ADAPTATION OF TREES TO LOW-LIGHT ENVIRONMENTS: EFFECT ON BRANCHING PATTERN OF FRAXINUS AMERICANA

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Abstract. Newly planted trees are often moved from the full sun environment of the nursery to shady locations around buildings or in urban canyons. Trees must adapt in order to survive. An adaptive strategy for trees exposed to changing irradiance levels in forest settings is the ability to change branching habit to maximize whole tree photosynthesis. The genetic ability to alter branching habit has potential adaptive value for survival in the low-light environment found in many urban landscapes. The ability to alter branching habit when growing in shady versed bright habitats was tested on *Fraxinus americana* (white ash) trees by measuring branching habit, as expressed by bifurcation ratio, on native stands of trees growing in a sunny old-field habitat and an adjacent shady understory habitat. Bifurcation ratios were similar for trees growing in both habitats, indicating an inability of white ash to change basic branching pattern when exposed to different irradiance environments. Other possible adaptive mechanisms and implications for planting in shady environments are discussed.

The urban landscape can be hostile to tree growth in many ways. The above ground environment to which we subject our street trees in many cities can more closely resemble a desert than the nearby forest. This is because the increased heat load from reflected and reradiated solar radiation combined with an accompanying lower relative humidity creates very high transpirational demands. The resulting stresses are severe, and tree water deficits occur even when soil supplied moisture is adequate (12,13). Planting trees in shady urban sites, however, can also impose severe stress. Certain downtown environments are known as urban canyons because the shade patterns cast by buildings are somewhat analogous to the shade cast by canyon walls. Kjelgren and Clark (4) found that some urban canyons receive only about 20% of total seasonal potential irradiance. The amount of irradiance can be extremely site specific, with one site being in full sun and another in total shade only a few feet away (Fig.1). Many other landscape settings are shady because buildings and existing trees block the sun. Trees that cannot acclimate to such low irradiance levels may not have sufficient root growth or overall vigor for survival. Knowledge of long term tree response to low irradiance will aid the landscape designer in making intelligent plant selection decisions.

Tree species have evolved many strategies to cope with irradiance changes naturally occurring in forests, such as canopy closure and gap openings. They differ in ability to tolerate shading since diverse strategies are needed for exploitation of different niches in the forest ecosystem. (10). Although there are distinct differences between the irradiance patterns of the forest understory and the city street (3), the adaptive strategies utilized by trees in forests are also required when they are planted in our cities.

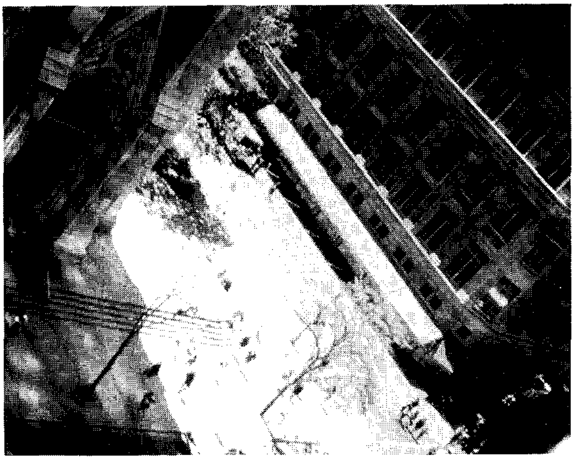

Figure 1. Shade patterns can vary drastically over short distances. The tree on the left is in dense shade and is dying. The tree on the right is in full sun and is thriving.

The arrangement of leaves within a canopy is one way in which plants maximize the efficiency of photosynthesis under differing light regimes (2). This is evident in the branching habits of plants that have evolved in shade (shade plants) and sun environments (sun plants) (14). A shade plant often maximizes irradiance in a low light environment by holding its branches in a somewhat flat plane parallel to the earth, approaching a monolayer. Leaf shape and branching habit may also differ within the canopy of a single tree because of the extinction of irradiance in the lower parts of the canopy (2). These structural responses to low irradiance levels are in a large part due to differences in spectral quality. Shady areas are enriched in far red light compared to red. Typical responses to low irradiation are increased stem extension rates and loss of apical dominance (6).

Leopold (5) and Oohata and Shidei (7) applied a method of quantifying branching habit for streams to the branching habit of trees. The adaptive ability to alter branching habit appears to differ among species. For example, the branching habit of *Quercus phillyraeoides* was insensitive to light levels (7), but *Acer saccharum* (11), *Cornus florida* and *Acer rubrum* (8) expressed different branching habit in high-light verses low light environments. For example, the bifurcation ratio of forest-grown *Acer saccharum* was 3.19, whereas the ratio for open-grown trees was 7.05 (11).

The purpose of this study was to compare the effect of a shady forest understory habitat and that of a sunny old field (formerly agricultural land undergoing natural reforestation) on the branching habit of *Fraxinus americana* (white ash). The forest-field habitat comparison was chosen because tree populations could be statistically sampled and because the contrast was a good model for testing the adaptive potential for branching habit modification of white ash. The potential for change in branching habit may be masked in a newly planted tree which is suddenly exposed to heavy shade, because the tree may not be able to express that potential before succumbing to reduced photosynthesis and other post-transplant stresses. Once the potential for change in branching habit is established, further studies in the urban environment should be undertaken to test whether it is expressed. Specific questions considered in this study were 1) Is branching habit as defined by bifurcation ratio species or habitat dependent? and: 2) What other effects of habitat are apparent?

Materials and Methods

Ten replicates of trees 2-3 m (6 - 10 ft) in height from each of two populations of white ash were sampled. One population consisted of trees growing as understory plants in a dense forest on the edge of an old field, and the other consisted of trees growing in full sun in the adjacent old field. Canopy trees above the sampled understory trees were almost exclusively white ash, affording a relatively homogeneous dense shade to the plants below, whereas trees in the oldfield habitat were exposed to unobstructed irradiance. The canopy trees were apparently the seed source for the field-grown trees as well as the understory trees. The field was farmed approximately 16 years before, as determined by the age of pioneer trees. Samples were taken along two transects deliberately placed in areas of relatively dense populations of target trees on 12 October, 1990 near the town of Dryden, N.Y. Samples were taken by randomly picking a distance from the beginning of the transect, a side (left or right) from the center and a distance from the center of the transect with a random number table. A replicate was then chosen as the nearest tree within the desired height range. Samples were harvested and the bifurcation ratio was determined for each entire tree, as explained by Picket and Kemp (8). The bifurcation ratio is a ratio of distal branches (number in all branch orders minus the number in the most proximal order) to proximal branches (number in all branch orders minus the number in the most distal) (See Fig. 2).

Height, trunk diameter 5 cm above the soil line and length of each branch were measured. Age of each replicate was determined by sanding a cross section of the trunk and counting the annual growth rings. All branches of each bifurcation order of each tree were dried to a constant weight at 70°C and the weights subsequently recorded.

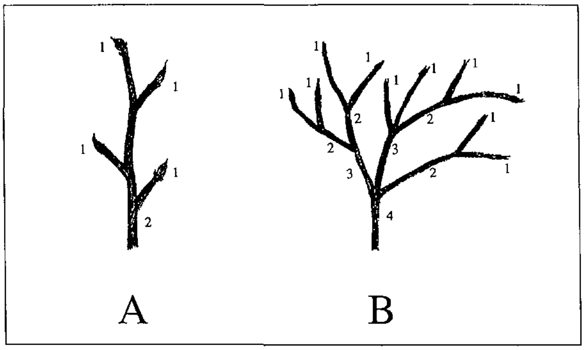

Figure 2. Method of branch ordering and calculation of bifurcation ratio used for *Fraxinus americana* trees from a forest and an oldfield habitat. A represents a plant well-adapted for sunny conditions, such *Liquidambar styraciflua*. Bifurcation ratio = [(4+1)-1]÷[(4+1)-3] = 4.0. B represents a tree well-adapted for shady conditions, such a *Cornus florida*. Bifurcation ratio = [(10+4+2+1)-1]÷[(10+4+2+1)-10] = 2.3.

Results and Discussion

First order (distal) branches of forest-grown trees weighed less ($P < 0.003$), and were fewer in number ($p < 0.004$) than those of field-grown trees, but there was no differences in total first order branch length between trees from each habitat (Table 1). Forest-grown trees also had less total branch dry weight than field-grown trees ($p < 0.0009$), but there was no difference in total length of all branches between habitats. Bifurcation ratios were similar for both populations. Total branch length was constant between trees from the contrasting habitats. Forest-grown trees had smaller trunk diameter ($p < 0.007$) and were younger ($p < 0.006$) than field-grown trees.

The most obvious environmental difference between the forest habitat and the field habitat was the difference in the amount of solar radiation incident on plant leaves. There was likely severe below-ground competition in both habitats, as the forest was heavily populated with canopy trees, and the field was heavily populated with herbaceous species. *Fraxinus americana* has been characterized as a mid-successional (occurs midway in the time line between habitat disturbance and climax vegetation) species, and it is well-adapted to the exploitation of sunny environments (2). As such, it might be expected to express a limited ability to change (plasticity) architectural habit when growing in shady environments, analogous to the observation that 'water spenders' (plants that exploit soil water resourses rapidly) have a low plasticity in tolerance to water deficits (1). *Fraxinus americana* is probably less shade tolerant than later successional species, such as *Acer saccharum*, which often spend considerable time early in their life history in shady understory environments. Population density of trees of the desired sample height (2-3 m) was in fact much less in the forest than in the adjacent field (data not shown). However, other strategies such as changes in leaf arrangement and size (8) may be important in the absence of plasticity in branching habit in a low-light environment.

Early successional or shade intolerant species would be expected to have high bifurcation ratios because higher numbers of distal branches result in greater whole tree solar radiation interception efficiency in high radiation environments. Late successional species would be expected to have lower ratios since a more forked branching habit (more proximal branches) is more efficient in the whole tree interception of low solar radiation (14). *Fraxinus americana,* however, had a lower than expected bifurcation ratio in relation to other relatively shade intolerant species tested by Whitney (14). This was explained as a result of the rachis of the compound deciduous leaves not being counted as short shoots. The bifurcation ratio found for *Fraxinus americana* in this study (mean = 4.9) was larger than that found by Whitney (14) (mean = 4.2) or Pickett and Kempf (8) (mean = 3.9). However, the fact that bifurcation ratios were similar for trees from both habitats concurs with data obtained both in the study by Whitney and the study by Picket and Kempf. Our study supports the theory that the branching habit of earlier successional species such as *Fraxinus americana* is fixed within the species, and morphological plasticity is not expressed by change in irradiation. The plasticity of *Acer saccharum* found by Steingraeber et al (11) and for *Cornus florida* and *Acer rubrum* by Pickett and Kempf (8) probably reflect the later-successional character of the species. All are generally considered shade tolerant but are opportunistic in the sense that they are capable of exploiting higher irradiances (such as in the opening of a gap in the forest canopy).

Although bifurcation ratios were similar between forest-grown trees and field-grown trees, other differences were apparent. The fact that field-grown trees had more terminal branches than forest-grown trees suggests that the field-grown trees were exploiting the higher irradiance with an increased number of leaves. Field-grown trees were older (Table 1) and somewhat shorter (data not shown) than forest-grown trees. They also had stouter branches, as reflected in the greater weight/length for terminal branches, greater overall weight, and a larger trunk diameter than forest-grown trees.

Trees growing in the field had an overall structure that would be acceptable for a street tree, but trees growing in the forest understory did not. The taller and thinner nature of the forest-grown trees is typical of growth processes of other plants which are moved from a sunny to a shady environment (9). Smith (10) indicates that trees classified as 'shade avoiders' tend to favor an internode expansion over leaf development since this strategy may result in young leaves which are exposed to more irradiation. This appeared to be the case for forest-grown white ash.

There was no difference between the two populations in total branch length, but the total number of branches was less for forest-grown trees. The forest-grown trees were therefore taller and less branched than the field-grown trees. 'Shade tolerators', on the other hand, have an energy conservation strategy that allows them to have a positive carbon balance by exhibiting a lower respiration rate. However, they also express a lower photosynthetic capacity and consequently have a slower overall growth rate than 'shade avoiders'. The results of this study indicate that *Fraxinus americana* trees are 'shade avoiders', not 'shade tolerators'. Seedlings were able to survive, however, for at least 11 years in the understory (Table 1). Forest-grown trees had reached the sample height in less time than the field-grown trees. This early height growth would be advantageous since reaching the higher irradiance at the top of the forest canopy quickly is essential for long-term survival.

There was no evidence of a 'self thinning' of short lateral branches due to low irradiance on forest-grown trees as discussed by Whitney (14). Such a 'self thinning' would theoretically decrease the bifurcation ratio as the tree went toward a monolayer. Although there was a decrease in the number of terminal branches on the forest-grown trees compared to oldfield-grown trees, there was a concomitant decrease of the number of second order branches (data not shown) which resulted in no net change in bifurcation ratio.

Summary

It is apparent that *Fraxinus americana* saplings are able to survive to some degree in a low light environment since the mean age of forest understory trees was almost 11 years. However, trees growing in the shady understory had poor general form, and they probably would not be acceptable for a landscape setting. This study indicates that survival ability is likely due to factors other than a change in branching structure. Possible candidates include a change in individual leaf morphology or inclination and a shift in the biochemistry of the photosynthetic apparatus. Other adaptive mechanisms besides branching

Table 1. Effect of habitat on distal (1°) and total branching, bifurcation ratio, caliper and age of white ash[z].

Habitat	Wt 1° (g)	Length 1° (cm)	Wt/Length	Number 1°	Wt, total	Length total	Bifurcation ratio (R_b)	Caliper	Age (years)
Forest	18.7(3.6)[y]	260(49)	.066(007)	5.5(1.7)	235(16)	561(61)	4.96(.95)	21.7(.9)	10.8(.53)
Old field	38.0(4.3)	301(31)	.115(.006)	13.9(4.4)	462(48)	603(64)	4.85(.41)	28.6(1.4)	13.2(.55)
p-[x]	.0031	.48	.001	.0035	.0009	.64	.92	.007	.0062

[z] Mean of 10 trees.

[y] Number in parentheses is standard error of the mean.

[x] P-value for mean(forest) vs. mean(field) for respective column.

plasticity may be in place, but a more 'shade tolerant' species should probably be chosen. On-site inspection of shade patterns throughout the day and consideration of seasonal solar radiation shifts are needed in order to make an intelligent species selection. White ash trees have the potential for short term survival in shady landscapes, but lowered photosynthesis will predispose trees to additional urban stresses or disease. White ash should therefore should only be planted in relatively high light environments.

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Résumé. Les arbres nouvellement plantés proviennent souvent d'une pépinière dont l'environnement est très ensoleillé pour être installés sur des sites ombragés autour des édifices ou dans les «canyons urbains». Les arbres doivent alors s'adapter pour survivre. Une stratégie d'adaptation pour les arbres exposés au changement des niveaux d'irradiation est alors la capacité qu'ont ceux-ci à modifier la structure de disposition de leurs branches afin de maximiser la photosynthèse sur l'ensemble de l'arbre. La capacité de modifier la disposition des branches, lorsque la croissance est en milieu ombragé versus un milieu en pleine lumière, fut testée sur des *Fraxinus americana* (frênes blancs) en mesurant la disposition des branches, mesure exprimée par le ratio de l'angle des fourches, sur des groupes d'arbres en milieu naturel. Les ratios d'angles étaient similaires pour les arbres en milieu ensoleillé à ceux en milieu ombragé, indiquant de ce fait une incapacité pour le frêne blanc à changer le patron de base de construction des branches lorsque celui-ci est soumis à différents environnements d'irradiation.

Zusammenfassung. Neugepflanzte Bäume werden oft von dem vollsonnigen Standort in der Baumschule an einen schattigen Standort um Gebäude oder in eine Strassenschlucht versetzt. Die Bäume müssen sich anpassen um zu überleben. Eine Anpassungsstrategie der Bäume, die wechselnden Strahlungsbedingungen ausgesetzt sind, ist die Fähigkeit, die Anordnung der Äste so zu ändern, daß die Baumphotosythese maximiert wird. Diese Fähigkeit zur Änderung der Aststellung, wenn der Baum in einem schattigen versus einem sonnigen Umfeld wächst, wurde an *Fraxinus americana* (Weiße Esche) an deren natürlichem Standort getestet durch die Messung der Aststellung, ausgedrückt im Vergabelungsverhältnis. Die Vergabelungsverhältnisse in sonnigem und schattigem Umfeld waren einander gleich, was darauf hinweist, daß die Weiße Esche nicht fähig ist, ihr Grundvergabelungsmuster zu ändern, wenn sie verschiedenen Einstrahlungen ausgesetzt ist.