Shade adaptation and shade tolerance in saplings of three Acer species from eastern North America

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Summary. Saplings of three, co-occurring maple species in a mature maple-beech forest differed in a suite of structural and physiological characters that separated the canopy species, *Acer saccharum*, from the two subcanopy species, *A. pensylvanicum* and *A. spicatum*. *Acer saccharum* had both more dense wood and tougher and heavier but thinner leaves than the subcanopy species. *Acer pensylvanicum* had the largest, lightest leaves with high stomatal density and its canopy architecture was the most effective in terms of leaf display for light interception. *Acer spicatum* had weaker wood similar to that of *A. pensylvanicum* but also small, soft and relatively poorly displayed leaves. Both subcanopy species maintained marginally higher average rates of photosynthesis over the growing season in the understory environment. We consider juvenile *A. saccharum* only shade-tolerant, capable of persisting through long periods in the closed canopy until a gap occurs but not specifically adapted to the understory environment. Juvenile *A. saccharum* appears to be constrained functionally by the requirements set by the canopy environment that adults will occupy. Characters such as high wood density are already expressed in the understory sapling; this investment in denser wood slows the growth of saplings, but is necessary for structural reasons in the adult. Juvenile *A. saccharum* have morphological and photosynthetic characters better suited to gas exchange and extension growth under the increased photon flux densities in large forest gaps, characteristics that will also be advantageous in the sunlit canopy environment of adults.

Both subcanopy maples appear to be more truly shade-adapted, although in somewhat different ways. *Acer pensylvanicum* has characteristics that enhance the potential for capture and utilization of sunflecks and is able to sustain higher growth rates than *A. saccharum* in the shaded subcanopy environment. *Acer spicatum* shares some shade-adapted features with *A. pensylvanicum*, and its habit of lateral spread through stem layering may confer an additional advantage in foraging for small light gaps.

**Key words:** *Acer saccharum* – *A. pensylvanicum* – *A. spicatum* – Photosynthesis – Leaf anatomy

Two distinct growth habits associated with differences in the levels of the forest canopy where reproduction occurs are apparent among maples in the temperate forests of northeastern North America. Sugar maple (*Acer saccharum* Marsh) typically grows to 30 m in height and at maturity forms a component of the forest canopy (Fowells 1965). Both mountain maple (*Acer spicatum* Lam.) and striped maple (*Acer pensylvanicum* L.) are smaller, subcanopy trees reaching only 5–6 m at maturity (Hibbs and Fischer 1979; Post 1969). *Acer saccharum* during its growth to reproductive maturity moves from a shaded understory environment to essentially full insolation in the forest canopy. After several episodes of accelerated growth under ephemeral gaps in the canopy, individual *A. saccharum* trees reach the forest crown (Canham 1985) and only then reproduce. In contrast to *A. saccharum*, both *A. pensylvanicum* and *A. spicatum* reproduce as relatively small trees in the forest subcanopy. *Acer pensylvanicum* does require light gaps to reach reproductive maturity, but the gaps can be small and of short duration (Hibbs et al. 1980).

Given these intrageneric differences in growth habit and life history, we might expect either of two modes of functional organization in juvenile *A. saccharum*. Sugar maple saplings could have structural and physiological characteristics much like those of the two subcanopy species with which they share the understory environment. Alternatively, juvenile sugar maples may be distinct and have characteristics better suited to the canopy environment that they will occupy as adults. In other words, we expect juveniles of the subcanopy maples to show shade-adapted features, but will a comparable-

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sized *A. saccharum* sapling in the same understory environment show similar patterns of adaptation? In this paper, we attempt to answer this question by comparing the structural and physiological traits of the three maple species in a natural population of coexisting saplings in the understory of a mature maple-beech forest.

**Methods and materials**

In summer 1986 we studied juveniles of all three maple species (*A. saccharum*, *A. pensylvanicum* and *A. spicatum*) in a natural, old-growth forest on Mont St. Hilaire, Quebec, Canada (45°33'N, 73°09'W). The size frequency distributions of saplings for the three species were comparable in the area of about 800 m² that we sampled on a north-facing, 37° slope. The saplings grew in the shade of codominant *A. saccharum* and *Fagus grandifolia* that had been only moderately damaged by a glaze ice storm three years earlier (Melanon and Lechowicz 1987).

We randomly selected 7 sets of 3 saplings (one per species) for detailed monitoring. The saplings in each set were within a 3 m radius to minimize environmental heterogeneity, and the 7 sets were treated as blocks in subsequent statistical analyses. To minimize extraneous sources of error variance, only saplings between 1 and 2 m high with an undamaged, single apical shoot were sampled.

To assess the functional basis for variation in shade adaptation among these three maple species, we made a variety of structural and physiological measurements on the selected plants from June to September, 1986. A total of 26 sets of gas exchange measurements under ambient environmental conditions was taken throughout the growing season with a portable infrared gas analyzer (LiCor 6000, Lincoln, Nebraska). These assays were made at different times between 0830 and 1650 h Eastern Standard Time on days when the foliage was not wet. A typical series of measurements took 2.1 h to complete. In each series of LiCor 6000 readings, the sampling sequence of blocks and the plants within each block were randomized and three randomly chosen leaves were measured per plant. The gas exchange characteristics of the three maple species are compared using the means of these 26 sets of assays. Each species mean is based on 576 independent readings taken throughout the growing season (3 leaves/sapling, 7 saplings/set, 26 sampling sets). These sets were treated as blocks in subsequent statistical analysis of the gas exchange characteristics of each species in this understory environment.

The light environment in which the saplings of each species grew was compared using the mean photon flux density (PFD) measured over the approximately 2 min interval of each LiCor assay. During each assay PFD was measured by the LI-190-1 quantum sensor attached to the 1 liter chamber of the LI-6000 photosynthesis system. Care was taken to orient the chamber and the quantum sensor in the natural position of the leaf being assayed; during the assay the operators were careful not to shadow the chamber with their bodies.

All above ground parts of the sampled saplings were harvested on September 10 to determine leaf toughness, specific leaf mass (SLM), leaf area and oven-dry biomass. Leaf toughness was determined with a leaf penetrometer (Feeny 1970) for 5 randomly chosen leaves per plant. Specific leaf mass (SLM) was estimated from ten to twelve 3.8 cm² discs per plant each taken from a different randomly chosen leaf. Stomatal densities were measured on clear nail polish impressions of fresh leaves (Simpson 1961). The area of all the leaves harvested in September was measured with a Paton Electronic Planimeter (Paton Industries Ltd, South Australia). The leaf display index (LDI) was measured in subsequent statistical analyses. The extension growth index (EGI) was used to describe canopy form of each plant. The wood density of oven-dried two-year-old twigs was determined by weighing and volumetric displacement of water. The plants were aged by basal ring count. Fresh leaf tissue samples were fixed in FAA, dehydrated in a series of ethanol solutions and sectioned in paraffin; leaf anatomical measurements were made by light microscopy on these sections stained with 0.05% toluidine blue.

Character differences among the three species were tested by pairwise comparisons using a nonparametric Wilcoxon test (Procedure NPAR1WAY in SAS, 1988). A multivariate comparison considering a variety of characters together in a canonical discriminant analysis (Procedure CANDISC in SAS, 1988; Cittins 1985) was used to illustrate the overall pattern of differences among the three maples.

**Results**

***Understory light regime***

The understory environment shared by these three maples is characterized by persistently low, diffuse light punctuated by short pulses of sunflcks. In a sample of 58 h over 16 days in June through September 1986, sunflcks (defined as PFD greater than 100 μmol·m⁻²·s⁻¹) occurred only 13% of the time but contributed 53% of the total photon flux. The median PFD for the three species were *Acer saccharum* 63 μmol·m⁻²·s⁻¹ (20, 89; first and third quartiles), *A. pensylvanicum* 46 (26, 135), and *A. spicatum* 72 (58, 78), less than 5% full sunlight, and did not differ significantly among species (Kruskal-Wallis Test P > 0.8).

***Character variation among species***

The three species did not differ significantly in height, basal diameter or total aboveground dry weight (a reflection of our sampling criteria), but did differ in age (Table 1). *Acer spicatum* saplings were younger than the other species; we attribute this to the fast-growing, layered stems that occur only in *A. spicatum* (Post 1969). Layering, basal sprouts, and numerous short branches combined with characteristically small leaves gives *A. spicatum* a distinct, shrubby appearance. *Acer pensylvanicum* tends to be sympodial with large leaves on long spreading lateral branches (Extension Growth Index, Table 1). *Acer saccharum* is strongly monopodial with intermediate-size leaves displayed on short stiff branches. The significant progression of increasing leaf size from *A. spicatum* to *A. saccharum* to *A. pensylvanicum* persists in the total leaf area per plant but the differences there were not significant. Leaf display index was lowest in *A. spicatum*. The LDI of *A. saccharum* was similar to the 8.28 ± 0.3 cm²·cm⁻¹ reported by Canham (1988).

*Acer saccharum* had the highest specific leaf mass (SLM), slightly higher than in an earlier report (Hagen and Chabot 1986) that found SLM values for the other two species similar to ours (Table 1). Laminar thickness and SLM showed inverse trends with *A. pensylvanicum* having the thickest yet least dense leaves; between species, laminar thickness and SLM were not significantly correlated (Pearson's r = 0.08, P = 0.73, n = 20). Although *A. saccharum* had the thinnest leaves and *A. pensylvanicum* the thickest, the heavily lignified sclerenchy-
Table 1. Summary of sapling characters of the three *Acer* species (X ± SD). Extension Growth Index is the ratio of terminal shoot length to the first pair of lateral shoots. Leaf Display Index is the total leaf area divided by the total shoot length. Within rows, means with the same letter are not significantly different at the 0.05 level (Wilcoxon’s two-sample test).

<table>
<thead>
<tr>
<th>Trait</th>
<th><em>A. saccharum</em></th>
<th><em>A. pensylvanicum</em></th>
<th><em>A. spicatum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole Plant</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height (m)</td>
<td>1.36 ± 0.41 a</td>
<td>1.61 ± 0.56 a</td>
<td>1.37 ± 0.39 a</td>
</tr>
<tr>
<td>Basal Diameter (cm)</td>
<td>0.95 ± 0.17 a</td>
<td>1.00 ± 0.15 a</td>
<td>0.95 ± 0.10 a</td>
</tr>
<tr>
<td>Mass (g dry wt)</td>
<td>50.6 ± 30.8 a</td>
<td>62.3 ± 42.6 a</td>
<td>36.0 ± 23.1 a</td>
</tr>
<tr>
<td>Age (year)</td>
<td>15.3 ± 6.1 a</td>
<td>10.1 ± 3.0 b</td>
<td>7.0 ± 3.9 b</td>
</tr>
<tr>
<td>Total leaf area (cm²)</td>
<td>3026 ± 1604 a</td>
<td>4131 ± 2492 a</td>
<td>2293 ± 1411 a</td>
</tr>
<tr>
<td>Wood Density (g·m⁻³)</td>
<td>0.70 ± 0.04 a</td>
<td>0.57 ± 0.07 b</td>
<td>0.55 ± 0.02 b</td>
</tr>
<tr>
<td>Extension growth index (cm·cm⁻¹)</td>
<td>4.36 ± 6.04 a</td>
<td>1.16 ± 0.87 a</td>
<td>1.32 ± 0.80 a</td>
</tr>
<tr>
<td>Leaf display index (cm²·cm⁻¹)</td>
<td>9.8 ± 1.7 a</td>
<td>11.7 ± 1.3 a</td>
<td>7.1 ± 1.6 b</td>
</tr>
</tbody>
</table>

Leaf structure

| Mean size (cm²)            | 44.1 ± 5.4 a  | 66.3 ± 11.0 b    | 22.3 ± 5.3 c  |
| Specific leaf mass (g·m⁻²) | 33.4 ± 7.4 ac | 27.2 ± 4.4 b     | 30.6 ± 3.5 bc |
| Leaf toughness (g·cm⁻²)     | 2109 ± 221 a  | 1900 ± 217 a     | 1218 ± 143 b  |
| Leaf thickness (µm)         | 75.8 ± 5.3 a  | 93.7 ± 9.8 b     | 85.8 ± 8.5 b  |
| Stomatal density (mm⁻²)     | 329 ± 57 a    | 443 ± 55 b       | 315 ± 63 a    |
| Stomatal pore length (µm)   | 8.9 ± 0.3 a   | 12.5 ± 1.0 b     | 9.5 ± 0.4 c   |

Leaf Physiology

| Mean seasonal photosynthetic rate (µmol·m⁻²·s⁻¹) | 1.52 ± 0.88 a | 1.83 ± 1.08 a | 1.74 ± 0.47 a |
| Water use efficiency (µmol·mmol⁻¹)              | 1.29 ± 0.38 a | 1.42 ± 0.27 a | 1.30 ± 0.1 a  |

*Ma* cells forming the bundle sheath in *A. saccharum* increased SLM and leaf toughness without increasing laminal thickness (personal observation; Hagen and Chabot 1986). *Acer spicatum* significantly less tough leaves than either *A. pensylvanicum* or *A. saccharum*.

*Acer saccharum* had significantly higher wood density. Both stomatal density and stomatal pore length were highest in *A. pensylvanicum*. Seasonal mean photosynthetic rate and water use efficiency estimates were lowest in *A. saccharum* but not significantly so (Table 1).

Although the differences among the three maple species in any given trait were not always great, the species were distinctly different from one another when a suite of traits was considered together (Fig. 1). This multivariate analysis emphasizes that while the two subcanopy maples are distinct from *A. saccharum*, they also differ from one another. Both subcanopy species have less dense wood and lower leaf specific mass, and over the growing season their average photosynthetic rate is marginally higher. The two subcanopy maples primarily differ from one another in leaf-related traits. *Acer pensylvanicum* has tougher leaves with higher stomatal density that are arrayed more closely along the branches compared to *A. spicatum*.

**Discussion**

Shade adaptation can involve the participation and interaction of many plant functions including traits associated with leaf physiology, morphology, branching structure and phenology (Canham 1988; Givnish 1988). This complicates the comparative analysis of sun and shade adaptation because there is no assurance that the basic relationships among relevant traits are phylogenetically invariant (Pagel and Harvey 1989). For example, the functional significance of a particular trait such as specific leaf mass can depend on other traits as diverse.
as photosynthetic capacity and the hydraulic conductivity of stemwood. Some of these traits may well vary among genera or families for reasons that have nothing to do with adaptation to sun or shade environments. Such effects of phylogenetic differences are less likely to confound the comparative analysis of sun-shade adaptation within a single, natural genus like 

*Acer*. We therefore compared co-existing samplings of three maple species growing together in a forest understory to decide if these congers differed in traits typically associated with shade adaptation. In this intrageneric analysis based on a wide variety of traits, we were able to show that saplings of the canopy species, *A. saccharum*, appear to have a lower level of shade adaptation than co-occurring subcanopy maples.

*Acer saccharum* had higher SLM, a common characteristic of sun- rather than shade-adapted species (Givnish 1988). In a two-year study, Jurik (1986) also found higher SLM in understory leaves of *A. saccharum* compared to *A. pensylvanicum*. *Acer saccharum*’s greater SLM is not due to the usual increase in leaf thickness associated with sun leaves (Jackson 1967; Givnish 1988).

*Acer saccharum* leaves were actually thinner than those of the subcanopy maples, and the increased SLM was attributable to heavy investment in sclerenchyma (personal observation; Hagen and Chabot 1986). This more scleratized and tougher leaf may represent the juvenile expression of an adult character necessary to reduce tearing in the more wind-exposed canopy environment (Nobel 1981). Increased scleratization can also be interpreted as an investment in defense against herbivores (Hagen and Chabot 1986), again an investment one expects to be higher in the slow-growing and long-lived canopy species (Coley et al. 1985; Loehle 1988). Higher SLM in a closed canopy environment was also observed in seedlings of two other canopy species (*Liriodendron tulipifera* and *Acer rubrum*) compared to a co-occurring subcanopy tree, *Cornus florida* (Wallace and Dunn 1980). Whether through increased sclerenchyma to strengthen leaves or to defend against herbivores, higher SLM may be a general characteristic of canopy compared to subcanopy trees even as saplings.

The denser wood of *A. saccharum* compared to the two subcanopy maple species can be interpreted as a juvenile character necessitated by the emergent nature of the adult tree. Higher wood densities provide greater tensile strength to withstand windthrow, and are typical of late-successional canopy dominants (King 1986). The shoot form of *A. saccharum* also suggests that even as a juvenile it is functionally more suited to the canopy rather than subcanopy environment. Variations in shoot growth form in saplings of Japanese maple species have been related to interspecific differences in light requirements (Sakai 1987). In these Japanese species, lower terminal compared to lateral shoot growth (i.e., lower EGI) indicates an increased adaptation to shade. Sakai’s elongation type of shoot growth form, which characterizes *A. saccharum*, is typical of species in large canopy gaps where higher insolation prevails. The greater investment in bole strength by *A. saccharum* rather than in a more extensive or taller shoot system indicates a weaker functional adaptation to the shaded forest understory, especially considering its lower rates of photosynthesis compared to the two subcanopy species (Chazdon 1985; Givnish 1988).

Because the rate of growth figures so strongly in the life history and competitive ability of woody species (Harcombe 1987), it can be taken as an overall measure of the juvenile performance of these three co-occurring maples. Considering the age differences of our sampled saplings, the growth rate of *A. saccharum* as a sapling is the lowest of the three species both in terms of height and whole plant mass. The slower height growth of *A. saccharum* is contrary to the expectation for canopy species based on intergeneric comparisons (King 1990). This surprisingly slower growth of juvenile *A. saccharum* is at least in part attributable to the substantial number of juvenile characteristics that are actually more advantageous to adults in the sun-lit forest canopy. Rather than an ontogenetic shift, the functional organization of *A. saccharum* appears to be constrained by a relatively invariant template from juvenile through adult. Because of this, we suggest that sugar maple is better considered to tolerate shade as a sapling that to be truly shade-adapted.

The subcanopy *A. pensylvanicum*, in contrast, has characteristics that suggest a consistent functional adaptation to the understory environment throughout its ontogeny. In addition to having larger and lighter leaves that are more efficiently spaced along the lateral branches, *A. pensylvanicum* also has a more sympodial shoot extension pattern. This branching architecture tends to produce a monolayer leaf display that coupled with lighter wood creates an efficient and economical surface for the interception of sunflecks (Horn 1972). King (1990) found similar patterns of greater leaf display efficiency in saplings of understory trees in a Panamanian forest. *Acer pensylvanicum* with its shade-adapted characters and relatively higher photosynthetic activity achieved the highest annual gains in height and biomass.

While relatively weak wood, lighter and more flaccid leaves and relatively high photosynthetic rates define *A. spicatum* as a shade-adapted plant compared to *A. saccharum*, it differs somewhat from *A. pensylvanicum*. *Acer spicatum*, with 60% more leaves borne on nearly twice as many shoots, has a shrubbier and less efficient light-capturing surface area than *A. pensylvanicum*. Given its low rates of regeneration by seed (personal observation) together with its habit of producing basal sprouts and spreading laterally through stem layering, *A. spicatum* appears to rely heavily on vegetative means to more effectively discover and exploit light gaps. Rapid height growth of layered shoot sprouts fed by the parental stem enables a quicker response to the presence of even very small light gaps. This foraging behaviour (Bell 1984; Rincon and Grime 1989) as an alternate mode of adaptation to the understory environment deserves further study.

The short term dynamics of gas exchange responses to sunflecks also require study in these three co-occurring maples. In the forest understory, the critical marginal gain in carbon depends on the balance between con-
struction and maintenance costs of leaves, shoots and roots and the effective capture and utilization of available light (Bjorkman 1981). As sunflecks contribute a major fraction of the daily and seasonal light energy flux in the forest understory in temperate (Weber et al. 1985) and tropical (Pearcy 1983) forests, and between 10% and 60% of daily carbon gain comes from sunflecks (Chazdon 1988; Pearcy and Calkin 1983; Weber et al. 1985; Pearcy 1987), there should be strong selection for characters that increase the capture and utilization of sunflecks (Chazdon 1988). An integrated analysis incorporating belowground energetic balance and an analysis of dynamic physiological responses to sunflecks, such as photosynthetic induction (Chazdon and Pearcy 1986a, b; Pearcy 1988), would yield a more complete appreciation of adaptation to the understory light environment in these three maple species.

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