

Tree canopy displacement at forest gap edges

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Abstract: Although plants are sessile organisms, they can forage for resources and avoid neighbors by growing towards areas with high resource availability and reduced competition. Apparently because of this morphological flexibility, tree canopies are rarely positioned directly above their stem bases and are often displaced. To determine if contrasts in light availability lead to the development of canopy displacement, we investigated the responses of tree canopies to the heterogeneous light environments at the edges of six experimental gaps. Canopies and trunks of gap edge trees were mapped, and their spatial distributions were analyzed. We found that tree canopies were displaced towards gap centers. The magnitude and precision of canopy displacement were greater for subcanopy trees than for canopy trees. The magnitude and precision of canopy displacement were generally greater for earlier successional trees and hardwoods than for later successional trees and conifers. Canopy depth was significantly greater on gap-facing sides of trees than on forest-facing sides of trees. Thus, trees along gap edges foraged for light by occupying both horizontal and vertical gap space. This morphological flexibility has implications for individual plant success, as well as forest structure and dynamics.

Résumé : Même si les plantes sont des organismes sessiles, elles peuvent fouiller pour trouver des ressources et éviter les voisins en poussant vers les endroits où la disponibilité de ressources est élevée et la compétition réduite. Apparemment, en raison de cette flexibilité morphologique, les cimes sont rarement positionnées directement au-dessus de la base de leur tige et elles sont souvent excentriques. Pour déterminer si des différences dans la disponibilité de lumière provoquent un déplacement de la cime, nous avons examiné la réponse de la cime de quelques arbres à des environnements lumineux hétérogènes en bordure de six trouées expérimentales. La cime et le tronc des arbres en bordure des trouées ont été cartographiés, puis leur répartition spatiale a été analysée. Nous avons constaté que la cime des arbres était déplacée vers le centre des trouées. L'ampleur et la précision du déplacement des cimes sont plus grandes pour les arbres en sous-étage que pour ceux de l'étage dominant. L'ampleur et la précision du déplacement des cimes sont en général plus grandes pour les arbres de début de succession et les feuillus en comparaison des arbres de fin de succession et des conifères. La cime des arbres était significativement plus profonde du côté faisant face à la trouée que du côté de la forêt. Donc, les arbres qui bordent les trouées cherchent la lumière en occupant à la fois l'espace horizontal et vertical des trouées. Cette flexibilité morphologique a des implications sur le succès individuel des plantes, de même que sur la structure et la dynamique de la forêt.

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Introduction

The growth and survival of any organism are dependent upon its ability to capture resources. The ability of an organism to capture resources depends, in turn, upon the size of the resource foraging organs, their physiological competence, and their placement relative to the resource pools (Bazzaz 1996, 1997). Plants, because of their modular nature, are exposed to relatively large areas and can experience multiple environments (Bazzaz 1991; Sprugel et al. 1991). Modules in high-resource environments are likely to have increased growth and survival relative to modules in low-resource environments (Jones and Harper 1987; Umeki 1995a; Stoll and Schmid 1998). The result of these asym-

metrical demographic processes is a system of foraging organs (either a canopy or a root system) that is displaced from the stem base and concentrated in resource-rich patches. Focusing on the displacement of the entire shoot or root system is an effective way to integrate a variety of small-scale demographic processes into a relatively simple measure of whole-plant resource foraging (Franco 1986).

In forest systems, light is a critical resource (Wales 1972; Hutchinson and Matt 1977) that is particularly patchy and may be disproportionately available to different regions within an individual plant canopy (Balodochi and Collineau 1994). Presumably because plant modules tend to grow most actively in areas of high light, plant canopies in forests are rarely positioned directly above their stem bases and are often displaced (Young and Hubbell 1991; Holmes 1995; Rouvinen and Kuuluvainen 1997; Do-Soo et al. 1999). Forest gaps provide a natural environment where an individual plant's canopy is exposed to two greatly contrasting light environments (Bazzaz and Wayne 1994). Trees along gap edges receive high light levels on one side and low light levels on the other side. Thus, gaps are an ideal natural system in which to ask questions about response flexibility, resource foraging, and canopy displacement.

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A plant's degree of physiological and morphological flexibility is a critical aspect of its competitive ability and life-history strategy (Bazzaz 1996), and this degree of flexibility may vary among plant species and size classes. Canopy displacement, in turn, represents a critical aspect of flexibility among forest trees; however, comparison of canopy displacement across tree species or size classes has been extremely limited (Young and Hubbell 1991; Umeki 1995b; Do-Soon et al. 1999). The magnitude and precision (sensu Campbell et al. 1991) of canopy displacement are likely to vary across these groups and may reflect contrasting light environments, growth rates, biomechanical capabilities, or resource foraging strategies. Learning more about species and size class contrasts in foraging by tree canopies will enhance our understanding of forest competition, succession, and dynamics.

We hypothesized that contrasts in light availability lead to the development of displaced canopies and that canopy displacement responses differ among tree size classes and species. To test our hypotheses, we investigated the responses of tree canopies to the heterogeneous light environments at the edges of six experimental gaps. Our objectives were (*i*) to determine whether trees along the edges of forest gaps forage for light by displacing their canopies towards gap centers and (*ii*) to examine differences in the magnitude and precision of canopy light foraging across tree size classes and species.

Materials and methods

Study site and species

This study was conducted in six experimental gaps located in a mature mixed hardwood stand at the Harvard Forest Long-Term Ecological Research (LTER) site in central Massachusetts, U.S.A. (42°30'N, 72°15'W). The natural vegetation of this region is classified as transition hemlock – white pine – northern hardwoods forest (Westveld 1956). The study site included a variety of tree species, both hardwood and coniferous. The most common species were *Quercus rubra* L. (northern red oak), *Acer rubrum* L. (red maple), *Fagus grandifolia* Ehrh. (American beech), *Betula lutea* Michx. f. (yellow birch), *Betula lenta* L. (black birch), *Castanea dentata* (Marsh.) Borkh. (American chestnut), *Tsuga canadensis* (L.) Carrière (eastern hemlock), *Pinus strobus* L. (eastern white pine), and *Betula papyrifera* Marsh. (paper birch). These species span a wide range of traditional tolerance rankings from the very tolerant *T. canadensis* and *F. grandifolia* and the tolerant *A. rubrum* to the intolerant *B. papyrifera* (Baker 1949). The remaining species common to this site can be considered intermediate in tolerance.

The experimental gaps were created in 1986 by the felling of selected canopy trees (Sipe 1990; Sipe and Bazzaz 1994, 1995). The gaps are located primarily on Gloucester stony loam soils, with some portions on Whitman silt loam or Acton silt loam (Sipe 1990). All of the gaps are elliptical in shape, with the longer axis oriented east to west. Measurements have shown that since their creation, the gaps have decreased in size from a mean area of 287 m² to a mean area of 157 m² by horizontal encroachment of gap-edge trees

(T.W. Sipe and F.A. Bazzaz, unpublished data; C.C. Muth and F.A. Bazzaz, unpublished data). The lower portions of the gaps have been kept relatively open since their creation by periodic cutting of regenerating saplings. Light environments in the gaps differ markedly from those in the adjacent closed forest. On clear days, gap centers receive on the order of four times more light than the nearby understory; on overcast days, the gap and forest environments differ by a factor of about three (Sipe 1990). The experimental gaps are excellent replicates of one another, because they are the same age, size, and orientation and are located on the same soil and forest types. Thus, trees along the gap edges have been exposed to roughly the same experimental treatment for exactly the same time period. This experimental design is more controlled than previous studies (Young and Hubbell 1991; Young 1995; Do-Soon et al. 1999), which have measured trees along the edges of natural and artificial gaps of varying age, size, orientation, soil type, and forest type.

Field methods

We made detailed measurements of all gap-edge trees greater than 5 cm diameter at breast height (DBH). A tree was considered part of the gap edge if a portion of its canopy was directly adjacent to an experimental gap. We identified 140 such trees and measured them for height and DBH. A clinometer was used to determine canopy depth (the height of the top of the canopy minus the height of the bottom of the canopy) on both the gap side and the closed forest side of each tree. Trees were divided into two size classes: subcanopy and canopy. Trees were considered part of the subcanopy layer if at least 50% of the canopy was overtapped by neighbors. Trees were considered part of the canopy layer if less than 50% of the canopy was overtapped. All subcanopy trees were species with the potential to eventually attain a canopy position. The designation of a tree as subcanopy thus reflects current size and not future potential.

To determine the location of each gap-edge tree relative to its corresponding gap center, we used a compass and measuring tape to measure the distance and direction from gap center to each tree trunk. Canopy extent relative to trunk base was determined in eight directions around each tree (Young and Hubbell 1991). Tapes were laid out in eight subcardinal directions around the trunk. We then used a densitometer to locate the position along each tape where the canopy edge was directly overhead. Thus, for each tree, eight measurements of canopy extent were recorded along with corresponding subcardinal directions. The canopy extent measurements were conducted in July and August 1999.

Data analysis

A polar coordinate system was developed for each gap, with the location of gap center defined as the origin. We used measurements of distance and direction from gap centers to gap-edge trees to calculate polar coordinates for each trunk. Canopy extent measurements were used to reconstruct canopy size, shape, and position relative to trunk base. To adjust for bole width, the radius of the corresponding trunk was added to each canopy extent measurement. Polar coordinates of the eight canopy extent points were then calculated based on the adjusted canopy extent measurements. Maps of

stem bases and their corresponding canopies were created for each gap using a geographic information system (ArcView version 3.2a; Environmental Systems Research Institute, Inc.). Tree canopies were plotted by connecting the canopy edge points of each tree into a polygon (Fig. 1).

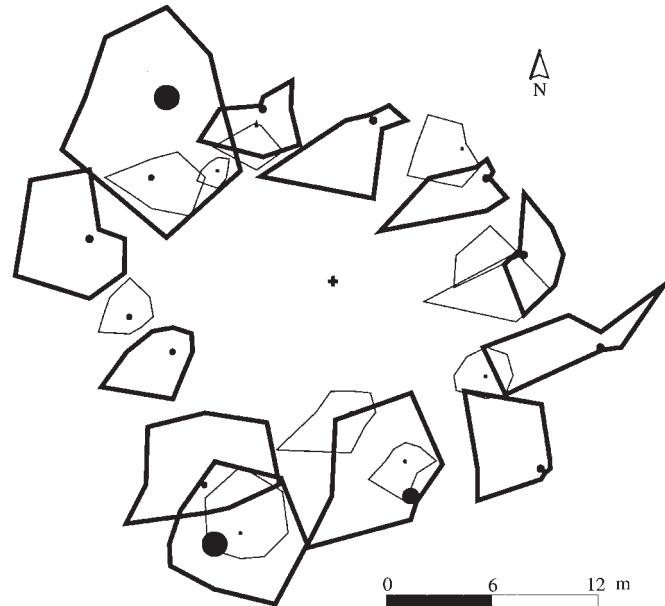
Canopy center of mass was calculated based on the eight canopy edge points of each tree (Batschelet 1981). The magnitude and direction of canopy displacement were defined as the length and direction of the vector pointing from stem base to canopy center of mass (Franco 1986; Brisson and Reynolds 1994; Rouvinen and Kuuluvainen 1997; Umeki 1995a, 1995b, 1997). To compare canopy displacement across a range of tree sizes, we calculated a relative canopy displacement value for each tree. Relative canopy displacement was defined as the distance between stem position and canopy center of mass divided by the mean of the eight canopy extent measurements. Thus, relative canopy displacement is a unitless measure, and a value of zero represents a tree with its canopy placed directly above its stem base. A value greater than one represents a situation in which the canopy is displaced entirely from the stem base. For the majority of forest trees, relative canopy displacement values tend to range between zero and one, indicating that the canopy is displaced but that the stem base is still positioned at some location beneath the canopy.

Relative canopy displacement was used to assess the magnitude of canopy displacement. This parameter was compared across tree species and size classes. A multifactor analysis of variance (ANOVA) (Sokal and Rohlf 1995) was carried out to determine the significance of these comparisons (Data Desk version 4.2; Data Description, Inc.). Gaps were considered blocks in this study and, thus, were analyzed as random factors. Because some species were restricted to one size class, it was not possible to examine interactions between species and size class in the multifactor ANOVA. We used Fisher's least significant difference (LSD) (Sokal and Rohlf 1995) as a post-hoc test for evaluating species differences in relative canopy displacement.

We evaluated the precision of canopy displacement (*sensu* Campbell et al. 1991) based on the strength of correlations between the direction of gap center and the direction of canopy displacement. A strong positive correlation between these two factors was used as an indication that tree canopies were foraging in the resource-rich gap environment and, thus, demonstrated high foraging precision. Because data were directional and not uniformly distributed, correlations were investigated using circular–circular rank correlation tests (Batschelet 1981).

A two-tailed, paired *t* test (Sokal and Rohlf 1995) was used to compare canopy depth on the gap-facing versus forest-facing sides of trees. To compare asymmetry in canopy depth across species and size classes, we created a new variable called canopy depth ratio. Canopy depth ratio was calculated for each tree and was defined as the difference in canopy depth between the gap-facing and forest-facing sides of the tree divided by tree height. A multifactor ANOVA (Sokal and Rohlf 1995) was carried out to determine if there were any differences in canopy depth ratio across tree size classes or species (Data Desk version 4.2; Data Description, Inc.).

Fig. 1. Map of tree stems and canopies along the edge of one of the experimental gaps. Tree stems are represented by circles scaled to stem DBH. Canopies are represented by lines connecting the eight canopy extent measurements into a polygon. Subcanopy trees are denoted by thin-lined polygons, and canopy trees are denoted by thick-lined polygons.



Results

Magnitude of canopy displacement

We found large values of relative canopy displacement among the 140 study trees. Gap edge trees examined in this study had relative canopy displacement values significantly greater than zero (mean 0.36, 95% confidence interval 0.32–0.40), indicating that tree canopies were displaced from their stem bases. With a few exceptions, canopy displacement was largely the result of differential branching rather than leaning of the main stem. For the vast majority of trees (138 of 140), relative canopy displacement was between zero and one, indicating that the canopy was not centered over the stem base but that the stem base was located at some point under the canopy. Two of 140 trees studied had relative canopy displacement values slightly greater than one.

Subcanopy trees had significantly greater relative canopy displacement than canopy trees ($F_{[1,137]} = 5.31, p = 0.023$) (Table 1, Fig. 2). The mean and standard error values of relative canopy displacement were 0.39 ± 0.028 for subcanopy trees and 0.32 ± 0.024 for canopy trees.

Species also differed in relative canopy displacement ($F_{[1,137]} = 2.90, p = 0.005$) (Table 1, Fig. 2). Species means in relative canopy displacement ranged from a low of 0.25 in *F. grandifolia* to a high of 0.53 in *B. papyrifera*. The results of Fisher's LSD post-hoc test are shown in Table 2. Overall, there was a trend of increasing relative canopy displacement with decreasing species tolerance ranking (Baker 1949). More specifically, the intolerant *B. papyrifera* had greater relative canopy displacement than did the highly tolerant *F. grandifolia* and *T. canadensis*. Species with intermediate

Table 1. Multifactor analysis of variance (ANOVA) for the effects of size class and species on relative canopy displacement.

Source	df	MS	F	p
Gap	5	0.009	0.22	0.952
Size class	1	0.224	5.31	0.023
Species	8	0.122	2.90	0.005
Error	123	0.042		

Note: Gap interactions were not included in this ANOVA since the factors gap, gap \times size class, and gap \times species were all nonsignificant. Because some species were restricted to one size class, it was not possible to examine interactions between species and size class.

tolerance rankings had intermediate canopy displacement responses that spanned a wide range. The two coniferous species (*P. strobus* and *T. canadensis*) had low relative canopy displacement values.

Because many of the species examined were restricted to one size class, it was not possible to examine the interaction between species and size class within the multifactor ANOVA. To investigate species variation in canopy displacement across the two size classes, we conducted two additional ANOVAs: one that included only the canopy trees and one that included only the subcanopy trees. Among subcanopy trees, species varied significantly in relative canopy displacement ($F_{[1,72]} = 2.82, p = 0.013$), but among canopy trees species differences were not significant ($F_{[1,64]} = 1.71, p = 0.147$). The fact that we found significant species differences within a single size class demonstrates that the species variation observed in the multifactor ANOVA was not simply due to size variation among species.

Direction of canopy displacement

The direction of canopy displacement was positively correlated with the direction of gap center, suggesting some level of foraging precision among tree canopies. The correlation coefficient for these two parameters was 0.44 ($p < 0.001$).

There was a much stronger positive correlation between the direction of gap center and the direction of canopy displacement for subcanopy trees than for canopy trees (Fig. 3). For canopy trees, there was a weak but significant circular-circular rank correlation between the two parameters ($r = 0.24, p = 0.05$), while for subcanopy trees, the relationship was stronger ($r = 0.61, p < 0.001$). Thus, foraging precision was greater for subcanopy trees than for canopy trees.

Species also differed in foraging precision (Fig. 4). Correlation coefficients for the relationship between the direction of gap center and the direction of canopy displacement ranged from values near 1.0 in *B. papyrifera*, *C. dentata*, and *B. lenta* to values less than 0.3 for *Q. rubra* and *P. strobus*. It was difficult to identify clear trends among species in terms of foraging precision. The four species with the greatest foraging precision (*B. papyrifera*, *C. dentata*, *B. lenta*, and *B. lutea*) were all intolerant or intermediate in tolerance (Baker 1949). None of the very tolerant (*F. grandifolia* and *T. canadensis*) or tolerant (*A. rubrum*) species showed high levels of foraging precision. However, it was two intermediate species (*Q. rubra* and *P. strobus*) that had the lowest foraging precision. Three of the four species with greatest

Table 2. Results of Fisher's least significant difference (LSD) post-hoc test on species differences in relative canopy displacement.

Species pair	Difference	SE	p
<i>F. grandifolia</i> – <i>A. rubrum</i>	-0.15	0.059	0.011
<i>F. grandifolia</i> – <i>Q. rubra</i>	-0.17	0.066	0.011
<i>F. grandifolia</i> – <i>B. lenta</i>	-0.22	0.100	0.027
<i>F. grandifolia</i> – <i>C. dentata</i>	-0.26	0.097	0.009
<i>F. grandifolia</i> – <i>B. papyrifera</i>	-0.37	0.133	0.006
<i>T. canadensis</i> – <i>Q. rubra</i>	-0.20	0.102	0.050
<i>T. canadensis</i> – <i>B. lenta</i>	-0.25	0.121	0.038
<i>T. canadensis</i> – <i>C. dentata</i>	-0.29	0.120	0.019
<i>T. canadensis</i> – <i>B. papyrifera</i>	-0.40	0.158	0.012
<i>P. strobus</i> – <i>B. papyrifera</i>	-0.34	0.166	0.043
<i>B. lutea</i> – <i>C. dentata</i>	-0.23	0.106	0.031
<i>B. lutea</i> – <i>B. papyrifera</i>	-0.35	0.141	0.015

Note: Only species pairs that differed significantly in relative canopy displacement are shown.

foraging precision were birch species. Neither of the coniferous species (*P. strobus* and *T. canadensis*) showed high foraging precision.

Asymmetry in canopy depth

Canopy depth was significantly greater on the gap sides of trees than on the forest sides of trees ($t_{[278]} > 20, p < 0.001$). Canopy depths were 10.5 ± 0.45 m (mean \pm SE) for gap-facing sides of trees and 7.4 ± 0.44 m for forest-facing sides of trees. A multifactor ANOVA revealed no differences in canopy depth ratio among tree size classes or species.

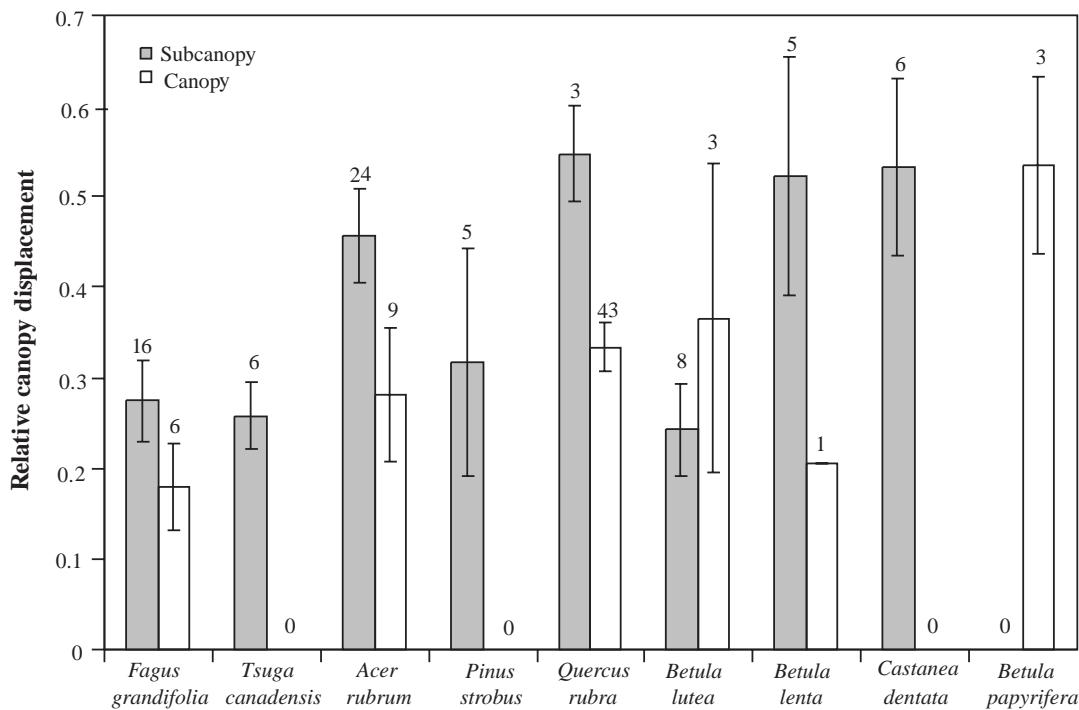
The tops of tree canopies were located at the same height on both the gap-facing and forest-facing sides of trees. The difference in canopy depth on opposite sides of trees was due to the canopy extending lower on the gap-facing sides of trees. In a separate branch demography study, K. Capecelatro and C.C. Muth (unpublished data) found that the lower canopies on the gap-facing sides of these trees resulted from both increased survival of existing branches and increased production of new epicormic branches relative to their forest-facing sides.

Discussion

Canopy displacement and tree light foraging

Plants can actively forage for resources by concentrating resource-acquiring structures in high-resource patches (Schmid 1985; Bazzaz 1991, 1996; Ackerly and Bazzaz 1995). We mapped tree canopies along the edges of forest gaps and found evidence of nonrandom displacement towards the gaps. More specifically, we found that trees growing along gap edges had canopies that were displaced towards gap centers and that were deeper on their gap-facing sides than on their forest-facing sides. Thus, we conclude that trees along gap edges foraged for light by occupying both horizontal and vertical gap space. Our results, based on a unique, replicated system of experimental gaps, strengthen and advance the findings of prior tree canopy displacement research. This small but growing body of work demonstrates that tree canopy displacement is an extremely common phenomenon in a variety of forest ecosystems, including moist tropical forest (Young and Hubbell 1991), seasonally dry

Fig. 2. Relative canopy displacement for the two size classes and nine tree species. Bars are shaded for subcanopy trees and open for canopy trees. Values above each bar are the sample size for each size class within each species. Error bars are 1 SE. Subcanopy trees had significantly greater relative canopy displacement than did canopy trees (ANOVA: $F_{[1,137]} = 5.31, p = 0.023$). Species differed significantly in relative canopy displacement (ANOVA: $F_{[1,137]} = 2.90, p = 0.005$). Species positions along the x axis approximate traditional tolerance classifications (Baker 1949), from very tolerant, later successional species on the left to intolerant, earlier successional species on the right. Because some species were restricted to one size class, it was not possible to examine the interaction between species and size class.



woodland (Holmes 1995), boreal forest (Rouvinen and Kuuluvainen 1997), and temperate deciduous forest (Young 1995; Do-Soo et al. 1999). Furthermore, there is increasing evidence that tree canopy displacement is nonrandom and is directed towards forest gaps (Young and Hubbell 1991) and away from neighboring trees (Young and Hubbell 1991; Holmes 1995; Umeki 1995b; Rouvinen and Kuuluvainen 1997).

Although the correlation between the direction of gap center and the direction of canopy displacement was strong, there was certainly some noise in the relationship. There are several reasons to expect that the direction of canopy displacement would not be perfectly correlated with the direction of gap center. First, the light environment at gap center may not always be the preferred light environment for every tree. The closed forest side of each tree was not uniformly shady and may have contained some high-light microsites. Also, light is inherently asymmetrical in northern temperate latitudes and comes primarily from the south, which differentially affects the timing and duration of direct solar radiation and the amount of diffuse radiation in contrasting parts of the gaps (Sipe 1990; Bazzaz and Wayne 1994; Rouvinen and Kuuluvainen 1997). Second, the structure of tree canopies is likely to reflect both past and present light environments (King 1991; Küppers 1994). The gaps were 13 years old at the time that we measured canopy displacement. While plant growth since gap formation should show a response, this amount of growth would not necessarily mask growth patterns that resulted from prior light environments.

Finally, light is not the only factor that contributes to canopy displacement. Herbivory, branch fall, water stress, wind stress, winter storm damage, belowground processes, physical abrasion by neighbors, and space availability may also affect the positioning and orientation of plant canopies (Givnish 1984; Franco 1986; Young and Hubbell 1991; Küppers 1994). In fact, it is likely that physical abrasion by neighbors on the forest-facing sides of trees and space availability on the gap-facing sides of trees were additional factors that contributed to the strength of the correlation. In crowded forest stands, space to grow and be free from abrasion could perhaps be thought of as a resource itself (sensu McConaughay and Bazzaz 1992).

Despite all the factors that are likely to mask the effect of gap light environment on tree canopy position, we still found a strong relationship between the direction of gap center and the direction of canopy displacement. This relationship provides compelling evidence that the canopy displacement that we observed was not simply due to random growth and survival of branches but was, in large part, active resource foraging by tree canopies towards high-light patches.

Variation in canopy light foraging across tree size classes

Subcanopy trees foraged for light with greater magnitude and precision than did canopy trees. These results support and expand the findings of Young and Hubbell (1991) and Do-Soo et al. (1999), which also demonstrated that smaller trees had greater magnitudes of canopy displacement than

Fig. 3. Direction of gap center versus direction of canopy displacement for the two size classes of trees. Some points were increased by 360° to make circular data trends easier to view along linear axes. For canopy trees, there was a weak but significant circular–circular rank correlation between the two parameters ($r = 0.24$, $p = 0.05$, $n = 65$). For subcanopy trees, there was a stronger circular–circular rank correlation ($r = 0.61$, $p < 0.001$, $n = 75$).

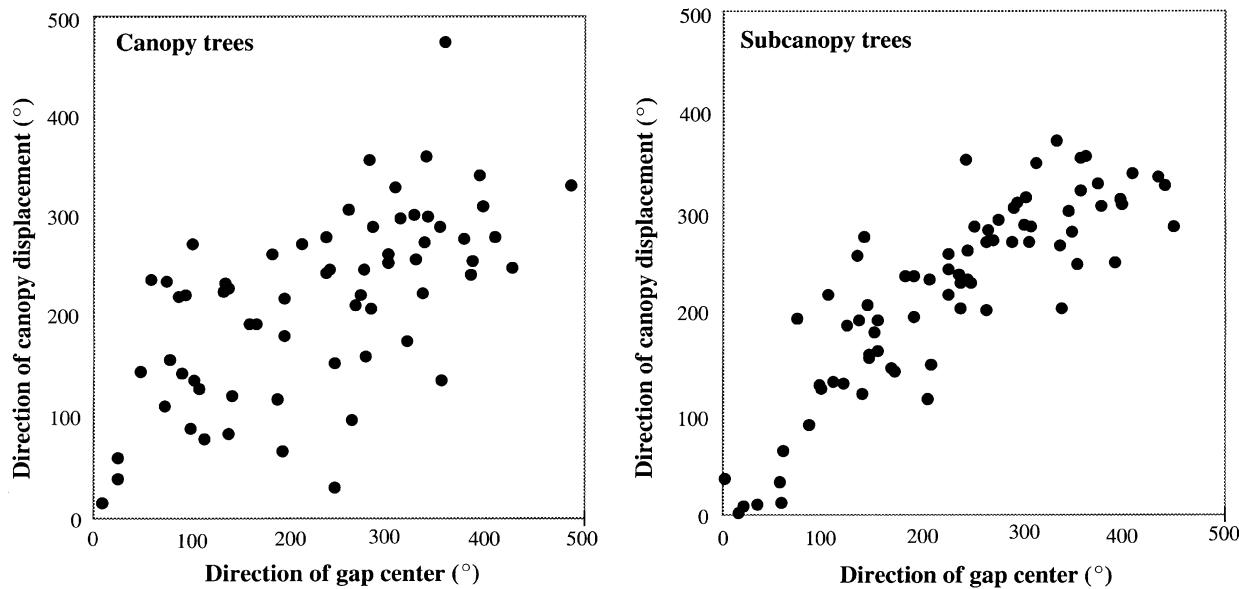
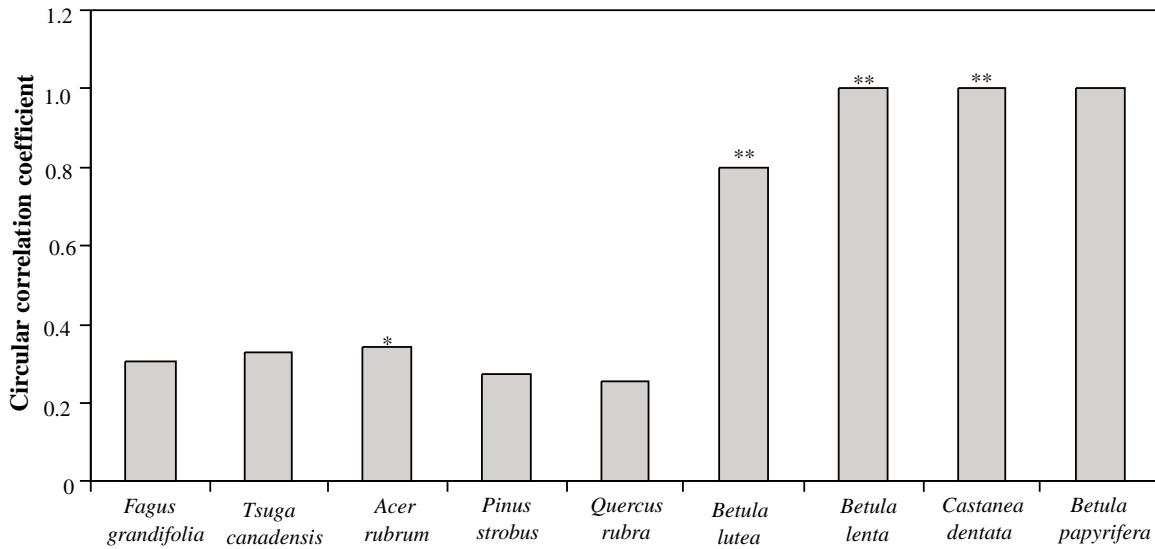


Fig. 4. Circular correlation coefficients for the relationship between the direction of gap center and the direction of canopy displacement for each of the study species. Bars are the correlation coefficients (r), and asterisks show the level of significance of the correlation (**, $p < 0.01$; *, $p < 0.05$). Species positions along the x axis approximate traditional tolerance classifications (Baker 1949), from very tolerant, later successional species on the left to intolerant, earlier successional species on the right.



larger trees. Differences in canopy light foraging across tree size classes are likely due to contrasting light environments, biomechanical constraints, and the portion of growth completed since gap opening. Subcanopy trees were overtapped by neighbors and clearly experienced a great contrast in light environments between their gap-facing and forest-facing sides, while canopy trees were exposed to full sun conditions over most or all of their canopy area. Canopy displacement can lead to increased costs of maintaining mechanical stability, since trees have increased risk of falling on their heavier sides (Young and Hubbell 1991; Young and

Perkocha 1994) or of loosing limbs (Young and Hubbell 1991). Subcanopy trees were generally shorter and lighter than canopy trees, so we can expect that they experienced smaller biomechanical constraints (Küppers 1989). Finally, if subcanopy trees were younger than canopy trees (which may not be the case for late-successional subcanopy trees), then we may expect the subcanopy trees to have greater foraging precision simply because a greater portion of their growth was completed after gap opening. As discussed above, a tree's crown is likely to reflect both past and present environments. For a young tree, the 13 years since gap

formation could make up the majority of its developmental history

Variation in canopy light foraging across tree species

We found species differences in tree canopy displacement. Earlier successional tree species generally had greater relative canopy displacement and thus foraged for light with greater magnitude than did later successional tree species; however, many species were intermediate in their responses. Trends among species in terms of foraging precision were less distinct, but the species with greatest foraging precision were intolerant or intermediate in tolerance. Overall, there appears to be an inverse relationship between tolerance and canopy light foraging. This relationship fits well with the limited data available on species differences in tree canopy displacement (Do-Soo et al. 1999) and with general ideas about differences among early and late successional species (Bazzaz and Wayne 1994; Bazzaz 1996, 1997).

Coniferous trees generally have excurrent growth and rigid architecture, so they might be expected to allow only limited flexibility in growth (Waller 1986; Young and Hubbell 1991). The two coniferous species (*P. strobus* and *T. canadensis*) had small values of relative canopy displacement and low precision of canopy light foraging. Umeki (1995b) similarly found low canopy displacement values for the coniferous *Picea abies* (L.) Karst. (Norway spruce) compared with the hardwood *Betula maximowicziana* Regel. (monarch birch). However, in contrast to our study, Umeki (1995b) concluded that the hardwood and the conifer had similar levels of foraging precision.

In an experiment with eight herbaceous plants of contrasting ecology, Campbell et al. (1991) found a trade-off between the magnitude and precision of resource foraging, such that some species had greater magnitude of foraging, and other species had greater precision of foraging. Our data revealed no such species trade-off. Instead, we found that in most cases, species that had the greatest magnitude of canopy light foraging also had the greatest precision of canopy light foraging. These high foraging species were generally early successional and hardwood species, as opposed to late successional and coniferous species.

The differences in canopy displacement that we observed across species and functional groups are likely due to different survival strategies and mechanical constraints among these groups, as well as the portion of growth completed since gap opening. Utilizing light resources in an adjacent gap is more critical for the survival of intolerant, earlier successional tree species than it is for later successional tree species. Also, fast-growing tree species are likely to have completed a greater portion of their growth since gap opening than slow-growing species (e.g., shade-tolerant trees or conifers). As discussed above, a greater portion of growth completed in the gap-edge environment provides opportunity for increased magnitude and precision of tree canopy light foraging. Finally, fast-growing, earlier successional tree species are generally composed of relatively low density wood (King 1991; Ackerly 1996) and, therefore, have weaker biomechanical constraints than later successional species, making it easier for them to displace their canopies while maintaining structural support. The high magnitude and precision of foraging that we observed for the midsuccessional *C. dentata*

may also be attributed to mechanical considerations. The *C. dentata* individuals measured in our study, like all *C. dentata* in the region, were sprouts of trees that had been exposed to chestnut blight. Thus, these trees likely had substantial root systems to anchor their small (5–10 cm DBH) stems securely, allowing highly displaced canopies with little risk of mechanical failure. The sprouting habit in general may provide increased light foraging capabilities to a variety of species.

Conclusions

Canopy displacement is an important form of plant resource foraging which allows individual plants to capture spatially heterogeneous light resources and avoid neighbors better than if they had fixed morphologies. Here we present evidence that trees along gap edges forage for light both horizontally and vertically by filling three-dimensional gap space. We also demonstrate differences in canopy light foraging abilities among tree species and size classes. Our data suggest that subcanopy, earlier successional, and hardwood trees generally forage for light with greater magnitude and precision than canopy, later successional, and coniferous trees.

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