TESTING HYPOTHESES FOR STEM BENDING IN TREE SAPLINGS

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We tested the prediction that the main stems of four common deciduous tree species grow phototropically as saplings in the forest understory in response to variable canopy structure. Our predictions were confirmed for *Fraxinus americana*, *Acer saccharum*, and *Ulmus americana*, which all had stems bent in the direction of greatest canopy openness. The fourth species, *Tilia americana*, did not demonstrate the predicted phototropic main stem bending. Our tests also enabled us to distinguish between alternative bending strategies, confirming that for three species, bending is associated with a phototropic shade avoidance response rather than a nonphototropic shade avoidance response and is not a consequence of biomechanical constraints. Additionally, we found evidence that the four species differ in the canopy conditions under which their saplings grow, suggesting niche separation along understory light environment gradients.

Keywords: biomechanical constraints, canopy openness, nonphototropic shade avoidance, phototropism, phototropic shade avoidance, stem bending.

Introduction

Young trees growing within forests are commonly found bending out over trails or away from the forest edge. These bent growth forms appear to represent a positive phototropic response, promoting access to a strongly unidirectional source of light. Phototropism has been widely demonstrated for many herbaceous plants (Hart 1996) but has been reported only rarely in trees. Main stem phototropism has been observed for trees growing at forest margins or along riverbanks (Loehle 1986) and has been credited with influencing crown orientation in tropical (Young and Hubbell 1991; Ackerly and Bazzaz 1995) and temperate (Olesen 2001) rain forests. Understory trees are also capable of responding rapidly to canopy gap formation (Canham 1988, 1989) as well as to lateral shading from neighbors (Holbrook and Putz 1989). What is particularly interesting is that these bent growth forms are not confined exclusively to trees that occupy forest edges, riverbanks, and trail margins (where phototropism has obvious benefits). Understory trees that are not growing near these obvious edges and their resultant light gradients also commonly show varying degrees of main stem bending. Most phototropic growth in plants has been observed when a light gradient of 20% or more is present (Hart 1996). Is it possible that tree saplings within a temperate forest understory characterized by ephemeral and unpredictable patterns of canopy openness experience sufficient gradients in available light to promote phototropic growth? This study was designed to examine how commonly and to what degree tree saplings bend in temperate forest understories, whether this growth form indeed represents phototropic growth and whether other factors may be at work in promoting bent stem growth in conditions away from forest edges.

At forest edges, even large, mature trees are often bent, whereas in the forest interior, a bent posture is typically confined to shorter individuals (i.e., <2 m; observations from this study). This suggests that bent saplings in the forest interior either straighten out as they grow or die before reaching the canopy. It is therefore unclear whether sapling bending in the understory is a temporary phenomenon and whether it represents an adaptive response to the local light environment.

Predictions for Adaptive Stem Growth Strategies in Forest Saplings

Phototropic shade avoidance. A shade avoidance strategy is characterized by multiple traits, including increased internode length, reduced lateral branching, and low leaf area (Henry and Aarssen 1997). A canopy opening that is not located directly overhead may elicit a growth response that includes not only rapid leader extension associated with apical control/dominance but also stem bending or inclination toward a distant canopy gap. If sapling bending can be classified as a phototropic shade avoidance growth strategy, we predict that the leader should demonstrate a phototropic orientation, bending toward areas of greater canopy openness.

Nonphototropic shade avoidance. Under conditions of limited canopy openness, specifically when there are no significant directional differences in canopy structure, a different shade avoiding strategy is possible. Sapling light interception may be improved by main stem bendiness through increasing the horizontal area over which leaves are presented, thus minimizing self-shading (Canham 1988; Henry and Aarssen 1997). Under such a strategy, phototropism may not be important. Hence, if main stem bending is related to a nonphototropic shade avoidance strategy, we predict that (1) saplings should be increasingly bent under lower canopy openness, (2) saplings should not be bent in any particular direction

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(i.e., not phototropic), and (3) bendiness of saplings—if it represents an adaptive strategy—should not be related to the spindliness of the sapling (i.e., biomechanical constraints).

Biomechanical Constraints

Rather than representing an adaptive strategy, bent growth forms in understory saplings may simply be a consequence of spindliness resulting from strong apical control/dominance, associated with the "race to the canopy," combined with effects of ice and snow loading (Henry and Aarssen 1997). If bendiness of understory saplings is largely due to biomechanical constraints, we predict that (1) main stem bending will not be in the direction of greater canopy openness and (2) bendiness (the degree to which a sapling is bent) will be positively related to the spindliness of the sapling—reflected by the extent to which leader extension growth is disproportionately greater than the growth of secondary support tissue (represented by the addition of stem girth). We tested these predictions (summarized in table 1) using data collected from natural populations of four temperate tree species common to northeastern North America.

Methods

Study Species and Site Choice

Sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), and white elm (*Ulmus americana* L.) were chosen for this study for several reasons: (1) they are co-occurring, mid- to late successional species that experience a variety of canopy conditions and likely experience competition for light in the early sapling stage of growth; (2) they are common within the study region; and (3) saplings of these species have been observed with variously bent main stems. Nomenclature for these four species follows Gleason and Cronquist (1991).

These four species are known to differ in the degree to which they are shade avoiding or shade tolerant. *Acer saccharum* is known to be very shade tolerant (Burns and Honkala 1965) and capable of surviving as a sapling in a light-limited understory for an extended time, but it can also respond quickly to the formation of light gaps with fast apical growth to reach a canopy position. *Acer saccharum*, therefore, employs growth strategies that represent both shade avoidance and shade tolerance. *Tilia americana* is also classified as being shade tolerant, although less so than *A. saccharum* (Burns and Honkala 1965). *Fraxinus americana* is shade tolerant when very young but becomes intolerant as it grows older (Burns and Honkala 1965). *Ulmus americana* is

classified as intermediately shade tolerant and possesses the ability to respond well with rapid growth when canopy openings occur (Burns and Honkala 1965)

All trees chosen for this study were growing in the understory of temperate mixed deciduous-coniferous forest tracts located at the Queen's University Biology Station, Chaffey's Locks, Ontario, Canada (44°34′N, 76°20′W) and were sampled between August 1 and September 1, 2002. The canopy composition of these forests also includes *Pinus strobus*, *Quercus rubra*, *Carya ovata*, *Carya cordiformis*, and *Tsuga canadensis*. These species made up a minor component of the forest understory and were therefore not included in this study on the basis of sample size challenges. Understory tree species in these forests included *Ostrya virginiana* and *Carpinus caroliniana*. Canopy trees in these forest tracts ranged from 20 to 30 m in height and are representative of mid- to late secondary succession. Sampled individuals were up to 2 m in height. Trees were sampled along linear transects spaced 10 m apart, with trees chosen to be at least 10 m distant from one another along transects. A total of 338 saplings were sampled, including 142 *A. saccharum*, 80 *F. americana*, 69 *T. americana*, and 47 *U. americana* saplings. Different sample sizes among species reflect the relative abundance of the four study species in the forest tracts considered.

Specimen Sampling and Measurements

Main stems were observed to deviate from vertical stature in two different ways: stem bendiness and stem inclination, with the latter involving largely straight but slanted or leaning stems associated primarily with effects of soil creep on sloped ground (e.g., Harker 1996) or because of unilateral root barriers. For this reason, trees with stems that were slanted or inclined from the base and trees growing on slopes were avoided. A number of saplings also showed bent or inclined stature because the main terminal shoot had been damaged earlier (e.g., from browsing) and a lateral shoot had taken over the main extension growth of the sapling or because a clump of stump sprouts had emerged following damage to a parent tree (observed especially in basswood). These damaged saplings and saplings sprouting from damaged stumps were also avoided. Additionally, we avoided saplings that were rooted within 1 m of a canopy tree. Such specimens were frequently very bent and obviously associated with a strong light gradient, but they were also bent because of physical obstruction from the trunk of a much larger neighbor. By employing these sampling restrictions, we were able to ensure a more conservative test of the direct role of light gradients affected by patterns of opening in the upper canopy.

Table 1

A Summary of Predictions Used in This Study to Distinguish between Possible Mechanisms for Sapling Main Stem Bendiness

Mechanism for stem bending	Sapling stems demonstrate positive phototropism	Canopy openness negatively related to stem bendiness	Stem bendiness is positively related to stem spindliness
Phototropic shade avoidance	Yes	No	No
Nonphototropic shade avoidance	No	Yes	No
Biomechanical constraints	No	Yes	Yes

For each sapling, we measured (1) stem length (L) along the (often curved or bent) length of the main stem starting at the base and extending to the limit of the furthest terminal bud (terminal point), (2) tree height (H) as the vertical distance from the terminal point to the ground, and (3) stem girth or diameter (D) at 10% of the tree's measured length (measured with calipers). The direction of bend was determined for each sapling using a compass.

Bendiness, or the degree to which a tree had a bent main stem, was calculated as a bending index, $BI = 1 - (H/L)$. This index scales bendiness between 0 and 1, where 0 represents a perfectly upright tree and 1 represents a tree with the terminal point bent down to ground level.

Spindliness, or the degree to which a stem is long relative to its girth, was calculated as the residual of the relationship between length and diameter of the main stem for all individuals in the sample (within species). A more positive residual represents a tree that is relatively less spindly, while a more negative residual represents a tree that is relatively more spindly.

Canopy Analysis

For each sampled tree, a canopy photograph was taken directly above the base of the main stem at the height of the terminal point using a 180° hemispherical (fish-eye) Nikon lens on a Nikon SLR camera. The camera was oriented toward magnetic north so that a given sapling's bend direction could be identified in the associated photo. The hemispherical negatives were scanned and analyzed with Gap Light Analysis (GLA) software (Frazer et al. 2000). Digitized canopy images were masked in CorelDraw with black semicircles to cover half the canopy image in the direction of the sapling's bend and then separately in the opposite direction to produce two images per sapling (fig 1). Canopy openness was quantified for each of these two images (percentage open sky) as well as for the full canopy. In this way, canopy openness
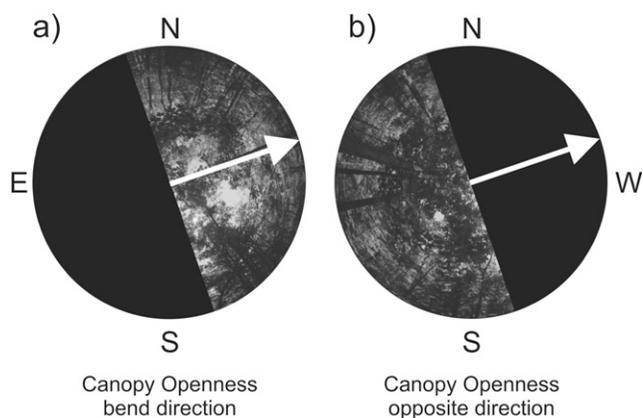

Fig. 1 Two versions of a canopy photo for a target sapling; the arrow points in the direction that the sapling was bending. *a* shows the photo half covered in black so that canopy openness could be quantified for the direction of sapling bend. Likewise, *b* shows the canopy with the other half of the photo covered such that canopy openness could be quantified in the direction opposite of that of the sapling's bend. Note that east and west are reversed because the images are looking upward.

in the direction of sapling bend and in the opposite direction was quantified for further analysis. Canopy openness was chosen as a measure of light availability to saplings because it reflects available diffuse light, which has been found to influence crown orientation more than direct light measures (Ackerly and Bazzaz 1995).

Data Analyses

All data were transformed as necessary to meet the normal distribution and homoscedacity requirements of regression analyses and t-tests. All transformations were done using the Box-Cox transformation in the JMP statistics package. Data that could not be normalized were considered using appropriate nonparametric statistics. The following analyses were performed to examine the hypotheses outlined above.

General analyses. To investigate whether saplings of each of the four species displayed significant bending, paired t-tests were applied to test for significant differences between height (H) and stem length (L) for each species. If the height of saplings was significantly smaller than the stem length for a given species, this was taken as evidence that saplings of this species had significant stem bendiness. Significance was assessed at $\alpha = 0.05$, and because the slope can only be less than 1 for this relationship, one-tailed P values were used to assess significance.

Given that this study was conducted in a northern temperate forest where the path of the sun during the growing season favors, on average, lower zenith angles in the southern portion of the sky (Canham et al. 1994), we tested the distribution of bend directions for each species to determine whether sapling bending tends to be southern in direction. We used directional statistics including Rayleigh's test, Rao's spacing test, Watson's U^2 test, and Kuiper's test (Zar 1999) to investigate the potential for nonrandom patterns in the frequency distributions of bend direction for each species. Since each of these tests has individual strengths and weaknesses, we used all of the tests and looked for strong evidence based on consistency in the results of these tests.

We tested for differences in stem bendiness (BI) between species using a nonparametric Kruskal-Wallis test. A nonparametric multiple comparisons test was used to determine which pairs of species significantly differed in their bendiness (Zar 1999).

We also investigated the possibility that when a sapling experiences greater asymmetry in canopy openness, the stem may have a larger BI. Asymmetry was calculated as the absolute difference in canopy openness between the bend direction and opposite direction, divided by total canopy openness. This was assessed using a model 1 regression analysis of asymmetry in canopy openness versus BI. To establish whether bendiness of saplings changes with increasing length of the main stem (i.e., an age/stage-specific effect on bendiness), model 1 regressions were generated for stem length versus BI for each species.

We further investigated whether each of the four tree species experienced differences in overall canopy structure. We used a Kruskal-Wallis test to compare canopy openness between all four species and used a nonparametric multiple comparisons test to identify significant differences between species pairs (Zar 1999).

Test for phototropic shade avoidance. We tested whether canopy openness was greater in the direction of sapling bend than in the opposite direction for each species. This is the main test of phototropic growth, and it involved paired *t*-tests between canopy openness in the bend direction and canopy openness in the opposite direction for each species.

Test for biomechanical constraints. Model 1 regression was used to assess the relationship between spindliness of a sapling and bendiness of that sapling. A significant positive relationship between these two factors suggests that increased bendiness may simply be due to the effects of ice/snow loading exacerbated by biomechanical constraints resulting from disproportionately greater leader extension relative to the addition of stem girth associated with strong apical control/dominance. This, combined with no evidence for phototropic growth, would fail to support a phototropic shade avoidance interpretation of bendiness.

Test for nonphototropic shade avoidance. For each of the four study species, we used model 1 regression analysis to test

whether the degree of sapling bendiness can be accounted for by overall canopy openness. A significant negative slope combined with no evidence for biomechanical constraints (above) can be interpreted as supporting the hypothesis that in low light conditions, trees employ a bent growth form to minimize leaf overlap and harvest limited light more effectively.

Results

Sapling length is significantly greater than sapling height for each of the four study species, establishing that all four species show significant stem bendiness (paired *t*-tests, $P < 0.001$). Not all patterns of bend direction are random (fig. 2). Both *Fraxinus americana* and *Acer saccharum* have statistically nonuniform distributions, while distributions of bend direction for *Tilia americana* and *Ulmus americana* are not statistically different from a uniform distribution (table 2). Neither *F. americana* nor *A. saccharum* has mean bend directions in the same direction, and both have irregular frequency
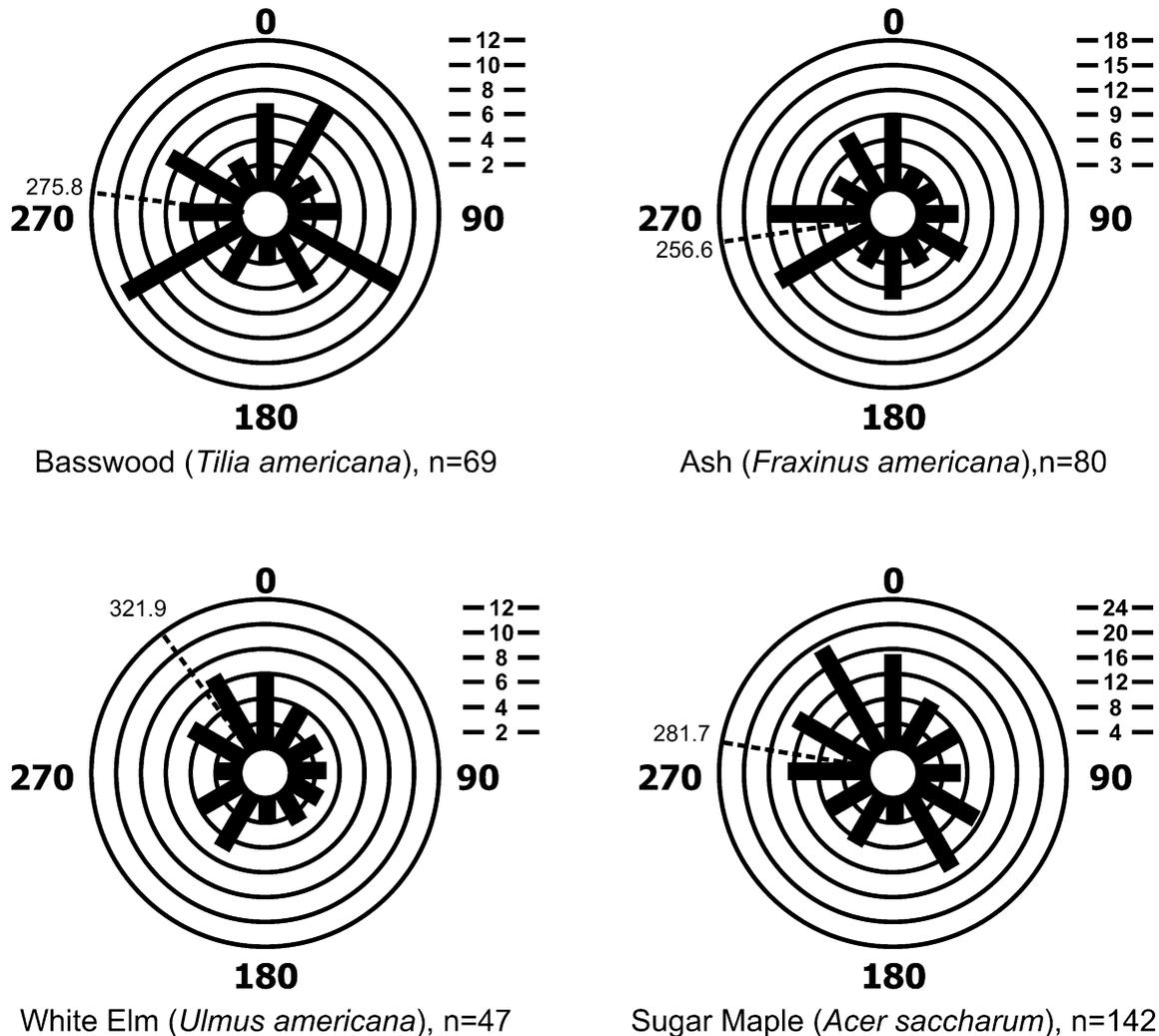

Fig. 2 Circular frequency histograms of bend direction in compass degrees for all four species considered. Dashed lines represent the mean bend direction in degrees from north. No obvious trend is observed in the direction of bend for any of the species. An examination of stacked histograms (not shown) ruled out the possibility that more bent individuals of each species show directional trends.

Table 2

A Summary of Statistics Testing for Uniform Frequency Distributions of Bend Direction for the Four Study Species

Species	Rayleigh's test		Rao's spacing test		Watson's U^2 test		Kuiper's test	
	Z	P	U	P	U^2	P	V	P
Fraxinus americana	3.884	.021	127.5	>.5	.231	<.025	1.851	<.05
Acer saccharum	.893	.409	150.02	<.01	.147	>.1	1.778	<.05
Tilia americana	.144	.866	128	>.5	.037	>.5	.968	>.15
Ulmus americana	1.301	.274	130.45	>.25	.099	>.25	1.309	>.15

Note. Underlined values are significant at $P < 0.05$.

distributions that are multimodal (fig. 2). There is no evidence of a predominantly southern bend direction.

The degree to which saplings have a bent main stem (BI) differs significantly among the four species (Kruskal-Wallis test, $P < 0.0001$). All four species differ significantly from one another in BI (nonparametric multiple comparisons test, $\alpha = 0.05$). *Ulmus americana* saplings have the highest degree of stem bending ($\overline{X} = 0.37$), followed by *T. americana* ($\overline{X} = 0.33$), *A. saccharum* ($\overline{X} = 0.26$), and finally *F. americana* ($\overline{X} = 0.23$).

Asymmetry in canopy openness does not predict the degree to which sapling stems are bent (BI) for *F. americana* ($P = 0.9568$), *A. saccharum* ($P = 0.18$), *T. americana* ($P = 0.2567$), or *U. americana* ($P = 0.0607$). Asymmetry in canopy openness differed significantly between *F. americana* ($\overline{X} = 0.36$) and *A. saccharum* ($\overline{X} = 0.25$) but not for other pairs (*T. americana*: $\overline{X} = 0.26$; *U. americana*: $\overline{X} = 0.33$).

Longer main stems have significantly greater bendiness in *F. americana* ($n = 79$, $r^2 = 0.1592$, $P = 0.0002$), *A. saccharum* ($n = 142$, $r^2 = 0.2333$, $P < 0.001$), and *U. americana* ($n = 47$, $r^2 = 0.17378$, $P = 0.0036$). However, longer main stems of *T. americana* saplings do not have more bent main stems ($n = 69$, $r^2 = 0.17866$, $P = 0.2735$). The degree of canopy openness experienced by each species differs significantly (Kruskal-Wallis test, $P = 0.0001$), with *F. americana* growing under the most open canopies ($\overline{X} = 2.86\%$), followed by *T. americana* ($\overline{X} = 2.58\%$), *U. americana* ($\overline{X} = 2.34\%$), and finally *A. saccharum* ($\overline{X} = 2.06\%$).

Canopy openness is significantly greater in the direction of sapling bend for *F. americana* (*t*-test, $t = -5.14$, $P < 0.0001$), *A. saccharum* (*t*-test, $t = -2.80$, $P = 0.0058$), and *U. americana* (*t*-test, $t = -4.29$, $P < 0.0001$) but not for *T. americana* (*t*-test, $t = -0.698$, $P = 0.487$) (fig. 3).

There is no significant relationship between spindliness and bendiness (BI) of *F. americana*, *T. americana* and *U. americana* saplings, although there is a significant positive relationship for *A. saccharum* (model 2, $r^2 = 0.1123$, $P < 0.0001$). There is also no significant relationship between overall canopy openness and the bendiness of saplings for any of the four species considered.

Discussion

Three out of the four study species (*Fraxinus americana*, *Ulmus americana*, *Acer saccharum*) demonstrated positive phototropism. Only *Tilia americana* did not show canopy-specific stem bending. While this is an indirect test of phototropism for these saplings, it makes a strong case that tree species growing under natural conditions respond, through patterns of growth, to even small differences in light availability in the canopy above them. While absolute differences in canopy openness between bending direction and the opposite direction were sometimes small, average canopy asymmetry was greater than 20% for all four study species. Phototropic responses have been recorded for plant species experiencing gradients in light intensity as low as 20% (Hart 1996). This type of inclined stem growth, typical of trees at forest edges and on riverbanks, clearly represents a broader strategy of phototropic shade avoidance employed by many tree species under a variety of canopy conditions, even within the forest interior. Our results add to previous work by Loehle (1986), who found that larger upland forest trees (>6 in dbh) do not demonstrate phototropic main stem bending and suggest that phototropic main stem bending is confined to younger/smaller saplings.

Tilia americana, which commonly has a very bent main stem in the study site (B. S. Schamp, M. Schurer, and L. W. Aarssen, personal observation) and was the inspiration for this study, was the only species in our study that did not show signs of phototropic bending. In fact, *T. americana* saplings had only the third-most bent main stems among the four species. The explanation for this probably lies in the exclusion of specimens growing close to suspected parent trees and the exclusion of stump sprout clumps (which are particularly common in basswood). These saplings are probably experiencing very strong asymmetry in light availability (Umeki 1995, 1997), but their bendiness is obviously affected also by physical obstruction, the effects of which we were not interested in measuring in this study.

The observed tree bending is likely the product of multiple years of growth. For many of these saplings, the extremity of canopy asymmetry that triggered main stem bending would have been diminished or even eliminated at the time that the study was conducted. Some of the saplings sampled may have, in fact, been undergoing the process of straightening out at the time the study was conducted. In spite of this, we observed a strong signal of phototropic growth for three of four species. This suggests that many saplings are capable of responding quickly to small, possibly short-lived differences in canopy structure. At the same time, variability in both sapling growing stage and the canopy structure at the time of this study makes it difficult to assess the degree to which a canopy must show directional asymmetry in openness for a tree sapling to begin actively growing a bent main stem. It is, however, reasonable to assume that the level of sensitivity to directional asymmetry of light availability will be species
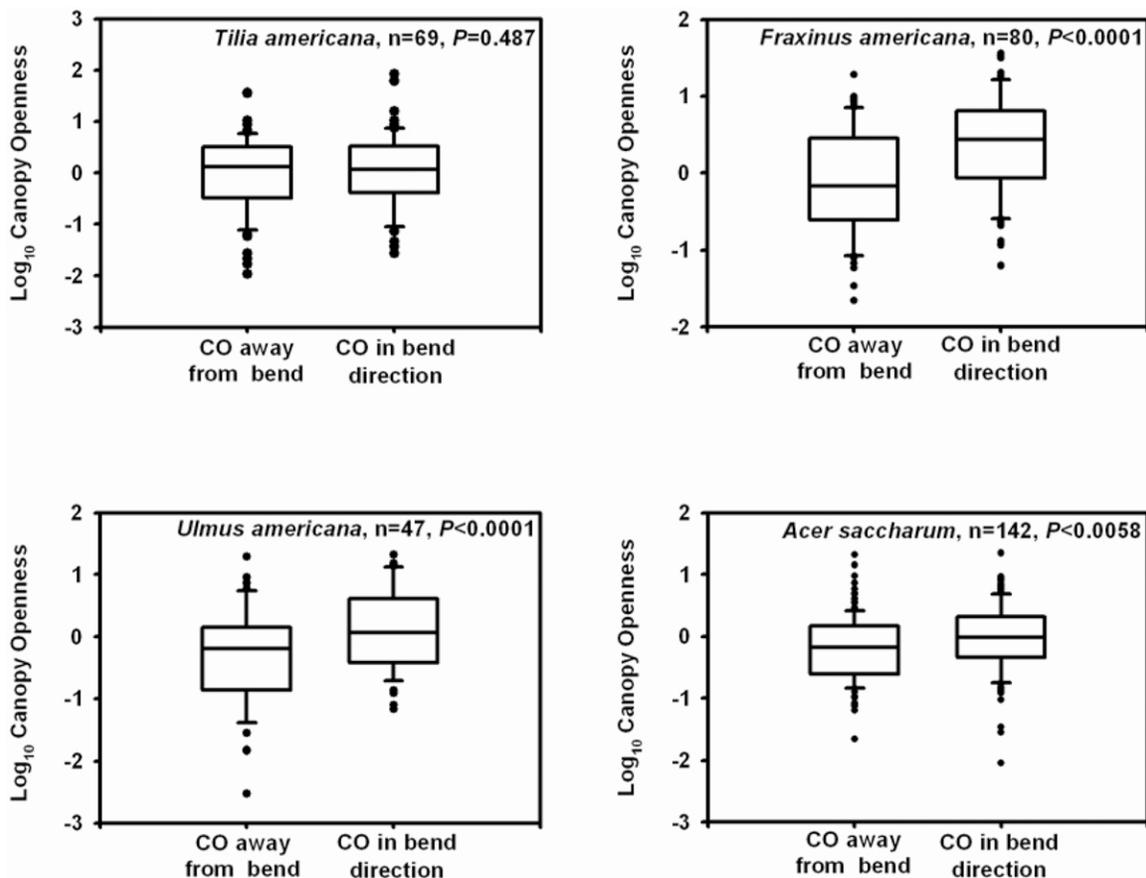
Fig. 3 Box plots comparing canopy openness (*CO*) in the direction of sapling bend to canopy openness in the opposite direction (i.e., away from bend). Boxes define the twenty-fifth and seventy-fifth percentiles, and whiskers represent the tenth and ninetieth percentiles of the data. The midline of boxes represents the median value of canopy openness, and data points represent those falling outside the tenth and ninetieth percentiles. For all species except *Tilia americana*, paired *t*-tests show that canopy openness is significantly greater in the bend direction than in the opposite direction.

specific. This sensitivity, on average, will fall within the range of canopy conditions observed for each species in this study. As indicated by our results, all four species can be differentiated by the level of both canopy openness and, for at least one pair, by the directional asymmetry of canopy openness that they experience. This may signify some degree of niche segregation along biotically defined gradients of light availability. Given that canopy species vary in the light levels they block (Canham et al. 1994), future study may be directed at examining the species combinations contributing to canopy conditions favoring the growth of saplings of each of these species.

A phototropic shade avoidance strategy typifies the race to the canopy that results from predominantly apical growth (Henry and Aarssen 1997). For *F. americana*, *U. americana*, and *A. saccharum* in this study, apical growth is augmented by directional growth toward more open parts of the canopy. The degree to which main stem bending is influenced by differential lateral growth along the main stem (Hart 1996) versus asymmetrical crown development (Ackerly and Bazzaz 1995; Umeki 1995) has yet to be determined. While biomechanical constraints were implicated only in the bending of

A. saccharum saplings, branching differences along the main stem may also contribute to the degree of stem bend (Umeki 1995). Unilateral branching intensity was not obvious when conducting this study; however, it represents an interesting direction for further research, especially for *A. saccharum*, the only species for which data from our study suggest that bending is related to biomechanical weakness. It is possible that main stem phototropism in *A. saccharum* simply results from a combination of stem weakness due to strong apical growth (leading to greater spindliness) and greater branching intensity in the direction of canopy gaps.

The degree to which this strategy is adaptive might be assessed in future studies through following the fates of tree saplings that employ stem bending as a method of shade avoidance. While a tree has the ability—through unilateral differences in secondary growth later on (i.e., the formation of reaction wood)—to straighten out, there may be limitations in the degree to which such a correction can occur. For example, a tree that has grown either too bent and/or too large may have difficulty in fully recovering to a vertical growth form and may also incur a greater mortality risk from gravity or wind (King 1986). Young and Hubbell (1991)

report that tropical trees with asymmetric crowns tend to fall in the direction that the canopy has asymmetrically spread. Given that such asymmetric crowns can result from asymmetrical branch growth/mortality (Umeki 1995) or from a bent main stem, there is a potentially large risk associated with phototropic bending, whereby a tree may remain competitive for available light but at an increased mortality risk. The relative stem inclination of dead saplings in the understory might provide some indication of the relative survival success of trees growing in this manner.

The bendiness of saplings was unrelated to the overall canopy openness, allowing us to reject the hypothesis that bendiness of the main stem functions to increase the lateral extent of leaf display beneath the canopy. This interpretation could benefit further from more data on what minimum level of light contributes to the bending of the main stem. We also observed that the degree of asymmetry of canopy light did not influence the degree to which a sapling was bent for any of our study species. The temporal variability of canopy openness most likely played an important role in this. The inevitable variability in a sapling's stage of bending or straightening probably obscured evidence of the effect of canopy asymmetry on the degree to which a sapling may have shown phototropic stem bending. A true test of this relationship would require a manipulative experiment artificially controlling canopy asymmetry.

In conclusion, we recorded evidence of phototropic growth of saplings for three out of four tree species in an upland forest understory. These results suggest that phototropic main stem bending can be listed among the suite of traits contributing to a phototropic shade avoidance growth strategy in *F. americana*, *U. americana*, and *A. saccharum*.

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