Trunk forking in *Acer saccharum*: a phototropic response to forest canopy gaps

Abstract

We examined trunk forking in *Acer saccharum* as an adaptation for filling canopy gaps. We measured diameter and distance to nearest neighbor around forked and unforked sugar maples and computed and compared the mean local basal area per sample area for these two groups. While these results were not statistically significant for each site, when taken together for all sites the data showed that sugar maples forked their trunks more often when the basal area around them was relatively low, indicating that forking allowed them to fill canopy gaps more effectively.

Introduction

Acer saccharum, the sugar maple, is a shade-tolerant, gap-phase species (Walters 1993). The growth of *A. saccharum* seedlings is typically restrained entirely by the limitation of light penetrating the forest floor by the canopies of overstory adult trees (Ricard et al., 2004). The seedlings persist on the forest floor as small juveniles for many years and grow quickly to fill gaps in the canopy created by disturbance (Marks and Gardescu 1998). The species has evolved phototropic responses to canopy gaps that allow it to avoid shade and quickly fill new gaps before its competitors (Brisson 2001). While in temperate North American forests *A. saccharum* is often found in conjunction with *Fagus grandifolia* (which is an even more shade-tolerant species), *A. saccharum* tends to out-compete *F. grandifolia* in the presence of very small canopy gaps by producing many short lateral branches that more effectively exploit these openings (Canham 1989).

The relationships of several phenotypic responses to light gaps have been examined, including stem orientation (King 2001), leaf structure and biomass allocation (Osada et al., 2004), root architecture (Cheng et al., 2005), and lateral branching

(Canham 1988). Though a recent study showed that trees, particularly shade-tolerant species, displace their canopies away from their neighbors to reduce competition and maximize resource exploitation (Muth and Bazzaz 2003), the tendency of sugar maples to branch early and form two trunks to fill the forest canopy more effectively has not been examined specifically. This experiment sought to demonstrate the effects of canopy density and light competition on the tendency of sugar maples to exhibit forked trunks. We hypothesized that trunk forking would allow sugar maples to fill canopy gaps more quickly and efficiently than a single trunk by creating a wider canopy area to absorb the light energy in these gaps and shade out nearby competitors. We expected that a forked trunk would be more effective than a single trunk at filling larger canopy gaps, while a single unforked trunk would be sufficient to fill smaller gaps.

We tested our hypothesis by comparing local basal area per sample area around forked and unforked sugar maples from three sites that differed in species dominance and overall basal area. We predicted that each site would have significantly different proportions of forked and unforked trees and that mean local basal area per m^2 would be significantly lower for forked trees than unforked trees. In addition we predicted that each site would have a significantly different mean local density for forked trees.

Methods

We sampled three sites: Grapevine Point, Sedge Point and Colonial Point. We selected these sites because they had significant populations of sugar maples but varied in species composition and overall basal area. In each site we established a 50m by 50m test area. We sampled each test area with five parallel 2m by 50m transects. We established these transects within the test area at a distance of 10m from one another measured from their centers. We used the following parameters in the sampling:

a) A height of 130cm was used for every diameter measurement (Brokaw and Thompson 2000).
b) In the case of trees of any species that exhibited trunk forking below 130cm, the dbh at 130cm of each trunk was recorded. These trunks were considered individual trees for the purpose of determining basal area and dominance within a site.
c) Trees (or trunks) with a dbh of less than 5cm were not included in any aspect of the study.
d) Only trees whose centers were within one meter of the center of a transect were counted as belonging to a transect.
e) Trees with forked trunks were defined as branching into two or more trunks (each with a diameter of atleast 5cm) below a height of 2m.
f) Distance between two trees was defined as the shortest distance from the surface of one tree to the surface of the next.

Within each transect we recorded the dbh and species of each tree. Every sugar maple encountered was recorded as being forked or not-forked, and we established a point-quarter system around the trees with one axis parallel to and the other perpendicular to the transect. Within each quarter we located the nearest neighbor and recorded its species, dbh and distance to the sugar maple.

We repeated these methods identically for each of the three sites. We calculated the relative dominance and basal area of each site from the transect data. We calculated the mean local density and basal area around forked and unforked sugar maples from the point-quarter measurements separately for each site and for all the sugar maples sampled in the study.

We used an ANOVA to analyze whether the mean local density for sugar maples differed between the three sites. We used a chi-square test to establish whether the proportion of forked and unforked sugar maples in the three sites was identically distributed to test the hypothesis that the sites would have significantly different proportions of forked and unforked trees. We used a t-test to examine whether the mean local density differed significantly for forked and unforked sugar maples for all the sites considered as a population. We examined this difference for the sites considered individually with additional t-tests.

Results

Colonial Point was dominated by relatively large trees and the understory was open with no light gaps and few recently fallen trees. The trees at Sedge Point tended to be much smaller and the understory was crowded with saplings of *Acer* and *Fagus*. The trees at Grapevine Point were intermediate in size and there were a few saplings rising to fill recently created light gaps. Because there was more distance between trees at Colonial Point and there were fewer trees overall, its basal area was almost equal to that of Grapevine Point. Though the trees were smallest on average at Sedge Point, this site had a substantially higher basal area than the other two because there were many more trees present (Table 1).

Colonial Point was dominated by very large old beeches, and several smaller red maples and sugar maples were growing between them (Fig 1). Colonial Point had the lowest dominance of sugar maples of all the sites. Sedge Point had an almost equal balance of dominance by red maples, sugar maples and beeches (Fig 2). The beeches at Sedge Point tended to be smaller than the maples but there were more beeches overall. Grapevine Point was different from the other two sites in that over 50% of its basal area was accounted for by sugar maples. Unlike the other two sites, there were no adult beeches or red maples, and several large ashes and basswoods were present (Fig 3.)

The difference in basal area per m^2 around the sugar maples between the three sites was statistically significant with a p-value of 0.013, however only the difference between Sedge Point and Colonial Point was significant (Table 2). All of the sugar maples at Colonial Point were unforked, while 47% of the sugar maples at Sedge Point and 24% of the sugar maples at Grapevine Point were forked (Table 3). The difference between these proportions was statistically significant with a p-value of 0.03 (Table 4).

Unforked sugar maples had an average local basal area per sample area of almost double that of the forked sugar maples (Table 5). This difference was statistically significant for the sugar maples of all three sites considered together, with a p-value of 0.007 (Table 6). This difference was statistically insignificant for Sedge Point (Table 7) and Grapevine Point (Table 8) considered individually, with p-values of 0.172 and 0.084, respectively.

Discussion

The results of the ANOVA (Table 2), which showed that the mean local basal area per m^2 of all sugar maples was only significantly different between Sedge Point and Colonial Point, are in reality not very meaningful because all the sugar maples at Colonial Point were unforked. It would be more meaningful to compare the local basal area per m^2 for all forked sugar maples or for all unforked sugar maples between the sites, however this would almost definitely be statistically insignificant because of the small sample sizes. The importance of this comparison is questionable because we would expect there to be variation in these numbers between sites based on differences in overall basal area in each site. In addition it would seem logical to compare the local basal areas per m^2 of sugar maples with the overall basal areas per m^2 at the sites, as lower values for the basal area around sugar maples would illustrate their preference for canopy gaps. However it would be unsound to make this comparison because we calculated basal area per m^2 in the transects and around the sugar maples using different sampling methods. The use of different sampling methods can lead to drastically different estimated densities, particularly when distribution is non-uniform (Engeman et al. 1994).

Because the canopy at Colonial Point was dominated by very tall, old trees that cast a thick uniform shade over the forest floor, it is not surprising that there were no forked sugar maples there. While it would seem unusual that the highest incidence of trunk forking occurred at Sedge Point (Table 3) where overall basal area was highest (Table 1), this site would also tend to have the most gaps because the trees in this site had lower basal areas and smaller canopies. This is supported by the fact that the difference between local basal area per m^2 for forked and unforked sugar maples was higher for Sedge Point than Grapevine Point. Furthermore average local basal area per m^2 for the unforked sugar maples at Colonial Point was close to the values for unforked trees at the other two sites (Table 5).

If the study were repeated, photometer readings would be taken randomly at several points in each site. Though more light would not reach the forest floor on average, a higher value for standard deviation in these readings at Sedge Point would show that this site has more canopy gaps than the other two sites. Likewise we would expect that though the similar values for basal area at Grapevine Point and Colonial Point should lead to similar mean light intensities at ground level, a lower standard deviation at Colonial Point would reflect a uniformly shaded environment for maple seedlings.

The fact that the difference between mean local basal areas per m^2 was statistically significant for all sites considered together (Table 6) but insignificant for the sites considered individually (Tables 7 and 8), despite the fact that the means were almost identical for each site (Table 5), shows that the sample sizes were too small in this experiment. If the study were continued, doubling the sampling regime at each site would probably lead to statistically significant results. This would further establish the role of trunk forking as an evolutionary adaptation of *Acer saccharum* to quickly fill light gaps.

Our study showed that trunk forking allowed sugar maples to fill large canopy gaps more completely. This was an original finding, however it was consistent with previous research. Shade-tolerant trees produce more lateral branches in canopy gaps (Canham 1989), and orient these branches towards areas with higher light (King 2001). Therefore in large canopy gaps trees tend to expand their canopies by producing several large radiating branches (Canham 1988). If two or more of the branches of a developing tree were highly successful in capturing light, it would be logical for them to continue to develop upwards towards different areas of the light gap and eventually form distinct trunks with individual canopies. The leaves of these canopies would detect light competition by means of the red to far-red irradiance ratio (Aphalo et. al 1999) and the branches of the tree would behave autonomously and avoid one another (Brisson 2001). At this point the canopy of one trunk would respond to shading by the canopy of its other trunks exactly as it would to shading from neighboring trees (Muth and Bazzaz 2003), and orient its trunks away from each other and neighboring trees to minimize the interaction between canopies. As long as the individual canopies were successful in capturing light, all the trunks would be maintained with their canopies oriented away from each other to minimize competition and exploit all available light.

Further support for our results could be provided by long-term studies in which the development of sugar maples is observed over time. Sugar maples would be grown under experimentally created canopy gaps with known values of canopy closure, and the incidence of forking could be observed to determine a threshold gap size under which forking is induced. Based on our observations we would expect that the threshold local basal area per sample area needed to induce forking would be somewhere between 0.00222 and 0.00408, however the experiment outlined above would give a threshold value for canopy closure which would be more relevant because this value more accurately represents the light environment in the microhabitat of a seedling (Jennings et al. 1999).

It is interesting to note that we observed several sugar maples which had trunks that forked, but one or more of the trunks was dead and rotting. The dead trunks always pointed into the canopy of a tall nearby tree. This suggested that the dead trunks had been aborted because their leaves were not receiving enough sunlight because they were being shaded out by a taller neighbor. A long-term study, perhaps performed as a follow-up to the one described above, could be performed to observe this process and determine that in fact the trunks die in response to their gaps being filled by surrounding taller trees, and not the other way around. This would be done by blocking sunlight to one of the trunks of several forked sugar maples and seeing whether the trees abort entire trunks in the same way that they abort unproductive smaller branches.

Trunk forking is an adaptation that has evolved in certain canopy gap-dependent species that improves their competitiveness and overall evolutionary fitness. Tree species with the ability to alter their form in response to their light conditions have an advantage and will tend to outcompete those that are morphologically rigid in settings where environmental heterogeneity is high. An improved insight into trunk forking as a response to light gaps will increase understanding of forest succession and tree species' adaptations to varying conditions.

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Tables and Figures

Table 1. Total basal area per m^2, average basal area and total trees at each site.

Site	Basal Area per Sample Area	Average Basal Area	Total Trees
Colonial Point	0.00476762	0.07011203	34
Grapevine Point	0.004535477	0.0503942	45
Sedge Point	0.00670734	0.03457391	97

Table 2. Results of an ANOVA comparing the mean local basal area per sample area around sugar maples.

Descriptives

BASAAll

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Sedge Pt	14	.00299342	.001797970	.000480528	.00195530	.00403154	.000466	.005925
Grapevine Pt	25	.00382678	.001618216	.000323643	.00315881	.00449475	.001056	.007086
Colonial Pt	13	.00535899	.002819610	.000782019	.00365512	.00706287	.001031	.011236
Total	52	.00398547	.002165721	.000300331	.00338253	.00458841	.000466	.011236

ANOVA

BASAAll

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.000	2	.000	4.763	.013
Within Groups	.000	49	.000		
Total	.000	51			

Multiple Comparisons

Dependent Variable: BASAAll
Tukey HSD

(I) Site	(J) Site	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Sedge Pt	Grapevine Pt	-.000833361	.000674859	.439	-.00246444	.00079772
	Colonial Pt	-.002365576(*)	.000778683	.010	-.00424759	-.00048356
Grapevine Pt	Sedge Pt	.000833361	.000674859	.439	-.00079772	.00246444
	Colonial Pt	-.001532215	.000691297	.078	-.00320303	.00013860
Colonial Pt	Sedge Pt	.002365576(*)	.000778683	.010	.00048356	.00424759
	Grapevine Pt	.001532215	.000691297	.078	-.00013860	.00320303

* The mean difference is significant at the .05 level.

Table 3. A summary of the sugar maples at each site.

Site	**Total Sugar Maples**	**Forked Sugar Maples**	**Unforked Sugar Maples**	**% of Sugar Maples forked**
Colonial Point	13	0	13	0%
Grapevine Point	25	6	19	24%
Sedge Point	17	8	9	47%

Table 4. Results of a chi-square test comparing the proportions of forked and unforked sugar maples at the three sites.

			Site			Total
			Sedge Pt	Grapevine Pt	Colonial Pt	
FNFAll	Not Forked	Count	8	19	13	40
		Expected Count	10.8	19.2	10.0	40.0
	Forked	Count	6	6	0	12
		Expected Count	3.2	5.8	3.0	12.0
Total		Count	14	25	13	52
		Expected Count	14.0	25.0	13.0	52.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	6.998(a)	2	.030
Likelihood Ratio	9.506	2	.009
Linear-by-Linear Association	6.816	1	.009
N of Valid Cases	52		

a 2 cells (33.3%) have expected count less than 5. The minimum expected count is 3.00.

Table 5. Average basal area per sample area around sugar maples at each site and overall.

	Sedge Pt.	Grapevine Pt.	Colonial Pt.	Overall Average
Forked	0.001965	0.002475	none	0.00222
Unforked	0.004160	0.004103	0.004	0.00408

Table 6. Results of a t-test comparing mean local basal area per sample area for all sites.

Independent Samples Test

	Levene's Test for Equality of Variances		t-test for Equality of Means						
	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
Equal variances assumed	1.046	.311	2.840	50	.007	.001897316	.000668047	.000555504	.003239129
Equal variances not assumed			3.363	24.703	.003	.001897316	.000564131	.000734758	.003059874

Table 7. Results of a t-test comparing the mean local basal area per sample area for Sedge Point.

Independent Samples Test

	Levene's Test for Equality of Variances		t-test for Equality of Means						
	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
Equal variances assumed	.039	.846	1.453	12	.172	.001354201	.000931998	-.000676448	.003384851
Equal variances not assumed			1.473	11.414	.168	.001354201	.000919577	-.000660857	.003369260

Table 8. Results of a t-test comparing the mean local basal area per sample area for Grapevine Point.

Independent Samples Test

	Levene's Test for Equality of Variances		t-test for Equality of Means						
	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
Equal variances assumed	.048	.828	1.806	23	.084	.001308399	.000724429	-.000190196	.002806994
Equal variances not assumed			1.788	8.291	.110	.001308399	.000731836	-.000368956	.002985754

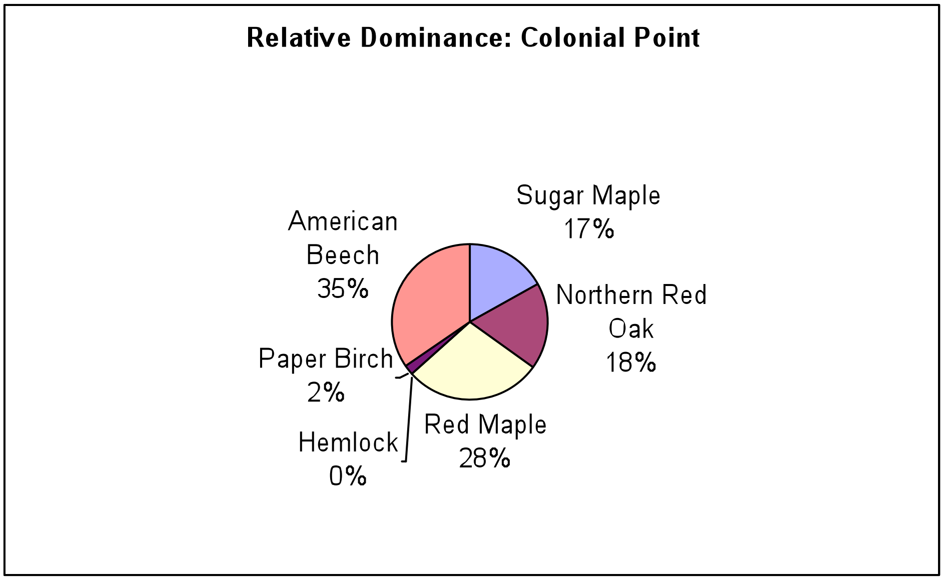

Figure 1. Relative dominance at Colonial Point.

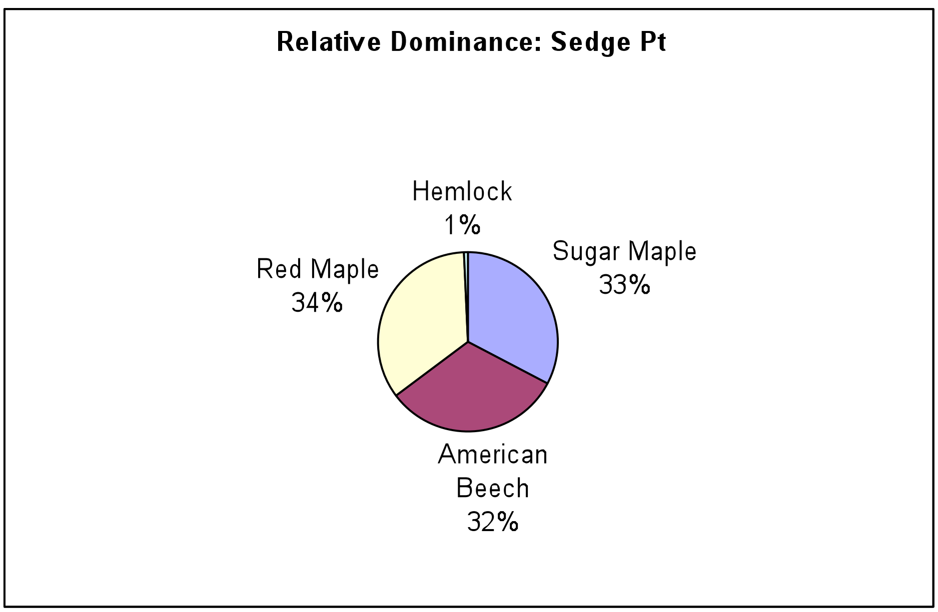

Figure 2. Relative dominance at Sedge Point.

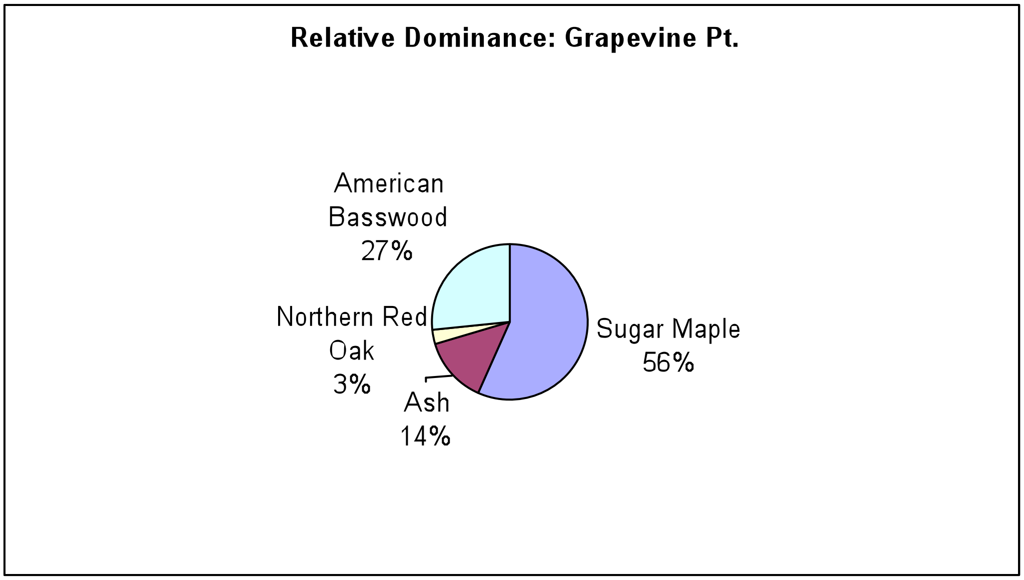

Figure 3. Relative dominance at Grapevine Point.