may also compensate to some extent by producing secondary foliage (Coulson and Witter 1984; Doane and McManus 1981; Kulman 1971) or by increasing rates of photosynthesis in damaged or adjacent, undamaged leaves (Detling et al. 1980; Dyer 1975, 1980; Dyer and Bokhari 1976; Hilbert et al. 1981; McNaughton 1976; Neales and Incoll 1968; Nowak and Caldwell 1984; Proctor et al. 1982; Reardon et al. 1972; Solomon 1983; Way and Cammell 1970). Damaged leaves may become a liability to the plant as emphasis shifts from growth and carbohydrate production to maintenance, promoting abscission of damaged leaves and replacement by secondary growth (Varley 1967). Leaf abscission also results from pathogenic infection (Addicott and Lyon 1973; Boote et al. 1983; Skarmoutsos and Millar 1982) and may be a natural defense strategy employed by plants to prevent the spread of disease (Kozłowski 1973). Abscission is a natural process leading to detachment of certain plant parts and, in leaves, "involves separation of a distinct layer of cells" at the base of the petiole (Woolhouse 1978). Discussion of abscission is usually restricted to that of leaves, flowers and fruits although twigs (Osborne 1973) and

stems (Addicott and Carns 1964) may also abscise prematurely. Premature abscission of herbivore-damaged leaves has been described in a number of forest systems including boreal beech forests (Nielsen 1978), Australian eucalypt forests (Journet 1981), subtropical mangrove forests (Onuf et al. 1977), and temperate deciduous forests (Thomas 1969). The existence of premature leaf abscission is sometimes acknowledged (e.g., Chabot and Hicks 1982; Fox and Morrow 1983; Ohmart et al. 1983) but not given serious attention. The few studies dealing explicitly with this phenomenon are concerned primarily with populations of leaf miners (Hileman and Lieto 1981; Maier 1983; Owen 1978; Pritchard and James 1984a; Proctor et al. 1982). Premature leaf abscission in response to folivore damage has been suggested to be a defensive mechanism used by plants to rid themselves of damaging organisms (Faeth et al. 1981). Initial reports of abscised, mined leaves described potential deleterious effects to the leaf miners, including mortality, but some current studies do not concur (Kahn and Cornell 1983; Pritchard and James 1984b).

The actual mechanism responsible for abscission is not clearly understood. The plant hormone auxin is recognized as a senescence and abscission inhibitor and its reduction in tissues is one factor associated with changes leading to abscission (Addicott 1982). However, according to Addicott (1982), enough auxin is present in midribs and leaf blades that partial defoliation has "little effect" on premature leaf abscission. Another plant hormone, ethylene, has received a great deal of attention with regard to its role in leaf abscission and is considered to be a promoter of the process (Addicott 1982; Sexton 1982; Thomas and Stoddart 1980). Ethylene is produced from most parts of higher plants (Sisler and Yang 1984) and is active in other plant processes including germination and fruit ripening. Its volatility and potential influence on adjacent plant parts may be important, although this activity under field conditions has not been emphasized (Addicott and Carns 1964). Ethylene acts by stimulating cell division in wound areas, indicating a wound repair mechanism (Yang and Pratt 1978). It further initiates a chain of events leading to activation of hydrolytic enzymes, cell wall breakdown, and reorientation of cell expansion in the abscission zone, resulting in mechanical stress and subsequent leaf abscission (Woolhouse 1978). Folivore activity stimulates production of ethylene (called wound or stress ethylene) near sites of leaf wounds (Jackson and Osborne 1970; Konze and Kwiatkowski 1981; Sisler and Yang 1984; Woolhouse 1978; Yang and Pratt 1978).

FOLIVORE RESPONSES TO ITS MILIEU

Folivore responses to their hosts are evidenced by physiological and behavioral adaptations. Physiological adaptations include maintenance of high gut pH (Feeny 1970) in order to deal more efficiently with tannins found in leaf tissues of most tree species (Bate-Smith and Metcalfe 1957). Recently discovered surfactants were reported to reduce protein precipitation by tannins within the guts of some folivorous caterpillars thereby aiding in digestion of leaves containing these refractory compounds (Martin and Martin 1984). Changes in host quality can be circumvented by the folivore through rapid inducement of a complex of oxidase enzymes which are effective in deactivating toxic compounds (Brattsten 1979). Folivores can also condition their host by directly modifying metabolic pathways via injected salivary compounds. For example, cytokinins inhibit leaf senescence

(Thomas and Stoddart 1980) and their injection by some species of leaf miners results in palatable "green islands" surrounding the herbivores (Engelbrecht et al. 1969; Engelbrecht 1971). Pectic enzymes from species of *Lygus* (HEMIPTERA: Miridae) (Hori 1975) and *Anthonomus* (COLEOPTERA: Curculionidae) disrupt hormone control mechanisms and may be responsible for flower and fruit abscission (Addicott 1982). Saliva from *Sirex noctilio* Fabricius (HYMENOPTERA: Siricidae), after contact with leaf tissues, promoted ethylene production in excess of that caused by mechanical damage alone (Shain and Hillis 1983).

Patterns of folivore feeding behaviors reflect adaptations to selective pressures of both hosts and predators. Behavioral responses to deterrent compounds in plants are present in a number of species. For example, plant trichomes, capable of penetrating the soft cuticle of caterpillars, are covered with silk by ithomiid butterfly, *Mechanitis isthmia* Bates, larvae in order to gain access to unprotected edges of leaves (Rathcke and Poole 1975). Leaf mining is considered to provide a protective habitat as well as a method for consuming foliar cell layers not laden with tannins (Feeny 1970). Over-dispersion of feeding damage in individual leaves of several species of herbaceous and woody plants was interpreted by Edwards and Wratten (1983) to be the result of avoidance behavior by which folivores escape halos of rapidly-induced inhibitory allelochemicals. In Mexico, a coccinellid beetle, *Epilachna tredecimnotata* (Latreille), was observed to cut circular trenches in squash (*Cucurbita moschata*) (*Curcubitaceae*) leaves, then feed on encircled tissue (Carroll and Hoffman 1980). The authors also observed monarch butterfly, *Danaus plexippus* (Linnaeus) (LEPIDOPTERA: Danaidae) and saddled prominent moth, *Heterocampa* spp. (LEPIDOPTERA: Notodontidae), larvae partially cutting petioles of host plant leaves prior to feeding on the same leaves. These examples of what the authors termed "wasteful feeding" suggest adaptations designed to circumvent induction of defensive compounds into otherwise palatable leaf tissue. In Costa Rica, a sphingid caterpillar, *Erinnyis ello* Linnaeus, constricts petioles of its host plant, *Cnidioscolus urens* (Linnaeus) (*Euphorbiaceae*) before feeding on the attached leaf. The constriction impedes flow of a sticky latex which would mechanically inhibit feeding and movement (Dillon et al. 1983). Heinrich (1971) described an unusual feeding behavior in the tobacco hornworm, *Manduca sexta* (Linnaeus), (LEPIDOPTERA: Sphingidae), on its host plants. Caterpillars of this species take a position near the petiole, grasp leaf edges with their thoracic legs, and bend the leaf toward them for feeding. If simple bending activity failed, chewing the midrib enabled a caterpillar to bring the leaf within reach of its mouthparts.

Behavioral adaptations by folivores, in response to their milieu, include activities designed to avoid predators. Some examples are jerky body movements, tumbling off substrate, nocturnal feeding, feeding while attached to undersides of leaves, and removing evidence of their feeding. A specialized form of behavior is associated with caterpillars palatable to insectivorous birds. Heinrich (1979) described a noctuid, *Catocala cerogama* Guenee, caterpillar which partially consumes a leaf, moves to the petiole, and systematically clips the leaf free. This behavior was thought to be a strategy employed by the caterpillar to avoid predators which utilized damaged leaves as a cue for the location of prey. In a later paper, Heinrich and Collins (1983) used black-capped chickadees, *Parus atricapillus*, to test the hypothesis that birds incorporate a search image for folivore damaged leaves in their foraging behavior. The results of their experiment lend credibility to the original explanation for leaf clipping behavior by palatable caterpillars.

SUPPORTING EVIDENCE

Analysis of seasonal patterns of herbivory, during 1981, in two forested catchments at the Coweeta Hydrologic Laboratory, U. S. Forest Service in North Carolina revealed that percent leaf area removed (LAR) did not accrue in an expected fashion (Risley 1983). Instead of steady increases in percent LAR there were early- to mid-season peaks followed by rather sudden decreases. Only after mid-season was there steady accrual of percent LAR until leaf senescence in the fall. Measurements of undamaged leaves and concentrations of foliar elements followed the same pattern. One explanation was that damaged leaves were shed and replaced by secondary growth (see Journet 1981). However, because the explanation was only supported circumstantially, a study was conducted in 1983 to explore insect-induced premature leaf abscission and the extent to which it occurred in a deciduous forest (watershed 18) at Coweeta.

The primary objective of the study was to measure premature leaf fall and compare the damage to leaves on the forest floor with those *in situ*. During the previous growing season, green leaves (greenfall) scattered on the forest floor were evidence that leaves had been shed prior to end-of-season senescence. It was expected that the blades of green-fallen leaves would have variable amounts of folivore damage and possess complete petioles.

Greenfall was collected and comparisons made with photographs taken of leaves in the canopy. Leaves from chestnut oak, *Quercus prinus*, hickories, *Carya* spp., yellow poplar, *Liriodendron tulipifera*, red maple, *Acer rubrum*, and flowering dogwood, *Cornus florida*, representing dominant tree species, were examined. Percent LAR data were submitted to an arcsine squareroot transformation (Sokal and Rohlf 1969) and tested ($\alpha = 0.05$) using a method described by Goulden (1952) for unequal sample sizes and unequal variance. In almost every case, when comparing percent LAR of green fallen leaves to those *in situ*, the abscised leaves exhibited significantly more damage (Table 1). Comparisons with observed feeding damage from forest floor macroinvertebrates indicate that little contribution to percent LAR was made between the time leaves fell and the time they were collected. A green leaf appeared to remain "fresh" for 2 to 3 d. Differences among trees illustrate variable responses to damage and that damage thresholds may exist (Table 1). That is, leaves may be shed when damage exceeds thresholds of acceptability. For example, dogwood appears to exhibit a low threshold as evidenced by very low percent LAR *in situ* and significantly higher (but low relative to other tree species) percent LAR in green-fallen leaves. Chestnut oak leaves illustrate a similar pattern but at a considerably higher level. Occasionally, entire leaves from mockernut (*C. tomentosa*) and pignut (*C. glabra*) hickories were found with very little damage, and although petioles were complete, the bulbous proximal portion of each has hollowed out. An examination of terminal leaf buds in the canopies of several hickory trees led to the discovery of weevil, *Curculio* sp. (COLEOPTERA: Curculionidae), larvae boring inside the buds and weakening leaf attachment points.

As collections were made, it became evident that leaf blades of some green-fallen leaves were not accompanied by complete petioles, and in fact, many petioles were only vestiges of the originals. Green-fallen leaves normally supporting relatively long petioles (yellow poplar, red maple, chestnut oak) were reexamined. Yellow poplar greenfall was exemplary in the observed pattern of partially consumed (up

Table 1. Comparisons of percent leaf area removed between green-fallen leaves (greenfall) and those *in situ*. Collections were made in 1983 at the Coweeta Hydrologic Laboratory, U. S. Forest Service, North Carolina. Number of leaves measured is indicated in parentheses. YP = Yellow Poplar, RM = Red Maple, DW = Dogwood, CO = Chestnut Oak, H = Hickory spp, * = significant ($\alpha = 0.05$) difference between means, ns = not significant.

Tree		Mean percent leaf area removed			
		Jul	Aug	Sep	Oct
YP	Greenfall	7.05 (45) *	18.13 (15) *	24.40 (103) *	8.45 (5) ns
	<i>in situ</i>	0.54 (88)	0.70 (115)	1.36 (111)	0.99 (161)
RM	Greenfall	1.49 (41) ns	4.98 (74) *	9.96 (106) *	1.75 (18) ns
	<i>in situ</i>	1.99 (94)	2.45 (120)	2.90 (126)	3.71 (178)
DW	Greenfall	3.38 (18) *	6.53 (15) *	6.02 (20) *	0.05 (1) -
	<i>in situ</i>	0.27 (133)	0.44 (139)	0.62 (103)	0.35 (218)
CO	Greenfall	10.17 (94) *	12.38 (150) *	8.35 (248) *	2.45 (153) *
	<i>in situ</i>	4.18 (144)	7.14 (131)	5.06 (130)	4.39 (216)
H	Greenfall	3.51 (30) ns	7.41 (144) *	1.57 (148) ns	1.32 (27) ns
	<i>in situ</i>	1.09 (90)	1.40 (267)	1.17 (253)	0.92 (498)

to 50% LAR) leaves combined with abbreviated petioles (Fig. 1). Clipping behavior was observed in 1985 and the result of this behavior was evident during the growing season. The proportion (percent dry weight) of clipped leaves in greenfall samples ranged from 25% in June to over 80% in early October.

Although greenfall occurred consistently and was measurable through the growing season, the contribution by weight to total annual foliar litterfall was small. The sampled tree species contributed 60% to total foliar litterfall in 1983 and greenfall was 1.3% of that total. While small, inputs of greenfall increased the flow of materials from herbivores to forest floor decomposer communities. In any year, these inputs may be important in maintaining and possibly stimulating decomposer activity.

SUMMARY

A review of the rapidly expanding literature on plant responses to insect damage and folivore responses to both plant host and predators illustrated the many questions and avenues of query challenging current research in this area. Emphasis was placed on the selective abscission of insect-damaged leaves as well as insect feeding behaviors resulting in petiole clipping. Premature leaf abscission is a host-plant response to damage including that caused by insects and pathogens. The action of wound or stress ethylene partially explains the mechanism leading to premature abscission of damaged leaves. More importantly, folivores may contribute directly to seasonal leaf-fall by attacking petioles before or after feeding on



Fig. 1. Green-fallen yellow poplar leaves with abbreviated petioles. A typical example of greenfall exhibiting evidence of caterpillar petiole-clipping behavior. Note considerable damage to each leaf.

the attached leaf blade. Petiole girdling before feeding enables a folivore to avoid induced compounds deleterious to feeding and/or digestion. Post-feeding clipping of petioles may be a predator avoidance strategy employed by palatable caterpillars to escape detection by insectivorous birds. Evidence supporting the role of herbivores in accelerating seasonal leaf-fall was presented from an investigation in a deciduous forest in North Carolina. Contribution by weight of greenfall during the growing season was small but consistent. A major implication of greenfall is an expanded role for canopy folivores by increasing input, above what is normally suggested, to decomposer communities on the forest floor. A study now underway at the Coweeta Hydrologic Laboratory is designed to measure the quantity, quality, and fate of greenfall in several watersheds.

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