

Tree canopy displacement and neighborhood interactions

Christine C. Muth and F.A. Bazzaz

Abstract: Competitive interactions among plants are largely determined by spatial proximity. However, despite their sessile nature, plants have the ability to avoid neighbors by growing towards areas with high resource availability and reduced competition. Because of this flexibility, tree canopies are rarely centered directly above their stem bases and are often displaced. We sought to determine how a tree's competitive neighborhood influences its canopy position. In a 0.6-ha temperate forest plot, all trees greater than 10 cm DBH ($n = 225$) were measured for basal area, height, canopy depth, and trunk position. Canopy extent relative to trunk base was determined in eight subcardinal directions, and this information was used to reconstruct canopy size, shape, and position. We found that trees positioned their canopies away from large neighbors, close neighbors, and shade-tolerant neighbors. Neighbor size, expressed as basal area or canopy area, was the best indication of a neighbor's importance in determining target tree canopy position. As neighborhood asymmetry increased, the magnitude of canopy displacement increased, and the precision with which canopies avoided neighbors increased. Flexibility in canopy shape and position appears to reduce competition between neighbors, thereby influencing forest community dynamics.

Résumé : La réaction des plantes face à la compétition est largement déterminée par la proximité spatiale. Cependant, malgré leur nature sessile, les plantes ont la capacité d'éviter les voisins en se développant vers les zones où la disponibilité des ressources est plus grande et ainsi de réduire la compétition. À cause de cette flexibilité, la cime des arbres est rarement centrée directement au-dessus de la base du tronc et souvent excentrique. Nous avons entrepris de déterminer comment la compétition avoisinante d'un arbre influence la position de sa cime. Dans une parcelle de forêt tempérée de 0,6 ha, la surface terrière, la hauteur, la hauteur de cime et la position du tronc de tous les arbres plus gros que 10 cm au DHP ($n = 225$) ont été mesurées. L'étendue de la cime relativement à la base du tronc a été déterminée dans huit directions correspondant à la rose des vents et cette information a été utilisée pour reconstruire la dimension, la forme et la position de la cime. Nous avons observé que les arbres disposent leur cime de manière à éviter les voisins de grande dimension, les voisins les plus près et les voisins tolérants à l'ombre. La dimension d'un voisin exprimée en surface terrière ou en surface de cime est le meilleur indicateur de l'importance de ce voisin dans la détermination de la position que recherche un arbre pour sa cime. À mesure que l'asymétrie du voisinage s'accroît, l'ampleur du déplacement des cimes et la précision avec laquelle elles évitent les voisins augmentent. La flexibilité dans la forme et la position de la cime semble réduire la compétition entre les voisins, influençant ainsi la dynamique de la communauté forestière.

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Introduction

Because plants are sessile organisms, an individual's position plays a critical role in setting up competitive interactions and determining resource availability. Plants are, however, able to control the location of particular modules by altering patterns of allocation and growth (Bazzaz 1991, 1996, 1997). Plants have the ability to forage for resources and avoid neighbors by growing towards areas with high resource availability and reduced competition (Franco 1986; Brisson and Reynolds 1997; Stoll and Schmid 1998). In for-

ested ecosystems, light is a critical and often limiting resource (Wales 1972; Hutchinson and Matt 1977; Pacala et al. 1996). Forest light environments are highly heterogeneous, so light may be disproportionately available to different regions within an individual plant canopy (Baldocchi and Collineau 1994). If well-lit regions of a canopy grow vigorously and poorly lit regions grow slowly, then the resulting canopy will be displaced towards the side with more light (Bazzaz 1984; Canham 1988; Young and Hubbell 1991; Ackerly and Bazzaz 1995; Muth and Bazzaz 2002). Because of this flexibility, tree canopies are rarely positioned directly above their stem bases. Canopy displacement is likely to have important consequences for light interception of individual plants and for competitive interactions between neighbors (Franco 1986; Ackerly and Bazzaz 1995; Umeki 1995a).

Plant canopies not only take up resources, but also influence the amount of resources available to neighbors (Tremmel and Bazzaz 1995; Canham et al. 1994). In forests, neighboring trees are the primary determinants of local light availability (Harper 1977). Previous work has shown that trees

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C.C. Muth^{1,2} and F.A. Bazzaz. Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, U.S.A.

¹Corresponding author (e-mail: cmuth@email.unc.edu).

²Present address: Department of Botany, University of North Carolina, Chapel Hill, NC 27599-3280, U.S.A.

position their canopies away from neighbors (Young and Hubbell 1991; Holmes 1995; Umeki 1995*b*; Brisson 2001; Muth and Bazzaz 2002). It seems likely that neighbor size and distance help determine how strongly a neighbor affects target tree canopy position (Brisson 2001). However, most studies of canopy displacement have failed to clearly establish a relationship between target tree canopy displacement and neighbor size and distance (Holmes 1995; Rouvinen and Kuuluvainen 1997) or have not directly investigated this relationship (Young and Hubbell 1991; Muth and Bazzaz 2002). Neighbor identity has been shown to affect target plant performance in some herbaceous communities (Barnes et al. 1990; Tremmel and Bazzaz 1993) and may play a role in forest neighborhood interactions as well. For example, Canham et al. (1994) found a strong relationship between the shade tolerance of a tree and its light-extinction characteristics, such that shade-tolerant species have denser foliage and thus cast significantly deeper shade than intolerant species. Thus, from a resource-based perspective, one might expect trees to preferentially grow away from more shade tolerant neighbors. The influence of neighbor distance, size, and identity on canopy displacement has yet to be adequately explored among trees, even though the positioning of tree canopies largely determines their ability to successfully forage for light.

A target tree's competitive neighborhood has traditionally been characterized in terms of the total magnitude of competitive pressure (e.g., Weiner 1982; Pacala and Silander 1985). The same neighborhood can also be characterized in terms of the spatial distribution, or symmetry, of competitive pressure (Brisson and Reynolds 1994; Brisson 2001). A target tree's neighborhood may be asymmetrical because the neighbors are clumped to one side or because one neighbor is particularly important (i.e., has a disproportionately strong impact on the target tree). For trees in highly asymmetrical neighborhoods, canopy displacement may provide an effective means of reducing competition. Thus, we might expect trees in highly asymmetrical neighborhoods to show stronger canopy displacement away from neighbors than trees from more symmetrical neighborhoods.

We conducted a descriptive field study in which tree canopies were mapped, and parameters of tree canopy displacement and neighborhood interactions were examined. Our objective was to determine how a tree's competitive neighborhood influences its canopy position. More specifically, we asked the following questions. (i) Do trees position their canopies away from neighbors? (ii) What is the relative importance of neighbor distance, size, and identity in influencing tree canopy position? (iii) Do more asymmetrical neighborhoods lead to larger canopy displacement responses? (iv) Do more asymmetrical neighborhoods lead to more precise canopy displacement responses?

Materials and methods

Study site and species

The study was conducted in a 50 × 120 m permanent plot 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 research plot was located on a north-facing 7° slope, which likely provided some protection from the hurricane that devastated this area in 1938 (Foster and Boose 1992). According to Harvard Forest records, this stand experienced moderate (11–25%) damage in the hurricane (Harvard Forest Archives, Petersham, Mass.). Pit and mound topography and the presence of large boulders suggest that the study area was never plowed and may have remained in forest continuously. The study site included a variety of hardwood species, the most common of which were *Acer rubrum* L. (red maple), *Acer saccharum* Marsh. (sugar maple), *Betula lenta* L. (black birch), *Betula lutea* Michx. f. (yellow birch), *Betula papyrifera* Marsh. (paper birch), *Fraxinus americana* L. (white ash), and *Quercus rubra* L. (northern red oak).

Field methods

Tree stems in the study plot were previously mapped using the methods of Canham et al. (1998) (George 1996; Harvard Forest Archives, Petersham, Mass.). All trees greater than 10 cm diameter at breast height (DBH) were relocated, measured for height, DBH, and canopy depth, and identified to species. A clinometer was used to measure canopy depth (the height of the top of the canopy minus the height of the bottom of the canopy). A total of 225 trees were measured.

Canopy extent relative to trunk base was determined in eight directions around each tree (Young and Hubbell 1991; Muth and Bazzaz 2002). Measuring 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, up to eight measurements of canopy extent were recorded along with corresponding subcardinal directions. For highly displaced leaning trees, the canopy was entirely absent in some directions. In such cases, fewer than eight canopy extent measurements were recorded. The canopy extent measurements were conducted in July 1997 and June 1998.

Data analysis

Canopy extent measurements were used to reconstruct canopy size, shape, and position relative to trunk base. To adjust for the 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. A map of all stem bases and their corresponding canopies was created, and tree canopies were plotted by connecting the canopy edge points of each tree into a polygon (ArcView version 3.2a, Environmental Systems Research Institute, Inc., Redlands, Calif.) (Fig. 1).

Canopy area was calculated for each tree by dividing the canopy into eight pie-shaped sections, each one centered on a subcardinal direction. We then estimated the area of each section by assuming that the canopy radius at the subcardinal direction was equal to the radius throughout that section. The area of a given section was defined as $(\pi r^2)/8$, where π was equal to 3.1416, and r was equal to the canopy extent measurement for that subcardinal direction. To determine the total canopy area of a given tree, we added up the areas of the eight sections.

Fig. 1. Map of stems and canopies of all trees greater than 10 cm DBH in the 0.6-ha study plot. Tree stems are represented by dots. Canopies are represented by lines connecting canopy edge points into polygons. Polygons for subcanopy trees (trees with less than 50% of their canopies exposed to full sun conditions) are drawn with broken lines, and polygons for canopy trees (trees with at least 50% of their canopies exposed to full sun) are drawn with solid lines.



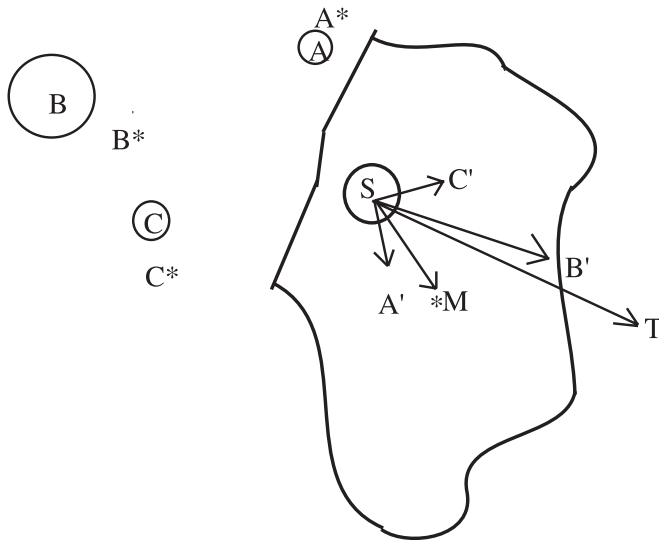
Canopy center of mass was calculated based on the eight canopy edge points of each tree (Batschelet 1981). The magnitude and direction of canopy displacement were defined as the length and direction of the vector pointing from stem base to canopy center of mass (Franco 1986; Brisson and Reynolds 1994; Rouvinen and Kuuluvainen 1997; Umeki 1995a, 1995b, 1997; Brisson 2001; Muth and Bazzaz 2002). 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 centered directly above its stem base. For a canopy the shape of a regular polygon, 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.

To characterize a tree's competitive neighborhood, we defined a parameter for each target tree called the vector of neighborhood asymmetry (Brisson and Reynolds 1994; Brisson 2001) (Fig. 2). We defined the outer 8 m of the plot as a border region where trees were used as neighbors only, and not as targets. Of the 225 trees measured, 129 were analyzed as target trees. For each target tree, we identified all neighbors with their canopy center of mass within 8 m of the

target tree's stem base and with a height greater than or equal to (± 2 m) the target tree's height. By requiring that neighbors be as tall or taller than the target tree (± 2 m), we explicitly assumed that competition was asymmetric. This assumption seems reasonable because competition for light appears to play a particularly strong role in forest ecosystems. For each neighbor, we created a vector with origin at the target tree's stem base, direction equal to the direction from the neighbor canopy center of mass to the target stem base, and length equal to an importance value (Brisson and Reynolds 1994; Brisson 2001). We then summed all the neighbor vectors to produce a vector representing the integrated neighborhood asymmetry. Canopy center of mass was used as a measure of neighbor location because it is a neighbor's canopy, rather than its stem, that is largely responsible for modifying local light environments (Umeki 1995b). We used six importance values related to neighbor distance (distance⁻²), size (basal area, canopy area, height, canopy depth), and identity (species tolerance ranking). For species tolerance rankings, we assigned importance values of one through five based on the five tolerance classifications in Baker (1949). These rankings are based on assessment of a species' ability to survive and grow in a forest understory. An importance value of five corresponded to Baker's "very tolerant" category, and an importance value of one corresponded to Baker's "very intolerant" category.

Neighborhood asymmetry is unlike traditional competition indices (e.g., Weiner 1982; Pacala and Silander 1985), because it reflects the spatial distribution of neighborhood

Fig. 2. Calculation of the vector of neighborhood asymmetry. For each target tree, we identified all neighbors within 8 m of the target tree's stem base and with a height greater than or equal to (± 2 m) the target tree's height. Here, S represents the target tree's stem base, and A, B, and C represent neighbor stem bases. M* represents the target tree's canopy center of mass, and A*, B*, and C* represent neighbor canopy centers of mass. For each neighbor surrounding each target tree, we created a vector with origin at the target tree's stem base, direction equal to the direction from neighbor canopy center of mass to target stem, and distance equal to an importance value (e.g., basal area). Here, the vectors for neighbors A, B, and C are SA', SB', and SC', respectively. We then added all the neighbor vectors to get the vector of neighborhood asymmetry (ST).



competitive pressure, rather than the total amount of neighborhood competitive pressure (Brisson and Reynolds 1994; Brisson 2001). The length of the vector of neighborhood asymmetry represents the magnitude of neighborhood asymmetry, with higher values occurring where neighbors are clumped primarily in one direction, and lower values occurring where neighbors are distributed fairly evenly around the target plant in spatial arrangement and importance. The direction of the vector of neighborhood asymmetry represents the direction towards which neighbors are “pushing” the target plant. If a target plant is growing directly away from the area of greatest neighbor pressure, then its direction of canopy displacement will exactly match the direction of neighborhood asymmetry.

To characterize how well these two directions corresponded, we calculated the difference in degrees between the direction of canopy displacement and the direction of neighborhood asymmetry. We refer to this new parameter as “canopy deviation from optimal”. Values can range from 0° to 180° , with higher values representing greater deviation of the direction of canopy displacement from the direction of neighborhood asymmetry. A value of 0° represents the situation where a target tree's canopy is positioned directly away from greatest neighbor pressure and thus suggests high foraging precision.

Statistical analysis

To determine if trees position their canopies away from

neighbors, we examined correlations between the direction of neighborhood asymmetry and the direction of canopy displacement. A strong positive correlation between these two parameters was used as an indication that tree canopies were foraging away from the area of greatest competitive pressure and thus demonstrated high foraging precision. We conducted seven such correlations, one for each of the six importance values and one with equal weighting of each neighbor (i.e., each neighbor was given an importance value of one). By comparing correlations calculated with different importance values, we examined the relative importance of neighbor distance, size, and identity in determining tree canopy position. Because data were directional and not uniformly distributed, these correlations were investigated using circular-circular rank correlation tests (Batschelet 1981).

To examine the influence of the magnitude of neighborhood asymmetry on the magnitude of canopy displacement, we regressed relative canopy displacement against neighborhood asymmetry (Data Desk version 4.2, Data Description, Inc., Ithaca, N.Y.). A positive relationship between these parameters would indicate that more asymmetrical neighborhoods lead to stronger canopy displacement responses.

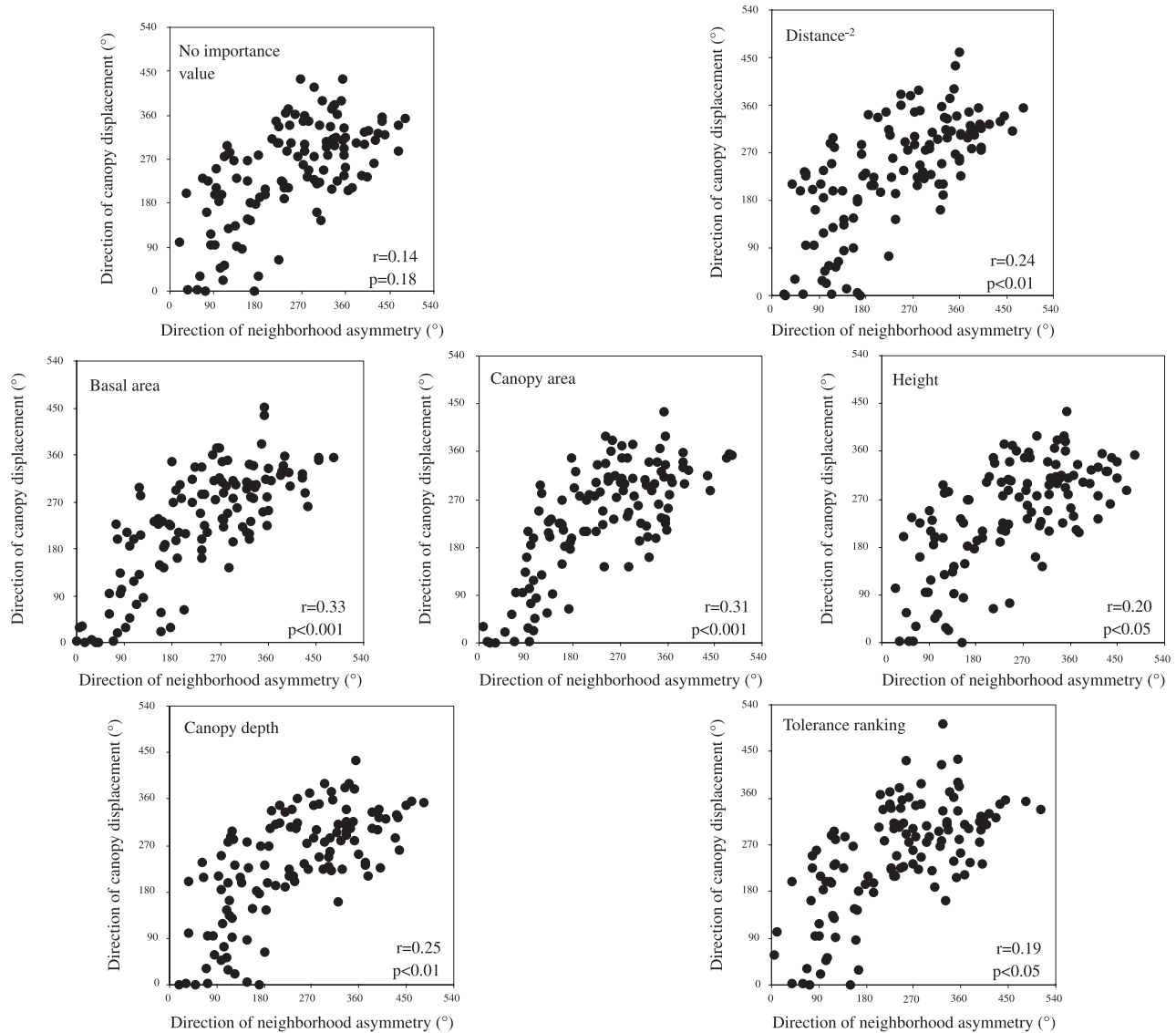
Finally, we wished to determine how neighborhood asymmetry affected the precision of canopy displacement. We predicted that in more asymmetrical neighborhoods, canopy deviation from optimal (i.e., the difference between the direction of neighborhood asymmetry and the direction of target tree canopy displacement) would be reduced. We tested this prediction by regressing canopy deviation from optimal against neighborhood asymmetry (Data Desk version 4.2, Data Description, Inc., Ithaca, N.Y.). A regression with a negative slope, with canopy deviation from optimal decreasing as neighborhood asymmetry increased, would support our prediction.

Of the 129 target trees, 9 were mature trees that had no neighbors of comparable height within the required distance of 8 m. These trees had neighborhood asymmetry values of zero, reflecting the even levels of competitive pressure on all sides, and they were used in the regression between relative canopy displacement and neighborhood asymmetry. However, it was impossible to assign these nine trees values for the direction of neighborhood asymmetry or canopy deviation from optimal. Thus, these trees were excluded from correlations between the direction of neighborhood asymmetry and the direction of canopy displacement and from the regression between the magnitude of neighborhood asymmetry and canopy deviation from optimal. Therefore, we had a sample size of 120 target trees for these analyses.

Results

We found large values of relative canopy displacement among the 225 study trees. Trees examined in this study had relative canopy displacement values significantly greater than zero (mean 0.35; 95% confidence interval 0.32–0.38), indicating that tree canopies were displaced from their stem bases. All of the study trees had relative canopy displacement values 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 beneath the canopy. These

Fig. 3. The direction of neighborhood asymmetry versus the direction of canopy displacement for each of the importance values. Each point represents one target tree. Some points were increased by 360° to make circular data trends easier to view along linear axes. Correlation coefficients and p values displayed are based on circular–circular rank correlation tests (Batschelet 1981).



values of relative canopy displacement are almost identical to values obtained for trees along 13-year-old gap edges in a similar forest type at Harvard Forest (mean 0.36; 95% confidence interval 0.32–0.40) (Muth and Bazzaz 2002).

Morphologically, a plant can respond to spatial variation in light availability either through differential growth and survival of individual branches and leaves or through leaning of the main stem (Bazzaz 1984; Young and Hubbell 1991). In the majority of cases, we found that canopy displacement was the result of differential branching rather than stem leaning. However, there were 11 trees in the stand that had stems leaning more than 10° from the vertical. *Betula papyrifera* had a strong tendency to lean (6 of 10 trees had leaning stems), and this tendency likely contributed to the large relative canopy displacement values for this species (mean 0.50; 95% confidence interval 0.39–0.61).

The mean direction of canopy displacement for all trees in the stand ($n = 225$) was 281° (Batschelet 1981). It is noteworthy that in contrast to the observations of other authors

(Koike 1985; Umeki 1995b, 1995c), the mean direction of canopy displacement did not correspond to the direction of the slope. Perhaps the 7° slope was not large enough to strongly influence the direction of canopy displacement. Also, the north-facing slope in our stand likely provides less pronounced light gradients than would a south-facing slope.

Tree canopies were displaced away from their neighbors. All of the correlations between the direction of neighborhood asymmetry and the direction of canopy displacement were positive, and six of the seven correlations were statistically significant (Fig. 3). The correlation in which all neighbors were weighted equally had a correlation coefficient of 0.14 and was the only correlation that was not statistically significant ($p = 0.18$). Correlations based on all six neighbor importance values were stronger than the correlation in which neighbors were weighted equally. Two importance values based on neighbor size produced the strongest correlations: basal area ($r = 0.33$, $p < 0.001$) and canopy area ($r = 0.31$, $p < 0.001$). Intermediate correlation coefficients were

obtained when canopy depth ($r = 0.25$, $p < 0.01$) and neighbor distance⁻² ($r = 0.24$, $p < 0.01$) were used as importance values. The lowest correlation coefficients were obtained for the importance values height ($r = 0.20$, $p < 0.05$) and species tolerance ranking ($r = 0.19$, $p < 0.05$). In representing these correlations graphically, some points were increased by 360° to make circular data trends easier to view along linear axes. By adding 360° to some points, we corrected for differences greater than 180°, which with circular units are actually less than 180° in the other direction.

To verify that there was no relationship between neighbor tolerance ranking and neighbor canopy area, we conducted a Pearson's correlation test and found no correlation between these parameters ($r = -0.05$, $p = 0.46$). This lack of correlation suggests that target trees displace their canopies away from shade-tolerant neighbors, not because of any relationship between tree size and shade tolerance, but because of the denser foliage of shade-tolerant trees (Canham et al. 1994).

There was a weak positive relationship between neighborhood asymmetry and relative canopy displacement ($R^2 = 0.072$, $p = 0.002$) (Fig. 4). In other words, trees in neighborhoods with high asymmetry generally had increased relative canopy displacement compared with trees in more symmetrical neighborhoods. The regression model for these parameters was $y = 0.06x + 0.27$, where x is neighborhood asymmetry, and y is relative canopy displacement.

More asymmetrical neighborhoods generally lead to increased precision of target tree canopy displacement away from neighbors (i.e., decreased canopy deviation from optimal). There was a weak negative relationship between neighborhood asymmetry and canopy deviation from optimal ($R^2 = 0.033$, $p = 0.048$) (Fig. 5). The regression model for these parameters was $y = -12.31x + 94.17$, where x is neighborhood asymmetry, and y is canopy deviation from optimal.

Discussion

Patterns of tree canopy displacement

We found clear evidence of tree canopy displacement away from neighbors. The direction of neighborhood asymmetry was positively correlated with the direction of canopy displacement across all neighbor importance values. These results add to a growing body of work suggesting that tree canopy displacement is a common means of neighbor avoidance across a range of forest types (Young and Hubbell 1991; Holmes 1995; Brisson 2001; Muth and Bazzaz 2002).

Each of the neighbor importance values that we examined provided information that strengthened the relationship between the direction of neighborhood asymmetry and the direction of canopy displacement. All of the correlations based on neighbor importance values were statistically significant and were stronger than the correlation in which neighbors were weighted equally. The two importance values that produced the strongest correlations, basal area and canopy area, characterize a neighbor's overall size. Basal area and canopy area are closely related allometrically and functionally, so it is not surprising that these importance values produced similar results. Our definition of a neighbor included height and distance requirements, and this may have decreased the rela-

Fig. 4. The relationship between the magnitude of neighborhood asymmetry and relative canopy displacement. Each point represents one target tree. Details of the fitted regression are given.

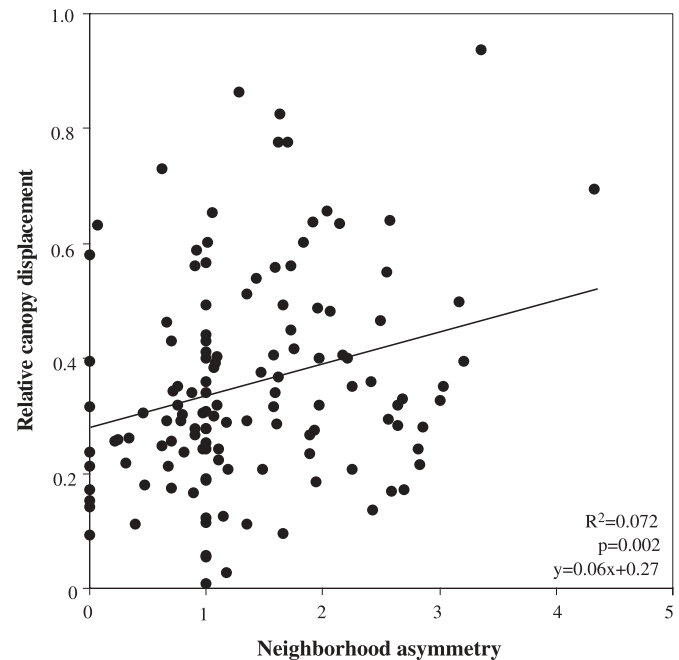
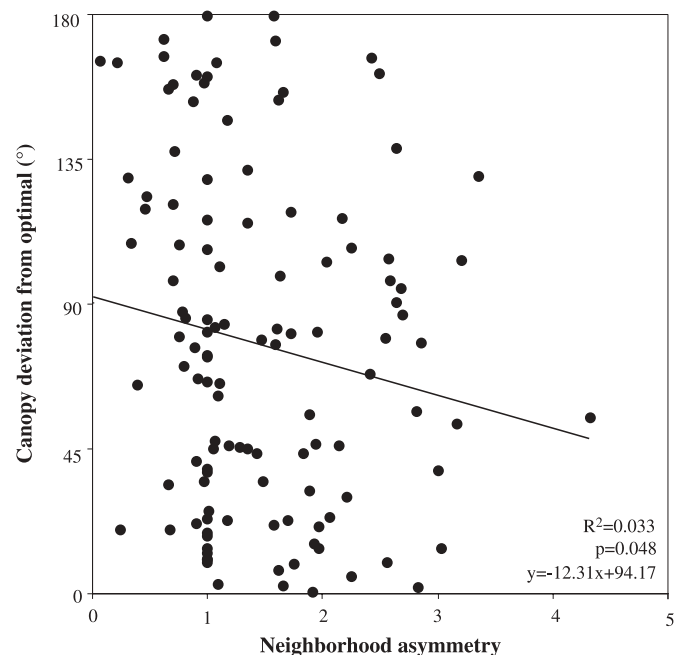


Fig. 5. The relationship between the magnitude of neighborhood asymmetry and canopy deviation from optimal. Each point represents one target tree. Details of the fitted regression are given.



tive strength of correlations based on the height and distance importance values. Overall, neighbor size, expressed as basal area or canopy area, was the best indication of a neighbor's importance in determining canopy position. However, tree canopies were displaced away from close neighbors and shade-tolerant neighbors, in addition to large neighbors. This was likely because close neighbors, shade-tolerant neigh-

bors, and large neighbors decreased local light availability more than distant neighbors, shade-intolerant neighbors, and small neighbors.

As neighborhood asymmetry increased, the magnitude of canopy displacement increased, and the precision with which canopies avoided neighbors increased (i.e., canopy deviation from optimal decreased). Brisson (2001) found a similar increase in the canopy displacement of *A. saccharum* as neighborhood asymmetry increased. For trees in highly asymmetrical neighborhoods, canopy displacement may be a successful way to avoid competition and increase access to resources. In contrast, trees in highly symmetrical neighborhoods have equal levels of competitive pressure coming from all directions, so canopy displacement offers such trees no clear benefits. Furthermore, canopy displacement appears to have potential costs, such as increased risk of mechanical failure (Young and Hubbell 1991; Young and Perkocho 1994) and decreased vascular efficiency due to reaction wood formation (Spicer and Gartner 1998). In fact, just 1 year after being measured and mapped for this study, one of the most highly displaced trees in the stand (relative canopy displacement = 0.88) fell on its displaced side, illustrating the likely biomechanical risk associated with strong canopy displacement. In asymmetrical neighborhoods, the costs of canopy displacement may be outweighed by increased resource availability. However, in more symmetrical neighborhoods, potential costs could further reduce the likelihood of strong canopy displacement responses.

We predicted that tree canopies would be displaced away from neighbors and that as neighborhood asymmetry increased, the magnitude and precision of canopy displacement would increase, and we found our predictions to be correct. There was, however, a large amount of scatter among our correlations and regressions, and this scatter was likely due to a number of factors. For example, the competitive neighborhood around a tree changes over time, and a tree's canopy structure is likely to reflect its development in both past and present neighborhoods (King 1994; Küppers 1994). In addition to neighbors, slope and aspect may play an important role in determining patterns of light availability for target trees, particularly in extreme northern and southern latitudes and on steep slopes (Rouvinen and Kuuluvainen 1997). Furthermore, canopy displacement is not always related to light availability. Other causes of tree canopy displacement include wind stress, water stress, winter storm damage, falling woody debris, and herbivory (Givnish 1984; Franco 1986; Young and Hubbell 1991; Küppers 1994). The fact that we found clear evidence of tree canopy displacement away from neighbors despite these other factors strongly suggests that the canopy displacement was due, in large part, to a combination of (i) decreased canopy growth and survival in areas of strong competitive pressure and (ii) increased canopy growth and survival in areas of weak competitive pressure (i.e., active resource foraging).

Tree canopy displacement and neighborhood interactions

The intensity of plant competition depends upon spatial relations between a target plant and its neighbors, the effects of neighbors on resource availability, and the ability of the target plant to compensate for neighbor effects through response flexibility (Tremmel and Bazzaz 1993). Canopy dis-

placement is a kind of response flexibility that both responds to and alters resource availability and spatial relations between neighbors. Consideration of canopy displacement is critical to a thorough understanding of competitive interactions among neighbors.

We have shown that target trees respond to the positioning and importance of neighbors and to the overall symmetry of their neighborhoods. Target trees in our study consistently had canopies that were displaced away from areas of greatest competitive pressure. It is important to remember that each neighbor also responds, in turn, to its neighbors in a dynamic and ongoing process. Thus, as the canopy of a target tree becomes displaced away from its neighbors, its neighbors' canopies may also become displaced away from the target. Alternatively, neighbors may respond by capturing any space that becomes available as the target's canopy changes position. The kinds of trees that are most avoided (e.g., trees with large basal area, shade-tolerant trees) will have less competitive pressure and more space available, and thus less need to be highly displaced. In fact, these types of trees tend to have low tree canopy displacement. In another study at Harvard Forest (Muth and Bazzaz 2002), we found that large trees and shade-tolerant trees had weaker tree canopy displacement responses to asymmetrical light environments than did small trees and shade-intolerant trees. Larger and more shade tolerant trees may demonstrate smaller canopy displacement responses owing to a combination of decreased competitive pressure and decreased response flexibility.

Competitive pressure and resulting tree canopy displacement responses may lead to more regular spacing of tree canopies than of tree stems. In experiments conducted on fast growing annuals, plant canopies were spaced regularly even though stem bases were not (Franco 1986; Umeki 1995a), providing evidence that flexibility in canopy shape reduces competition between individuals. If tree canopies in forest communities are positioned more regularly than their stem bases, then tree canopy displacement directing individuals away from their neighbors and towards gaps may actually increase stand level light interception and productivity and decrease light availability and heterogeneity in the understory more than would be expected based on stem positions. Thus, tree canopy displacement may have implications not just for individual plant success and neighborhood competitive interactions, but also for ecosystem pattern and process.

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