

Do Leaves Control Episodic Shoot Growth in Woody Plants?

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ABSTRACT. It has been generally observed that leaf removal alters the pattern of episodic shoot growth in certain species in such ways that suggest some type of foliar control. In the present study, the effects of periodic defoliation during the growing season on the shoot growth of 11 woody species were analyzed in an attempt to elucidate the control mechanisms of episodic shoot growth. Four types of responses to defoliation were observed: A) A second flush in red oak, shagbark hickory, and year-old seedlings of green ash and sugar maple; B) A small continued extension of stem elongation with the production of some additional leaves and a significant delay in terminal bud formation in white ash, green ash, pignut hickory, black walnut, and in year-old seedlings of green ash and sugar maple; C) No response in sweetgum and white pine; and D) Shoot die-back in sugar maple, silver-red maple, cottonwood, black walnut, and to a lesser extent, the ashes. Defoliation was most effective and sometimes only effective in causing the above-mentioned responses when given early in the flush period. Leaf control of episodic shoot growth may be due to foliar inhibitors and/or effects of competition for water and nutrients.

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INTRODUCTION

Episodic growth, which is characterized by intermittent periods of shoot elongation (flushes) interrupted by periodic dormancy, is a common phenomenon in woody species in temperate and particularly in tropical environments. The shoots of some species (for example, loblolly pine, citrus, mango) exhibit flushes throughout the growing season, whereas others (for example, red and white pine, ash) have only one spring flush and then cease growth for the remainder of the season (Kozlowski and Pallardy 1997). A spring flush may be as short as a few weeks (Cline and Deppong 1999). In any case, new terminal buds are formed at the end of each flush period. The number of flushes per growing season in species exhibiting reoccurring flushing generally decreases as trees mature.

Romberger (1963) has posed the fundamental question of episodic growth. Why is it that the terminal shoot meristem will cease growth even when conditions for growth are still optimal in late spring with respect to moisture, nutrient availability, temperature, irradiance and photoperiod? It is not uncommon for shoots of herbaceous plants to have continuous growth through most of the season. Why should woody plants stop growing early in the season? Why do some species exhibit recurrent flushing in a relatively stable environment?

There is evidence to support the hypothesis that the leaves of some woody plants inhibit the growth of the terminal meristem (Crabbé 1970; Borchert 1991; Doorenbos 1953; Collin and others 1994; Wilson 1984). Doorenbos (1953) cites Goebel (1880) as noting that defoliation of a dormant twig during the spring "has been shown again and again to cause the terminal bud to resume growth." It has often been observed that natural defoliation due to herbivory or hailstone damage during the flushing period causes precocious opening of terminal buds (Romberger 1963). The fact that leaf

inhibition of bud growth has been linked to competition for nutrients and water (Crabbé and Barnola 1996) or to inhibitors in leaves (Tinklin and Schwabe 1970) is highly suggestive of some role of leaves in the control of episodic shoot growth.

The present report focuses on the effect of defoliation on shoot elongation in woody species with the goal of elucidating the control mechanisms of episodic shoot extension. It is part of a larger study (Cline and Deppong 1999) to test the hypothesis that apical dominance is the primary source of control on lateral bud outgrowth in paradormancy.

MATERIALS AND METHODS

Intact twigs of mature trees of white ash (*Fraxinus americana* var. *americana* L., 15 years-old, 29 trees), red oak (*Quercus borealis* Michx. f.j., 50 to 60 years-old, 3 trees), green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl.) Fern, [Pat Moore] 9 years-old, 12 trees), shagbark hickory (*Carya ovata* (Mill.) K. Koch, 20 to 40 years-old, 3 trees), pignut hickory (*Carya glabra* (Mill.) or *Carya ovalis* (Wang. Sarg.), 7 to 35 years-old, 5 trees), and black walnut (*Juglans nigra* L., 7 years-old, 12 trees) were tagged for defoliation treatments and control in late March 1997. Twigs on lower order branches were selected. Diseased twigs and those exhibiting low vigor and small bud size were excluded. The same methods were employed in April 1998 with red oak (same species as above), 50 to 60 years-old (5 trees), white pine (*Pinus strobus* L., 20 years-old, 14 trees), sweetgum (*Liquidambar styraciflua* L., 12-15 years-old, 10 trees), cottonwood (*Populus deltoides*, 50 to 60 years-old, 2 trees), sugar maple (*Acer saccharum* Marsh., 11 to 14 years-old, 5 trees), hybrid silver/red maple (*Acer rubrum* L., ACER x *freemanii* 'Celzam' P.P. 7279, about 15 years-old, 8 trees) and one year-old seedlings of green ash and sugar maple grown in the greenhouse. All trees outside were located in or near Columbus, OH.

For greenhouse studies, one hundred green ash and sugar maple seedlings beginning their second year

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following the opening of a recently formed terminal bud, B) A small continued elongation of the stem with the production of some additional leaves and a significant delay in terminal bud formation, C) No response ("Control" in Figure 1), and D) Death of twig (not shown in figure).

Red oak responded according to category A in Figure 1. Defoliation early during the first flushing in 1997 caused a second flushing (preceded by the formation of the first terminal bud) with a small increase in shoot length as well as the formation of a second terminal bud and lateral buds along with bud scale scars from the first terminal bud (Table 2). Defoliation done late in the first flush or after the first flush had no effect. There was no die-back in any of the defoliated shoots of red oak. Similar results were obtained in 1998 (Table 1). The response of shagbark hickory to defoliation in 1997 was similar to that of red oak although not as strong (Table 2).

TABLE 2

Defoliation induction of second flushing of terminal shoots in 1997.

		Red Oak		Shagbark Hickory	
First flushing of intact control shoots					
Shoot length (cm)/node number \pm SD					
		10.8 \pm 7.5/9.1 \pm 3.1		8.9 \pm 5.1/6.7 \pm 1.1	
Second flushing (defoliated shoots)					
DD	%	Shoot length cm/node number	%	Shoot length cm/node number	
5-14	100	1.8 \pm 1.5/5.1 \pm 1.3			
5-15	71	1.6 \pm 1.0/5.4 \pm 1.1	0	(all shoots died)	
5-19	64	1.0 \pm 0.8/3.7 \pm 2.0			
5-20			100	1.9 (1/7 shoot survival)	
5-28	0				
6-6	0		57	0.9 \pm 0.6/--	
7-11			0		

DD = defoliation date.

% = percentage of shoots with second flushing.

Sample size (n) = 7-11.

White ash and green ash responded according to category B (Fig. 1). Defoliation during early flushing caused many of the shoots to continue elongation to a small extent, add a few new small leaves as is indicated by the increase in node number, and delay terminal bud formation (Fig. 2, white ash; Table 3). The additional nodes with shortened internodes resulted in a cluster-like appearance at the shoot apex. Similar responses were noted in some black walnut and pignut hickory twigs, but the time of response differed. Defoliation treatments which were carried out post-flushing or late in the season had no such effects in ash and appeared as controls (Fig. 1). However, defoliation later in the season did cause

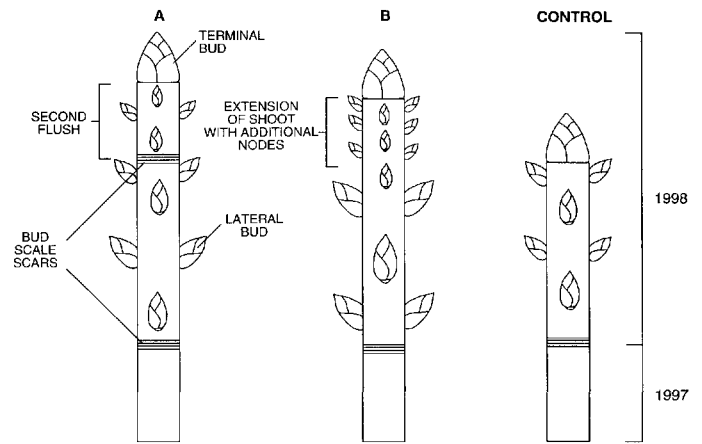


FIGURE 2. The effect of defoliation date on node number in white ash at four different sites, IA, IB, II, and III. Vertical lines represent \pm SD.

shoot elongation in walnut and pignut hickory in some cases (Table 3). There was also much die-back in many of the early defoliated ash, walnut and hickory shoots (data not shown).

A majority of sugar maple shoots defoliated early during flushing died (Table 1). Defoliation had no effect on those treated later in the season. A similar response was observed in the greenhouse seedlings. Completely defoliated twigs of white pine produced terminal bud second flushing in a few instances. No effect on the terminal bud was observed in response to defoliation in all other species tested.

Green ash and sugar maple greenhouse seedlings also exhibited a delay in terminal bud formation when defoliation was carried out during flushing (Table 1). They also responded to defoliation with a second flush but only if the defoliation treatment was given after the first flush had already ended. This was also observed in *Fraxinus excelsior* L. saplings under controlled conditions (Collin and others 1994).

DISCUSSION

Defoliation treatments did change the normal episodic growth patterns in some species. Second flushing was induced in red oak and shagbark hickory. There was some extension of shoot terminal bud growth, additional node formation on the stem and a delay of terminal bud maturation, particularly in white and green ash. These promotive effects of leaf removal on terminal bud growth suggest that this leaf inhibitory influence on the bud is, at least in part, of a paradormic nature, that is, the lack of visible growth of the terminal bud meristematic regions is regulated by factors within the plant but external to the dormant structure (Lang and others 1985, 1987). However, defoliation only promoted terminal bud growth when given early in flushing in the above-mentioned species and rarely or not at all in the other seven species tested. This suggests the existence of a multiplicity of processes and factors, both foliar and nonfoliar, which control terminal bud growth.

In cases where defoliation is known to promote some kind of terminal bud growth, the action of a foliar inhibitor is one possible mechanism of control. The

TABLE 3

Effects of defoliation on increased shoot length and node number in 1997.

DD	White Ash IA			White Ash IB			Black Walnut			Pignut Hickory		
	Shoot length (cm)/Node number \pm SD of intact control shoots											
	$11.2 \pm 5.1/3.5 \pm 0.9$			$7.7 \pm 1.5/3.7 \pm 0.5$			$12.6 \pm 5.3/12.1 \pm 5.4$			$13.3 \pm 11.1/9.1 \pm 3.2$		
	% shoots elongating	Increase in length cm	Increase node #	% shoots elongating	Increase in length cm	Increase node #	% shoots elongating	Increase in length cm	Increase node #	% shoots elongating	Increase in length cm	Increase node #
May 9	80	0.9 \pm 0.6	2.9 \pm 1.4	100	1.2 \pm 1.5	3.8 \pm 1.2						
May 12	14	0.4 \pm 0.1	1.6 \pm 1.2									
May 15							0	0	0	0	0	0
May 16	81	0.6 \pm 0.4	3.0 \pm 0.9	100	1.4 \pm 0.6	4.2 \pm 0.7						
May 20							0	0	0	0	0	0
May 23	83	0.9 \pm 1.1	2.8 \pm 1.5	100	0.9 \pm 0.7	3.8 \pm 1.5						
May 28										0	0	0
May 29							63	2.2 \pm 0.5	9.4 \pm 1.8			
May 30				0	0	0						
June 5							17	2.5 \pm 0	8.0 \pm 0			
June 6				0	0	0				14	2.5 \pm 0	8.0 \pm 0
June 26							13	4.8 \pm 0	20 \pm 0			
July 2							0	0	0			
July 11										17	2.4 \pm 0.6	10.5 \pm 2.1

DD = defoliation date.

Sample size (n) ranged from 6-16.

inhibitor, abscisic acid (ABA), which is known to be produced in leaves during the short days of late summer (Wareing and Phillips 1970) does not appear to be a viable candidate for terminal bud inhibition in May or June when the photoperiod is still increasing. If ABA does play such a role, then an ABA-deficient mutant should lack inhibition of terminal bud growth and its branches would be long. The search for such a mutant and for other possible inhibitors might well be fruitful.

Competition for nutrients and water by the leaves is another possible mechanism whereby the presence of leaves might result in the inhibition of terminal bud growth. Busgen and Munch (1929) have pointed out that the regulation of evaporation from leaves has been observed to influence the longevity of shoot tips thus suggesting competition between the leaves and terminal buds for water. Harmer (1989) has found increased flushing by nitrogen treatments in *Quercus petraea* seedlings. Critical experiments need to be carried out that demonstrate whether significant competition does exist for water and/or nutrients between the terminal bud and the leaves.

Doorenbos (1953) has suggested that the first indication of the onset of winter (endo) dormancy during the growing season may be when defoliation will no longer cause the terminal bud to break. He points out that the growth of the terminal meristem must stop early enough

in the season to allow terminal bud formation to occur and for the bud "to prepare itself for the winter cold."

The shoot die-back, which resulted from the defoliation treatment, could have been caused by dehydration associated with the cutting injury to the petioles. This hypothesis could be tested by placing wax or resin over the freshly cut petiole to prevent desiccation and to observe whether this prevents die-back. In one sense this injury/dehydration hypothesis for explaining shoot die-back appears in contradiction to the water competition hypothesis for explaining defoliation promotion of terminal bud growth. There might well be a fine-tuned balance between the two conditions.

Terminal bud die-back (shoot tip abortion) leading to sympodial branching is very common in nature and may be due to a variety of causes including severe competition by lateral shoots for water and nutrients (Brown and others 1967), accidental injury (Remphrey and Davidson 1992), or to genetic programming (Millington 1963).

Analyses of trees of various ages including greenhouse seedlings indicated that although defoliation promotion of terminal bud growth was greater in younger than in older trees, significant effects on second flushing, stem elongation, additional leaf formation, and delay of terminal bud formation were also found in certain older species. With respect to defoliation release of lateral bud outgrowth, Cline and Deppong (1999) have found

such an effect mainly in red oak among 11 different older woody species analyzed. Comparatively speaking, the observed effects of defoliation on the terminal bud were generally much more pronounced and consistent than those on the lateral buds. The fact that, under certain conditions, the terminal bud will continue to grow while the lateral buds remain inhibited, suggests some fundamental differences in their growth control mechanisms.

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