

Timing and intensity of herbivory: Its influence on the performance of clonal woodland herbs

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Abstract

Herbaceous woodland species account for a significant amount of the biodiversity of temperate deciduous forests. A wide diversity of life-history strategies is known for woodland herbs, and several systems have been used to categorize the range of life-history characteristics. Clonal growth, one common feature of many woodland herbaceous species, provides several benefits including the ability to respond to disturbances by sharing resources among ramets. There is evidence that resource sharing is common among ramets of some species of woodland herbs but not others. Herbivory is a common form of disturbance among woodland herbs, but little is known about effects of the timing and intensity of herbivory. In this paper, we use an existing system of classification of life-history traits of clonal species to make predictions about how woodland herbs would respond to the timing and intensity of defoliation. Examples from a preliminary study in Maryland, USA, are used to demonstrate that the timing and intensity of herbivory can play an important role in determining patterns of future growth and resource allocation.

Keywords: clonal growth, clonal herbs, deciduous forests, herbivory, Maryland, ramets.

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Three examples demonstrate that woodland herbs account for most of the vascular plant species biodiversity in temperate deciduous forests. In a study of the state of Wisconsin (USA), Curtis (1992) found that herbs accounted for 55–75% of all species in seven forest types. Further east in the deciduous forest biome of North America, 85% of the species recorded by Siccama *et al.* (1970) in the Green Mountains of Vermont were herbaceous. Between 60 and 86% of the species were herbaceous in slope and floodplain forests in the James River Gorge in Virginia (Ramsey *et al.* 1993). In addition to accounting for most of the vascular plant biodiversity in temperate deciduous forests, woodland herbs encompass a wide range of life-history strategies ranging from annual species to long-lived perennials (Kawano 1975; Givnish 1987). Most perennial woodland herbs are clonal and produce ramets through a wide variety of root- and stem-derived organs (e.g. Klimes *et al.* 1997). Purported benefits of clonal reproduction in woodland habitats include:

(1) Vegetative reproduction is more energetically and nutritionally efficient than sexual reproduction in light-limited environments where the probability of successful seedling establishment is low.

(2) Vegetative reproduction reduces the risks of genetic extinction in response to natural and human disturbances and to natural death of individual ramets.

(3) Vegetative reproduction allows for morphological plasticity in resource acquisition in patchy environments. Individuals can vary placement of ramets and, over time, the production of ramets in different locations can result in movement of the clone.

(4) Clonal reproduction allows for sharing (e.g. risk spreading) among connected ramets in response to patchy distributions of resources and disturbance (e.g. disease, herbivory).

In this paper we focus on the fourth purported benefit by considering the potential interactions between connected ramets in response to the timing and intensity of herbivory. We begin with a brief literature review of physiological integration among ramets of clonal woodland herbaceous species and responses of woodland herbs to herbivory. We then expand upon a classification proposed

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by Jónsdóttir & Watson (1997) to make predictions about how clonal woodland herbaceous species might respond to differences in the timing and intensity of herbivory. We end the paper with results from a preliminary study in Maryland, USA, to test some of the predictions.

Physiological integration among ramets of woodland herbaceous species

Physiological integration has been examined in only a few clonal woodland herbs, and most studies have been of species that form relatively large clonal patches (see Appendix in Jónsdóttir & Watson 1997). Only a few patterns of physiological integration have been demonstrated for clonal woodland herbs. *Aster acuminatus* may be typical of species which form large patches which have short-lived connections between parents and ramets with little, if any, physiological integration (Ashmun *et al.* 1982). *Clintonia borealis* and *Podophyllum peltatum* may be representative of species that form large patches and have a high degree of physiological integration among ramets that are connected for years (Ashmun *et al.* 1982; Landa *et al.* 1992). As much as 50% of the carbon fixed by *P. peltatum* can be translocated to older rhizomes for use in the next growing season to support new growth in the spring. *Aralia nudicaulis* (Flanagan & Moser 1985) and *Glechoma hederacea* (Price *et al.* 1992) have a high degree of clonal integration but differing patterns of resource movement. Most carbon movement among *A. nudicaulis* ramets is basipetal while in *G. hederacea* it is acropetal. A series of articles by Hutchings and his colleagues in the UK have clearly shown the complexity of resource sharing among ramets of clonal species (e.g. Slade & Hutchings 1987; Marshall 1990; Price & Hutchings 1992). They found that most species display some level of functional integration during ramet development (Hutchings & Bradbury 1986; Hutchings & Mogie 1990).

Herbivory

Almost all species of woodland herbs are affected by herbivory, and the consequences have been shown to be variable. Some woodland herbs contain chemicals that deter herbivores (Rooney & Dress 1997a). A few species have been shown to benefit by a moderate amount of herbivory (e.g. Schreiner *et al.* 1996) by ungulates. Some woodland herbs may be ignored by some animals but eaten by others (Knight 1964). Woodland herbs, however, are almost always negatively impacted by high levels of vertebrate and invertebrate herbivory (Brunet 1993), and forests with high densities of ungulates such as the white-tailed deer (*Odocoileus virginianus*) typically have a low diversity of understory herbs (Tilghman 1989; Balgooyen & Waller 1995; Rooney & Dress 1997a,b; Waller & Alver-

son 1997). The degree to which some species of woodland herbs are influenced by herbivory can even be used as indicators of deer density (Anderson 1994). Only a few species (e.g. ferns such as *Dennstaedia punctiloba*, *Dryopteris intermedia*, *Endymion nonscriptus*) that contain toxic chemicals are avoided by deer (Rooney & Dress 1997a,b), but they are also consumed at high deer densities (Rooney & Dress 1997a,b).

The range of effects that herbivores have on current and future growth and reproduction of woodland herbs has been studied in few species. Watson (1995) suggested that the influences of herbivores on native herbs depend on the nutritional quality of the plant, the part of the plant that is attacked by the herbivore, the mode of action of the herbivore, and the timing of herbivory relative to the plants developmental phenology. de Kroon *et al.* (1991) showed that rhizomes of *P. peltatum* that had shoots which were lost earlier in the growing season through senescence or herbivory only produced asexual shoots the next growing season. Temporal variations in herbivore density have been shown to play a role in long-term plant responses to herbivory (John & Turkington 1997). Complex interactions between woodland herbs and several groups of animals and disease organisms have also been demonstrated. Ericson and Wennström (1997) suggested that cycles of vole populations could influence the interactions between voles, scale insects, and smut-infected shoots of *Trientalis borealis*. Shoots of *T. borealis* which were infected by a smut fungus (*Urocystis trientalis*) were preferred by voles (*Clethrionomys glareolus*) and scale insects (*Arctothezia cataphracta*). Thus, herbivory by voles reduced the incidence of smut infection and potentially selected for a higher disease resistance in *Trientalis*. The effects of voles on woodland herbs were also examined by Ericson and Oksanen (1987). They found that the interactions between voles and plants were complex and were influenced by how productive the sites were. Voles had little effect in highly productive sites, and plant morphology was important as individuals with rosettes were eaten less than plants with umbrella shoots.

Ehrlén found that *Lathurus vernus* was damaged by insects, molluscs and deer, with the greatest influence on mortality being caused by meristem damage by molluscs. Insect damage to inflorescences of *Trillium erectum* was less for individuals producing two inflorescences (Davis 1981). Davis suggested insect damage should provide a selective advantage to individuals with two inflorescences but they were present at low frequencies in populations because of energy limitations. Pests and pathogens had few effects on *Silene dioica*, but mortality increased in response to grazing by animals that were not identified (Matlack 1987).

In addition to eating aboveground tissues, herbivores also consume the belowground parts of plants and

influence current and future growth and reproduction (Ericson & Wennström 1997). Rodents which ate the underground corms of *Tipularia discolor* had a greater significance on the long-term dynamics of populations than any other factor (Whigham & O'Neill 1991).

Several artificial defoliation studies have been conducted on woodland herbs, and responses have been so variable that no general patterns appear to be discernible relative to life-history strategies, degree of clonal integration or phylogeny. Even a small amount of leaf removal had a negative effect on biomass production of *G. hederacea* (Price & Hutchings 1992) and the consequences increased with greater amounts of defoliation. The effects of a given amount of defoliation depended on the pattern of leaf removal and source-sink relationships were modified by patterns of defoliation (Price *et al.* 1992). Male and female tillers of the dioecious sedge *Carex picta* were found to function as semiautonomous physiological units, and males and females responded differently to artificial defoliation (Delph *et al.* 1993).

Differential responses of species to defoliation have been shown by Rockwood and Lobstein (1994) who found that most responses were temporally delayed. Responses to herbivory also increase with increased frequency of defoliation. A 3-year defoliation study of *Tipularia discolor* showed that 100% leaf removal resulted in a cessation of flowering within 1 year, a progressive decline in below-ground biomass, and increased mortality (Whigham 1990). Plants that were 50% defoliated had the same responses but the consequences were delayed. Defoliation of *T. discolor* also resulted in decreased amounts of belowground biomass and concentrations of non-structural carbohydrates (Zimmerman & Whigham 1992). Zimmerman and Whigham concluded that non-structural carbohydrates were not used as much for recovery from defoliation as for initiation of new leaf growth and flowering. Leaf removal also resulted in a decrease in corm biomass in *Trillium grandiflorum* (Lubbers & Lechowicz 1989) but, unlike *T. discolor*, had no influence on seed production. Removal of flowers and leaves of *Primula veris* resulted in a decrease in flowering for 2 years (Syrjänen & Lehtil 1993). Increased fruit production only had an effect on future performance of *Cypripedium acaule* when it was combined with complete defoliation. Partially defoliated plants were able to compensate for the costs of fruit and seed production (Primack *et al.* 1994).

Model for predicting responses to timing and extent of herbivory

Jónsdóttir and Watson (1997) developed a framework for characterizing patterns of integration among clonal plants based on three characteristics: longevities of connections

between ramets, ramet longevity, and ramet generation time. They divided clonal plants into two groups: disintegrators and integrators. Disintegrators are clonal plants whose ramet connections break shortly after daughter ramets are formed. Integrators are clonal plants whose ramet connections are physically and physiologically maintained for varying periods of time after ramet birth. The integrator group was further subdivided into four categories based on the degree of physiological integration among ramets (full or restrictive integration) and clone size (small or large clonal fragments).

The framework developed by Jónsdóttir and Watson (1997) provides a useful model for predicting the effects of the timing and extent of herbivory (Table 1) on growth and reproduction of woodland herbs. Table 1 contains the same groupings and categories proposed by Jónsdóttir and Watson, but it has been expanded to include two components of herbivory (frequency and amount). The frequency of herbivory appears as three columns labeled early, late and frequent. We consider early herbivory to be the removal of leaf tissue during the period of leaf expansion. Late herbivory would occur during the middle of the growing season or later and frequent herbivory refers to removal of leaf tissue at least at three times (early, mid, late) during the growing season. The cells in the Table are proposed plant responses to different amounts of herbivory (high/medium/low). High, medium and low herbivory are arbitrarily defined as the percentage of leaf material removed and is equal to: high $\geq 75\%$, medium ≥ 25 and $< 75\%$, low $\leq 25\%$. Predicted responses to the timing and extent of herbivory are given as: 0 = no effect on growth or reproduction, - = negative response on growth and reproduction.

Four different predicted scenarios emerge from Table 1: -/-/-, 0/0/0, -/-/0, -/0/0. We predict that frequent herbivory would always have a negative effect (-/-/-) on growth and reproduction independent of the duration of integration (disintegrators or integrators), size of the clonal fragment, and degree of physiological integration. Studies of browsing by ungulates provide most of the information to support this prediction. Frequent herbivory by deer has been shown to result in local extinction or a significant negative repercussion on growth and reproduction (Rooney & Dress 1997a,b; Waller & Alverson 1997). A few experimental data also support this conclusion (Whigham 1990; Rockwood & Lobstein 1994).

We predict that species in both categories of 'disintegrators' would respond negatively to high and medium amounts of herbivory no matter how frequently it occurred. Differences between types of 'disintegrators' are predicted to occur mostly at low levels of herbivory (Table 1). For species which form large clones, we predict that differences would occur mostly in response to the

Table 1 Predicted responses to the amount and timing of herbivory

Functional types	Early herbivory	Late herbivory	Frequent herbivory
Disintegrators			
Regenerate new leaves	-/-/0	-/0/0	-/-/-
Don't regenerate new leaves	-/-/-	-/-/0	-/-/-
Integrators			
Restrictive integrators in small clonal fragments			
Regenerate new leaves	-/0/0	-/0/0	-/-/-
Don't regenerate new leaves	-/-/-	-/0/0	-/-/-
Restrictive integrators in large clonal fragments			
Regenerate new leaves	-/0/0	-/0/0	-/-/-
Don't regenerate new leaves	-/-/-	-/-/-	-/-/-
Full integration in small clonal fragments			
Regenerate new leaves	0/0/0	0/0/0	-/-/-
Don't regenerate new leaves	-/-/-	0/0/0	-/-/-
Full integration in large clonal fragments			
Regenerate new leaves	0/0/0	0/0/0	-/-/-
Don't regenerate new leaves	-/-/-	0/0/0	-/-/-

Table modified from Jónsdóttir and Watson (1997). Functional types for disintegrators and integrators refer to clonal size and whether plants do or do not produce new leaves following herbivory. The timing of herbivory is based on the three scenarios (early, late, frequent) as described in the text. The triplicates in each cell refer to responses (positive [+]) or negative [-] to different amounts of herbivory (high/medium/low) as described in the text. The terms 'disintegrators' and 'integrators' are defined in the text.

degree of clonal integration and the level of herbivory (Table 1). Herbivory later in the growing season would not have any affect on small and large clone-forming species unless the amount of herbivory is high and the clone has restrictive integration (Table 1).

Preliminary experiments on the impact of timing and amount of herbivory

We have conducted preliminary field experiments on the effect of the timing and amount of herbivory on three species of woodland herbs: *Claytonia virginica*, *Uvularia perfoliata* and *Podophyllum peltatum*. Herbivory was simulated by defoliating plants as described below. The experiments were conducted in the spring and summer of 1997 at the Smithsonian Environmental Research Center (SERC) near Edgewater, MD. The three species are common woodland elements in the older forests at SERC. *Claytonia virginica* is a widespread spring ephemeral (Schemske 1977) that occurs over a wide range of habitats, primarily in mature deciduous forests (Crozier & Boerner 1984). Various aspects of the ecology of *C. virginica* have been examined (e.g. Sparling 1967; Bazzaz & Bliss 1971; Peterson & Rolf 1982; Eickmeier & Schussler 1993). *Uvularia perfoliata* and *P. peltatum* are also common in deciduous forests throughout eastern North America (Wilbur 1963; Sohn & Policansky 1977). Both flower early in the spring but, unlike *C. virginica*, leaves of both species

persist into the summer and autumn. The ecological life history and various aspects of the ecology of *U. perfoliata* have been examined by Foerste (1891), Whigham (1974), Wijesinghe and Whigham (1997), and Kudoh *et al.* (in press). *Podophyllum peltatum* has been the subject of several ecologic studies (e.g. Sohn & Policansky 1977; Givnish 1983; Policansky 1983; Benner & Watson 1989; Landa *et al.* 1992; de Kroon *et al.* 1997; Gerber *et al.* 1997). All three species are clonal and produce both sexual and asexual ramets. Seeds of all three species are dispersed by animals (Whigham 1974; Handel 1978; Braun & Brooks 1987). *Claytonia virginica* reproduces asexually by corms, *U. perfoliata* reproduces by producing ramets at the ends of stolons, and *P. peltatum* reproduces by the production of a branched rhizome system. The three species would be categorized in Table 1 as: *U. perfoliata* = disintegrator which does not regenerate new leaves; *C. virginica* = disintegrator which does not regenerate new leaves; *P. peltatum* = fully integrated species that forms large clonal fragments and does not produce new leaves in response to defoliation.

Methods

Several patches of each species were located as plants emerged in the spring. Twenty-five individual ramets were randomly marked and assigned to all combinations of each of the following treatments.

Uvularia perfoliata

Two levels of defoliation: 50% and 100% (=medium and high, respectively) in Table 1. Herbivory was simulated by defoliating plants three times during the growing season: shortly after all leaves had unfolded during shoot development, 1 month after the first treatment, and 2 months after the first treatment. Only non-flowering ramets were used. Twenty-five plants were chosen as controls and received no simulated herbivory.

Claytonia virginica

Two levels of defoliation: 50% and 100% of each leaf emerging from the corms of individual plants. Herbivory was simulated by cutting leaves twice during the growing season, shortly after flowering began and in the middle of the growing season. All individuals reproduced sexually. Twenty-five plants were chosen as controls.

Podophyllum peltatum

Two levels of defoliation: 50% and 100% of each leaf. Herbivory was simulated twice during the growing season: shortly after full leaf expansion and in the middle of the growing season. Only non-flowering ramets were used in the study. Because *P. peltatum* produces a branched rhizome system, rhizomes were severed (e.g. de Kroon *et al.* 1991) so that all treated plants included a portion of each rhizome system of the same age (3 years). Twenty-five plants were chosen as controls.

Plants were sampled near the end of the growing season for the following variables: number of ramets produced, number of roots per ramet, root biomass, number of buds produced on ramets (*U. perfoliata*); number of flowering shoots per ramet, number of flowers per ramet, number of fruits per ramet, corm biomass (*C. virginica*); length of new rhizome segment(s) (*P. peltatum*).

Results and discussion*Uvularia perfoliata*

Measurements of the responses of *U. perfoliata* focussed on ramets produced by parent ramets. Fifty per cent and 100% leaf removal applied shortly after leaves had expanded resulted in decreased numbers of ramets produced and ramet root biomass (Fig. 1). Defoliation a month later resulted in decreased root biomass for the 100% leaf removal treatment only (Fig. 1). Treatments applied 2 months after shoot development had no noticeable influence on the number of new ramets or root biomass. None of the treatments had any effect on the

number of roots produced nor was there any clear pattern in the number of buds produced by ramets. Wijesinghe and Whigham (1997) showed that the size of parent ramets and light conditions (e.g. gap or nongap habitat) both played an important role in determining the size and number of ramets produced. Results of this preliminary study suggest that both the timing and amount of herbivory also influence both current (i.e. number of ramets produced) and future (e.g. ramet size) growth. Responses to different amounts of herbivory, however, appear to be small or non-existent later in the growing season. The observed results follow the patterns predicted in Table 1 for high herbivory (e.g. 100%). Moderate amount of herbivory (e.g. 50%) did not result in any changes in the response variables.

Claytonia virginica

Response variables measured for *C. virginica* focussed on current sexual reproduction (number of flowering shoots, number of flowers, number of fruits) and future growth (corm biomass). The amount of herbivory and timing of herbivory resulted in no clear responses in sexual reproduction (Table 2). These preliminary results suggest that spring ephemerals such as *C. virginica* are able to offset short-term effects of herbivory to support sexual reproduction by utilizing resources stored in corms. The timing and amount of herbivory, however, may influence future growth because total corm biomass was less for both levels of herbivory applied early in the growing season (Fig. 2). Like *U. perfoliata*, herbivory later in the growing season had no noticeable influence on either current or future growth. *Claytonia virginica* is a spring ephemeral, meaning that all of its growth and reproduction are completed during a short period of time (approximately 2 months) in the spring. *Claytonia virginica* responses did not follow any of the predicted patterns for sexual

Table 2 Responses of *Claytonia virginica* to varying amounts of herbivory (50% and 100%) applied twice (T1 and T2) during the growing season

Treatment	No. flowering		
	shoots	No. flowers	No. fruits
Control	3.9±0.6	41.3±5.9	25.5±3.9
T1-50%	3.1±0.3	34.5±3.9	20.5±2.5
T1-100%	3.6±0.3	47.9±11.0	20.6±2.5
T2-50%	3.8±0.7	45.0±12.2	29.5±8.9
T2-100%	3.6±0.8	39.6±8.7	34.3±8.3

All values are means±1 SE.

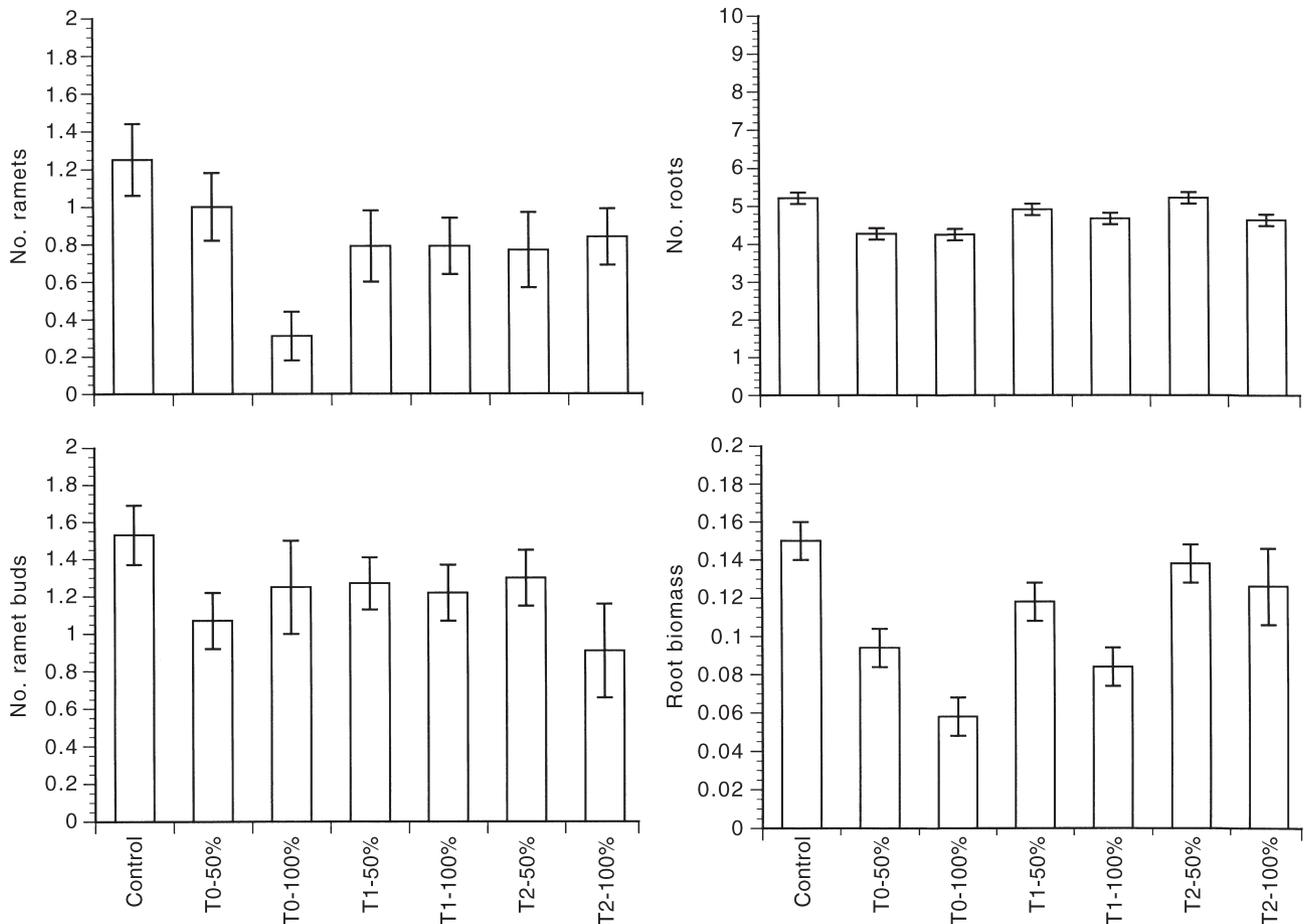


Fig. 1 Responses of *Uvularia perfoliata* to 0%, 50% and 100% defoliation applied at three different times during the growing season. T0, T1 and T2 refer to early, mid and late defoliation as described in the text. Values are means + 1 SE.

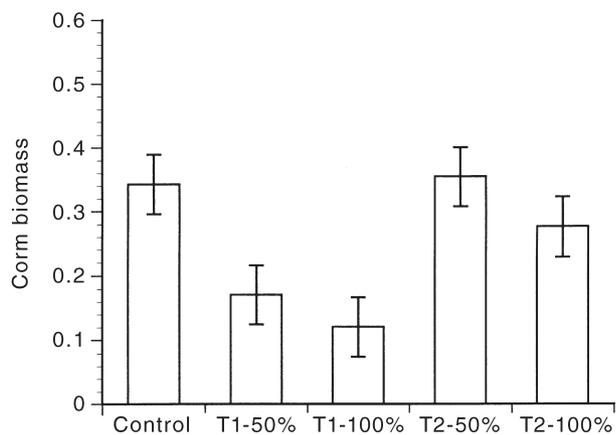


Fig. 2 Corm biomass of *Claytonia virginica* in response to 0%, 50% and 100% defoliation applied twice (T1 and T2) during the growing season. Corm weight is expressed as dry weight biomass in grams (mean + 1 SE).

production in the current growing season (Table 1). Only future growth (e.g. corm biomass) followed the predicted pattern, and the negative response was limited to early season herbivory.

Podophyllum peltatum

The total length of rhizome(s) produced during the growing season was influenced by both the timing and amount of herbivory (Fig. 3). Ramets that were treated shortly after leaves had expanded produced shorter rhizomes, and plants that were 100% defoliated produced the shortest rhizomes. These responses were predicted (Table 1). Rhizome length did not change in response to either level of herbivory later in the growing season as predicted in Table 1. These results confirm the earlier findings of de Kroon *et al.* (1991) but further suggest that the amount of early season herbivory is also important. *Podophyllum peltatum* responded to the pattern predicted by Table 1 for a fully integrated clonal species that suf-

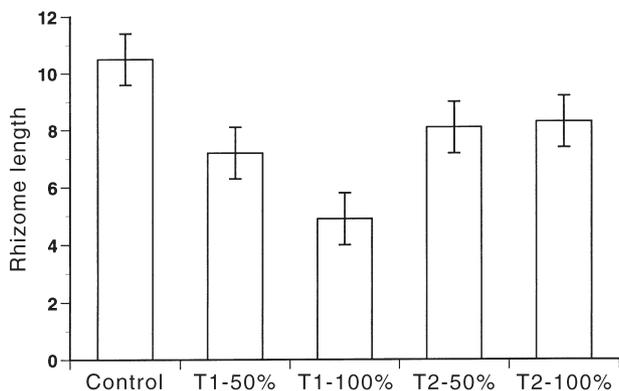


Fig. 3 Length of new rhizomes produced by *Podophyllum peltatum* in response to 0%, 50% and 100% defoliation applied twice (T1 and T2) during the growing season. Rhizome lengths are expressed in centimeters as means (+1 SE).

ferred herbivory during the early and middle of the growing season.

Conclusions

Our literature analysis suggested that the effects of herbivory have been examined in very few woodland herbs. The studies that have been done suggest that responses should vary among species depending on several life-history attributes. Results of our preliminary experiment suggest that the timing and amount of herbivory operate in an interactive way to determine growth and reproduction, particularly herbivory that occurs early in the growing season. However, clearly the predicted responses shown in Table 1 are an oversimplification of what might be expected. Few species are likely to be able to survive frequent herbivory no matter what level of herbivory occurs. This conclusion is supported by field observations and a limited number of experimental studies. The predicted responses to less frequent herbivory are even more interesting. Our preliminary study demonstrated that the responses will be complex and that the greatest consequences of herbivory will occur in response to varying amounts of herbivory early in the growing season. We suggest that the timing and amount of herbivory clearly influences current and future growth and reproduction of woodland herbs. There is a clear need for additional studies of species with different life-history strategies to determine the applicability of the predictions offered in Table 1.

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