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THE ECOLOGICAL SIGNIFICANCE OF LOBED AND TOOTHED LEAVES IN TEMPERATE FOREST TREES

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Abstract. Leaves with toothed and lobed margins are frequent in deciduous forests but are rare in moist tropical forests. We hypothesize that leaf teeth may be important to deciduous species as sites of precocious, early season photosynthesis. To test this hypothesis we dosed leaves with $^{14}\text{CO}_2$ and used autoradiography to examine the spatial distribution of photosynthesis within immature leaves of 18 woody species of North Carolina Piedmont forests. We found a significant concentration of early season photosynthesis on the margins of eight species with prominent teeth or lobes, but not in seven toothed or lobed leaf species and in none of the four entire-leaf species.

Key words: *drip tips, function; forest tree leaves, temperate cf. tropical; leaf expansion and growth; leaf margin characteristics; leaf teeth and lobes; North Carolina (USA) Piedmont forests; photosynthesis, early season.*

INTRODUCTION

Leaf-margin characteristics of tree species follow a predictable pattern based on climate. Tree species of cool, temperate forests generally have leaves with toothed or lobed margins, whereas moist, evergreen tropical forests contain almost exclusively species with entire-margined leaves (Bailey and Sinnott 1916, Cain and Castro 1959, Gentry 1969, MacArthur 1972, Givnish 1979). The proportion of tree species with non-entire leaves steadily increases along the tropical-to-temperate gradient of decreasing mean annual temperature and increasing seasonality (Bailey and Sinnott 1916, Wolfe 1978a). In addition, the moisture and seasonality gradient from moist tropical forest to dry tropical forest corresponds to a similar, albeit less pronounced, gradient of increasing proportion of non-entire-leaved tree species (Gentry 1969, Richards 1996). The correlations between climate and leaf margin are sufficiently strong that paleobiologists routinely use leaf-margin statistics from fossil floras as indicators of past climate (Bailey and Sinnott 1916, Wolfe 1978b, Givnish 1987).

The climate-based pattern of leaf-margin morphology is not constrained by taxonomic classification; Bailey and Sinnott (1916) cite numerous examples of plant

families wherein species characteristic of moist tropical forests have leaves with entire margins, whereas those species found in temperate forests generally have lobed or toothed margins. In addition, several genera that contain both tropical and temperate species have temperate species with toothed or lobed margins and tropical species with entire margins (e.g., *Quercus*; see Brenner 1902, MacArthur 1972). The fact that leaf margins with teeth or multiple lobes have evolved numerous times in unrelated temperate plant groups suggests that toothed and lobed margins represent adaptive traits. Although the polyphyletic origin of non-entire margins and the correlation between leaf margin and climate are well established and have been known since at least the beginning of the 20th century (Brenner 1902, Bailey and Sinnott 1916), the adaptive advantages conferred by non-entire leaf margins have remained uncertain (Richards 1996, Gentry 1969, MacArthur 1972, Givnish 1979, Grace 1983).

Lobed and toothed margins are advanced characteristics in the evolution of angiosperms, appearing later and under different ecological circumstances than entire margins (Hickey and Wolfe 1975). Angiosperms radiated from the moist tropical forests during the Cretaceous period when widespread climate changes brought decreased mean annual temperature, reduced rainfall, and increased seasonal variation in temperature and/or moisture (Axelrod 1952). The selective pressures associated with short growing seasons that alternated with cold winters or extreme dry seasons

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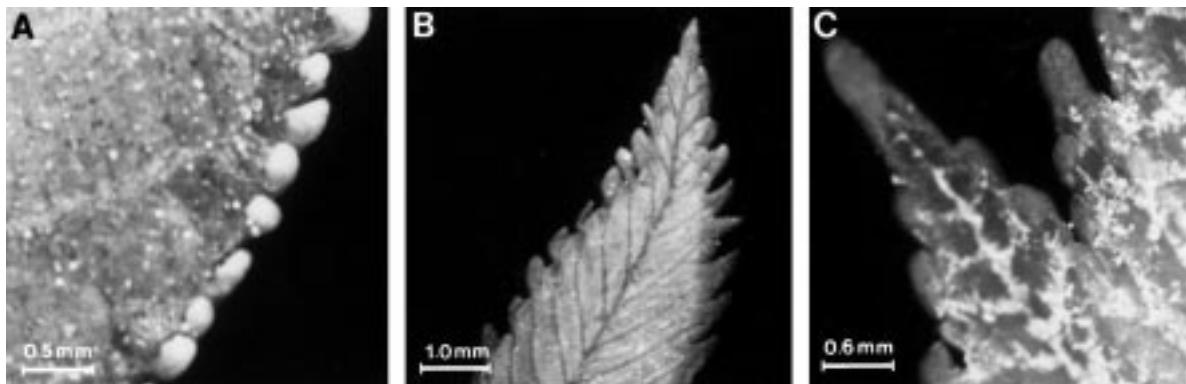


FIG. 1. Immature leaves showing swollen, mature tissue in the marginal teeth. (A) *Carya alba*; (B) *Ulmus alata*; (C) *Acer rubrum*.

favored tree species with a deciduous habit (Axelrod 1967, Wolfe 1978a). Deciduous forests are characterized by a seasonal leaf drop followed by a rapid flush of leaf re-growth when warm temperatures or available moisture return, during which time trees leaf out to nearly full leaf area in a brief 1–2 wk period. The success of the deciduous habit with its concomitant costs in nutrient- and carbon-use-efficiency appears to hinge on the lower construction costs of the thinner deciduous leaves and their more rapid rates of photosynthesis (Chabot and Hicks 1982). In many temperate deciduous angiosperm species, leaf-margin characteristics such as lobes and marginal teeth also appeared during the Cretaceous angiosperm radiation, potentially in response to the same lower temperatures and increased seasonality responsible for evolution of the deciduous habit (Hickey and Wolfe 1975). The nearly simultaneous evolution of the deciduous habit and non-entire leaves suggests a functional relationship.

Leaf teeth may be functionally important to deciduous species as sites of early-season photosynthesis. During the spring leaf flush, marginal teeth of some temperate deciduous species are turgid and relatively large when the leaves are still small, but fail to expand much more as the season progresses, with the result that they become proportionally smaller and less conspicuous as the leaf reaches full size. For example, the marginal teeth of young *Carya*, *Ulmus*, and *Acer* leaves are prematurely thickened and bright green when the inner portions of the leaf blade are still visibly thin and lacking in green coloration (Fig. 1). The serrations of juvenile *Ulmus* leaves have been reported to have well-developed spongy mesophyll, making them potentially capable of gas exchange long before the medial portions of the leaf (Billings 1905).

To test the hypothesis that marginal leaf teeth and lobes represent adaptations for more rapid initiation of photosynthesis in flushing leaves of temperate trees,

we examined changes in the spatial distribution of photosynthesis within immature leaves to determine whether marginal teeth and lobe tips represent sites of precocious photosynthesis.

METHODS

Leaves of 18 temperate woody plant species were collected from North Carolina (USA) Piedmont forests during spring leaf development. Representative leaves were collected periodically from budbreak to leaf maturity. The following groups of species were tested: entire margins—*Cornus florida*, *Fagus grandifolia*, *Cercis canadensis*, and *Nyssa sylvatica*; prominently toothed—*Ulmus americana* and *Viburnum rafinesquianum*; inconspicuously toothed—*Prunus serotina* and *Viburnum prunifolium*; compound and prominently toothed—*Aesculus sylvatica*, *Carya alba*, and *Rubus allegheniensis*; lobed with smooth margins—*Quercus alba*, *Quercus stellata*, and *Liriodendron tulipifera*; lobed with pointed or toothed margins—*Quercus rubra*, *Viburnum acerifolium*, *Liquidambar styraciflua*, and *Acer rubrum*. The botanical nomenclature follows Kartesz (1994).

Harvested leaves were placed in plastic bags in a cooler and immediately transported to the laboratory and analyzed for ^{14}C assimilation within 1 h of detachment. The leaves were subjected to a 30-sec pulse of $^{14}\text{CO}_2$ (74 kBq) in a LI-COR 1-L chamber (LI-COR LI-6200 Portable Photosynthesis System) at 23°C with optimum photosynthetic light levels ($\approx 500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) from an overhead lamp. The system employed was modeled after that described by McCrea et al. (1985). Constant air circulation was maintained by a chamber fan. After removal from the chamber, leaves were immediately dipped in liquid nitrogen to stop translocation, pressed, and dried between sheets of blotter paper. Once dry, the leaves were arranged on Kodak electron-microscope film (number 4489) to generate autoradiographic images

TABLE 1. Presence or absence of photosynthetic activity in the margins of juvenile leaves of 18 temperate forest tree and shrub species.

Species	Type†	Photosynthetic activity‡
Leaves with lobes/teeth		
With photosynthetic margins		
<i>Acer rubrum</i>	c	L, M
<i>Aesculus sylvatica</i>	u	M
<i>Carya alba</i>	c	M
<i>Liquidambar styraciflua</i>	c	L
<i>Quercus alba</i>	c	L
<i>Q. rubra</i>	c	L
<i>Q. stellata</i>	c	L
<i>Ulmus alata</i>	c	M
Without photosynthetic margins		
<i>Liriodendron tulipifera</i>	c	...
<i>Prunus serotina</i>	c	...
<i>Viburnum acerifolium</i>	s	...
<i>V. prunifolium</i>	s	...
<i>V. rafinesquianum</i>	s	...
Leaves with entire margins		
With photosynthetic margins		
None
Without photosynthetic margins		
<i>Cercis canadensis</i>	u	...
<i>Cornus florida</i>	u	...
<i>Fagus grandifolia</i>	c	...
<i>Nyssa sylvatica</i>	c	...

† c = canopy tree species, u = obligate understory tree, s = shrub.

‡ L = photosynthetic activity in lobe tip; M = photosynthetic activity in marginal teeth.

of the photosynthetically active areas of the leaves. The film cassettes were stored at -80°C for periods of up to 4 mo.

We quantified the dark regions (areas of photosynthetic activity) on the film with an "Imagequant" (Molecular Dynamics, Sunnyvale, California, USA) laser densitometer. We compared single pixel values (0.008

mm^2) from the marginal teeth or lobe tips to pixel values in the sinuses between the teeth to determine the spatial distribution of photosynthetic activity within individual leaves.

RESULTS

Photosynthetic activity of juvenile leaves was at first assessed qualitatively; areas appearing dark were considered photosynthetically active due to carbon assimilation. Laser densitometer data showed the clear areas of the film (e.g., the medial portions of the young leaves) had negligible optical densities, commonly two- to four-fold lower than leaf lobe tips and teeth. Enhanced activity was apparent in teeth compared to sinuses of some toothed species and in the lobe tips of several lobed species, although other species showed no precocious photosynthesis (Table 1). Species showing enhanced photosynthesis in marginal characters included *Quercus alba*, *Q. rubra*, *Q. stellata*, *Aesculus sylvatica*, *Acer rubrum*, *Carya alba*, *Ulmus alata*, and *Liquidambar styraciflua*; the latter four appear in Fig. 2. The entire-margined species (*Cercis canadensis*, *Cornus florida*, *Fagus grandifolia*, which is shallowly dentate, and *Nyssa sylvatica*) failed to show precocious photosynthetic activity in any part of the young leaf. Several lobed and toothed species showed no evidence of early photosynthesis at the margins or lobe tips (all three *Viburnum* species, *Rubus allegheniensis*, *Prunus serotina*, and *Liriodendron tulipifera*).

The developmental progression in the spatial distribution of photosynthetic activity of *Acer rubrum* and *Ulmus alata* leaves is shown in Fig. 3 as the ratio of photosynthetic activity in the marginal teeth to that in sinuses. Table 2 shows the developmental progression in mean optical density from six replicates at each leaf size. Upon budbreak (leaf size index = 1, Fig. 3), the marginal teeth of both *Ulmus alata* and *Acer rubrum* are more photosynthetically active than the sinuses between the teeth (Fig. 2). The level of photosynthetic

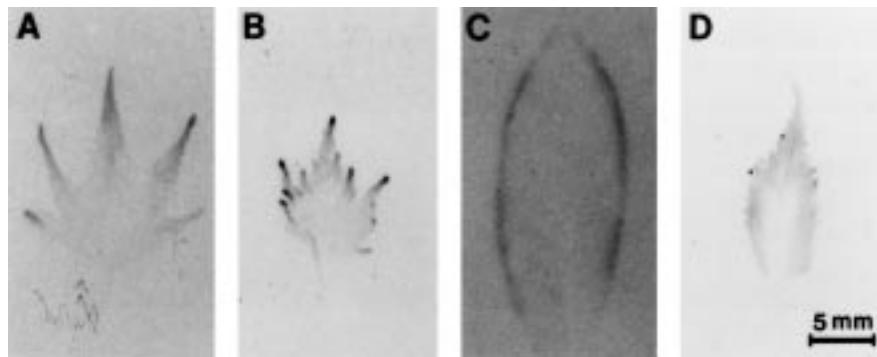


FIG. 2. Autoradiography of immature leaves. The dark regions indicate ^{14}C assimilation due to heightened photosynthetic activity in the marginal teeth and lobes. (A) *Liquidambar styraciflua*; (B) *Acer rubrum*; (C) *Carya alba*; (D) *Ulmus alata*.

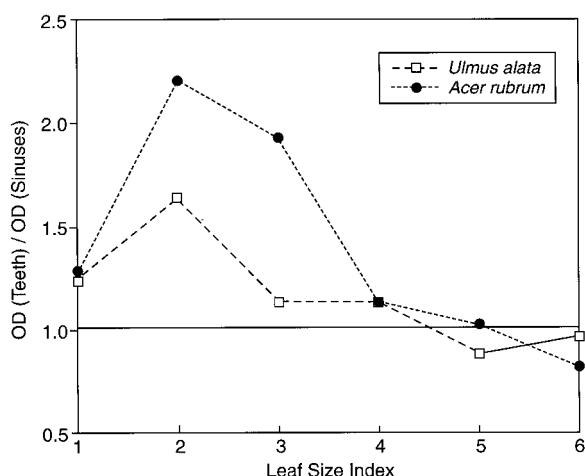


FIG. 3. Change in the ratio of tooth to sinus photosynthetic activity during leaf expansion in *Acer rubrum* and *Ulmus alata*. When the ratio equals 1, photosynthetic activity in the teeth is equal to that in the sinuses. Leaf size index: (1) *Ulmus* = 1.10 cm, *Acer* = 1.15 cm; (2) *Ulmus* = 1.60 cm, *Acer* = 1.30 cm; (3) *Ulmus* = 2.1 cm, *Acer* = 1.9 cm; (4) *Ulmus* = 2.3 cm, *Acer* = 2.0 cm; (5) *Ulmus* = 3.5 cm, *Acer* = 3.4 cm; (6) *Ulmus* = 9.2 cm, *Acer* = 7.5 cm. Measurements of optical density (OD) were taken at 699 nm.

activity in the medial portions of the lamina increases as the leaf expands. As the leaf reaches maturity (leaf size index = 6) and the sinus tissue becomes fully developed, photosynthetic activity in the teeth remains constant or decreases, whereas the photosynthetic activity in the sinuses increases until it is approximately equal to that in the teeth.

DISCUSSION

Lobed species including *Liquidambar styraciflua*, *Acer rubrum*, *A. saccharum*, *Quercus alba*, *Q. stellata*, and *Q. rubra* show heightened photosynthetic activity at the lobe tips in immature leaves (Table 1, Fig. 2). Like the lobe tips of the previously mentioned species, the marginal teeth of *Ulmus alata*, *Acer rubrum*, and *Carya alba* are highly photosynthetic at bud break, while the remainder of the leaf is less so (Figs. 1 and 2). The tissue of these teeth matures early compared to the medial and basal portions of the leaf. In most entire-margined species, leaf maturation progresses in a basipetal direction; the tip of the leaf matures first, becoming photosynthetically active, followed by gradual tissue maturation toward the base of the leaf (Turgeon 1989). As tissue matures and develops photosynthetic capacity, it swells due to cell division, cell expansion, and the development of the spongy mesophyll layer needed for gas exchange. The lobed species we studied appear to develop basipetally, but from the tip of each lobe toward the base. Although the entire-

TABLE 2. Variation in mean optical density with leaf size index, from outbreak on. There were six replicates at each leaf size.

Species	Leaf size index	Optical density	
		Teeth	Sinuses
<i>Ulmus alata</i>	1	.387	.312
	2	.201	.123
	3	.398	.349
	4	.360	.318
	5	.421	.478
	6	.483	.498
<i>Acer rubrum</i>	1	.206	.165
	2	.263	.119
	3	.221	.121
	4	.240	.212
	5	.297	.291
	6	.313	.396

margined species we observed probably develop basipetally, significantly heightened activity was not apparent in the leaf tip.

Our data indicate that leaf teeth and lobe tips of some species mature early, producing swollen and photosynthetically active tissue while the leaf is quite young and otherwise not photosynthetically active. These areas are protuberances of tissue and, like the leaf tip, are separated on all but one side from the rest of the leaf. This spatial arrangement allows the tissues of the leaf tip, lobe tips, and marginal teeth to swell to maturity early without reducing the leaf's ability to further expand the yet immature medial and basal leaf regions. As the leaf matures, cells located medially and basally in the leaf, as well as cells of the sinuses between the teeth, enlarge as the tissues and intercellular spaces expand to allow the gas exchange needed for photosynthesis (Fig. 3). However, leaf tissue loses much of its ability to expand with the expansion of intercellular spaces. Early maturation of the margin of an entire-margined leaf such as *Nyssa sylvatica* or *Cercis canadensis* is physically impossible because it would preclude or greatly limit subsequent blade expansion.

We failed to observe the predicted early marginal photosynthesis in four shrub species with prominent teeth or lobes: *Rubus allegheniensis*, *Viburnum acerifolium*, *V. prunifolium*, and *V. rafinesquianum*. The juvenile leaves of these species appear to have the overall basal level of photosynthetic activity like the entire-margined leaves we studied, but no concentration of photosynthesis was observed at the lobe tips or in the marginal teeth. These species are all shrubs and thus are confined to the forest understory. Several are known for their convergence in leaf shapes with common tree species (e.g., *Viburnum acerifolium* and *Acer rubrum*, *V. prunifolium* and *Prunus serotina*) and may well have leaf shapes that evolved because of the protection that

crypsis through leaf-shape mimicry affords. Herbivory avoidance by leaf-shape mimicry is well established for some woody plants (e.g., Gilbert 1975, Rauscher 1978), and the remarkable conformity of leaf margins within tropical forests and within temperate forests may partly result from the benefits of being inconspicuous to specialist herbivores.

The deciduous nature of temperate forests creates a situation where precocious photosynthetic structures may be beneficial to trees. In temperate deciduous forests, sunlight freely penetrates the canopy during the spring. Emerging leaves have brief access to intense solar radiation, unencumbered by the shade of other leaves. These plants face an adaptive dilemma in that photosynthesis cannot be initiated until intercellular spaces have expanded for gas exchange. This maturation, which is required for extensive photosynthesis, precludes further significant tissue expansion, but to wait for full leaf expansion for initiation of photosynthesis means greatly limited use of the transient intense light that occurs at the beginning of the short growing season. It is our hypothesis that marginal teeth and lobe tips in some species provide an evolutionary solution to this dilemma by maturing early while leaf expansion continues in the basal and medial portions of the leaf and in the sinuses between the teeth. Marginal teeth or lobe tips may provide a mechanism whereby leaves can take advantage of the abundant spring light and produce photosynthates in the juvenile stage while the leaves are still expanding.

Lobed and toothed margins should be expected wherever a seasonally bare forest canopy limits leaf longevity but provides an early season opportunity for rapid photosynthesis. Further evidence for this trend is apparent from the fact that lobed and toothed leaves are common in tropical dry forests, which experience a seasonal leaf drop (Richards 1996, Gentry 1969). Adaptations for rapid initiation of photosynthesis such as marginal teeth and lobes are unlikely to confer a significant evolutionary advantage under conditions of constant shade such as found in the understory of evergreen forests. Moreover, early maturation of leaf parts could be detrimental in moist tropical forest species where delayed greening contributes to herbivore avoidance in some species (Kursar and Coley 1992). However, some rapidly growing successional trees of large gaps in moist tropical forests, such as *Cecropia* and *Trema*, have lobed or toothed leaves, demonstrating again that where intense but transient sunlight is available, lobed and toothed leaves often occur.

The adaptive significance of drip tips, which are commonly observed on leaves of tropical forest trees and lianas, also has never been completely resolved (Whitmore 1984, Ellenberg 1985, Richards 1996). However, Raciborski (1900) and Ellenberg (1985) have

described precocious drip-tip development to be the norm, with only a small proportion of drip tips maturing with or after the primary leafblade. The long drip tips are first to mature and are exaggerated in size, dwarfing the remainder of the leaf while the leaf is still immature. As the leaf grows, the drip tip remains more or less constant in size as the basipetal parts of the leaf lengthen and widen. Drip tips may function like margin teeth as areas that mature early and facilitate the more rapid growth and maturation of the leaf, thereby limiting the period of vulnerability to herbivory.

Larson and colleagues (Larson and Gordon 1969, Larson et al. 1972, Larson and Dickson 1973) studied leaf development in *Populus deltoides* (cottonwood) and found that precocious photosynthesis in the leaf tip is beneficial, both to the developing leaf and to other parts of the plant. The precociously photosynthetic leaf tip provides photosynthates to the younger tissues of the apex, the vascular tissues of the leaf, and adjacent immature tissue of the leaf (Larson and Gordon 1969, Larson et al. 1972, Larson and Dickson 1973). The early maturation of the leaf tip produces a reservoir of photosynthates for use by the plant before the leaf is totally mature. Early maturation of leaf lobes and marginal teeth would provide a similar benefit to a plant, a benefit multiplied by the number of additional areas experiencing early photosynthesis.

We have established that multiple lobes and leaf teeth are, in some temperate tree species, areas of active early photosynthesis, and we suggest that such morphological structures provide a boost of photosynthates to trees during the spring leaf flush. In order to determine whether the amount of photosynthate transported from precocious leaf areas is a significant addition to that being transported from storage, translocation experiments that quantify the various contributions of photosynthate are needed.

Rarely will one explanation fully account for all the variation in a basic attribute such as leaf margin. Several plausible adaptive advantages for leaf-margin characteristics have been proposed. Non-entire margins of leaves may contribute to energy balance (Parkhurst and Loucks 1972, Grace 1983). Certain margin characteristics, especially spines such as those of *Ilex*, likely evolved in response to herbivore pressure (Ehrlich and Raven 1967, Givnish 1979). Givnish (1979) hypothesized that because deciduous leaves are thin, they are less effective in supporting tissue between main veins; a lobed shape minimizes inter-vein tissue. All of these hypotheses are likely to apply in some circumstances and could reinforce the advantages accrued from rapid initiation of photosynthesis.

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