Dependency of branch diameter growth in young Acer trees on light availability and shoot elongation

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Summary Many biomechanical and theoretical studies have been based on the pipe-model theory, according to which a tree is regarded as an assemblage of pipes, each having the same amount of leaf area or leaf mass. However, the physiological mechanisms underlying the theory have not been extensively examined, particularly at the branch level. We analyzed how branches and trunks thickened in nine young Acer mono Maxim. var. marmoratum (Nichols) Hara f. dissectum (Wesmael) Rehder, and A. rufinerve (Siebold & Zucc.) trees. In particular, we examined the roles of light, allocation of photosynthates and shoot heterogeneity. The cross-sectional area \( A \) of a branch was proportional to cumulative leaf mass or leaf area of the branch, and cumulative cross-sectional area of the daughter branches \( \Sigma A \) above a branching point was equal to the \( A \) of the mother branch. These results indicate the validity of the pipe-model theory. However, the theory was invalid for current-year growth of branch cross-sectional area \( \Delta A \). The \( \Delta A/\Sigma \Delta A \) for a branching point was greatest (nearly equal to 1) at the crown surface, decreased with crown depth, and tended to increase again at the trunk base, and \( \Delta A \) strongly depended on light interception and the yearly increment of leaves on the branch. We examined factors that influenced \( \Delta A \) with multiple regression analysis. The ratio of \( \Delta A \) of a branch to branch leaf area depended on both relative irradiance and mean current-year shoot length of the branch, suggesting that diameter growth of a branch is determined by the balance between supply of photosynthates, which depends on light interception by the branch, and demand for photosynthates, which is created by the high cambial activity associated with vigorous shoot elongation.

Keywords: Acer mono, Acer rufinerve, branch autonomy, current-year shoot growth, growth in cross-sectional area, Leonardo da Vinci’s rule, leaf increment, long and short shoots, pipe-model theory, sink–source balance, tree architecture, vigor index.

Introduction

The cross-sectional area (or sapwood area) of a branch is proportional to the leaf mass or leaf area of the branch—a relationship that was noted by Leonardo da Vinci more than 500 years ago (Richter 1970). On the basis of this proportional relationship, Shinozaki et al. (1964a, 1964b) proposed that a tree is an assemblage of pipes having the same number of leaves. This is called the pipe-model theory.


The ratio of leaf area (or leaf mass) to stem sapwood area is not always constant; it differs depending on site conditions as well as the particular environment of a tree (Mäkelä et al. 1995, Mencuccini and Grace 1995, Berninger and Nikinmaa 1997, Carey et al. 1998, Mäkelä and Vanninen 1998, Li et al. 2000). The ratio tends to decrease with increasing tree height (McDowell et al. 2002) and when sapwood area is measured at the stem base (Mäkelä et al. 1995). These findings suggest that hydraulic conductance declines with increases in path length or sapwood senescence, or both.

Photosynthates are translocated from source leaves to sink organs along a sugar concentration gradient. However, photosynthates produced in a given branch are rarely translocated to its sibling branches, despite the presence of a sugar concentration gradient between branches. This observation has given rise to the concept of “branch autonomy” (Sprugel et al. 1991) and has been invoked in many studies on the mechanisms that determine tree architecture (Takenaka 1994, Perttunen et al. 1996, Day and Gould 1997) and community structure (Takenaka 1994, King et al. 1997). For example, Takenaka (1994) succeeded in mimicking the growth of a stand of trees by assuming that each autonomous shoot produces daughter shoots or dies depending on how much light it intercepts.

However, it is misleading to treat all branches and shoots as perfectly equal and perfectly autonomous. Growth of a shoot
depends on its local light environment and its status among neighboring daughter shoots within a branch (Takenaka 2000, Sprugel 2002). Goulet et al. (2000) proposed the vigor index (VI) to express the relative status of a branch, which is calculated as follows. Consider a mother branch bearing several daughter branches at a branching point. The VI of the thickest branch among the daughter branches equals the VI of the mother branch. The VI of any other daughter branch is expressed as a product of the VI of the mother branch and the ratio of the cross-sectional area of this daughter branch to that of the thickest daughter branch. Thus, VI represents the relative size of each daughter branch. The calculation starts with the basal trunk and is repeated at every branching point. The VI for the branch segments of the main axis of the tree are set to 1. Accordingly, VI decreases as branching order increases. When branch sizes are similar, the branches in the upper part of the crown generally have greater VIs than those in the lower part of the crown (Goulet et al. 2000, Nikinmaa et al. 2003). In young trees of sugar maple (Acer saccharum Marsh.) and yellow birch (Betula alleghaniensis Brit.) (Goulet et al. 2000), and in Scots pine (Pinus sylvestris L.) (Nikinmaa et al. 2003), the growth of shoots depended on both the light environment and VI.

The construction and maintenance of branches, trunk and roots depends on photosynthates produced by young shoots. Diameter growth of branches downstream of the distal shoots is not determined solely by local conditions such as light interception and number of leaves on the branch. In photosynthetically active shoots, the ratio of photosynthates exported downward to photosynthates used within the shoot also varies among shoots. For these reasons, the patterns in which photosynthates are allocated should be more heterogeneous than predicted by the pipe-model theory. To understand how an entire tree is constructed, it is thus important to clarify the allocation pattern of photosynthates. Although Valentine (1985), Mikelä (1986, 1999, 2002) and Perttunen et al. (1996, 1998) developed plausible tree growth models that incorporate rules for the allocation of photosynthates, the physiological mechanism(s) underlying some of these rules has not been identified. One potential mechanism may depend on the abundance of long shoots or leader branches with high rates of auxin synthesis. Auxin synthesized in young leaves and at active apices is transported basipetally, and activates shoot elongation and cambial function (Mohr and Schopfer 1995). As a consequence, long shoots or leader branches might be expected to show vigorous diameter growth. Such heterogeneity can be incorporated into the pipe-model paradigm. In their pioneering study, Morataya et al. (1999) found that leaf mass was correlated with area and volume growth of the sapwood in Tectona grandis L.f. and Gmelina arborea Roxb.

Photosynthesis and transpiration depend on irradiance. In situ measurement of photosynthesis and transpiration for each shoot of the tree is impractical; however, light interception can be accurately estimated for each shoot. An instantaneous photosynthetic light-response curve (the rate of photosynthesis plotted against irradiance) shows light saturation, whereas daily photosynthesis plotted against daily photon flux density yields a more linear curve (Terashima and Takenaka 1986). Moreover, canopy leaves acclimate to their particular light environments (Björkman 1981). Therefore, light interception by a shoot should be a reasonable index of photosynthesis by that shoot over a period of weeks or months (Campbell and Norman 1998).

In the present study, we examined two maple species, Acer mono Maxim. var. marmoratum (Nichols) Hara f. dissectum (Wesmael) Rehder and Acer rufinerve (Siebold & Zucc.), whose leaves have been shown to acclimate to the light environment (Hanba et al. 2002). We measured light interception by each current-year shoot as an index of photosynthetic production and transpiration. We then examined: (1) relationships between current-year growth of the cross-sectional area of a branch and various leaf attributes, including leaf mass, area, light interception and current year increase in leaf number; (2) patterns of carbon allocation from shoot tips to the base of the trunk; and (3) the dependence of branch diameter growth on light availability and several attributes of shoot growth activity (mean current-year shoot length and VI). We interpreted our results in the context of mechanisms of diameter growth of branches and trunks.

Materials and methods

Study sites and species

The study was conducted in two deciduous, broad-leaved forests: the Ogawa Forest Reserve (36°56′ N, 140°35′ E, 600 m a.s.l.), where mean annual temperature is 9.0 °C and mean annual precipitation is 1800 mm; and the Ashu Experimental Forest of Kyoto University (35°20′ N, 135°45′ E, 700 m a.s.l.), where mean annual temperature is 12.3 °C and mean annual precipitation is 2400 mm.

Three 1 to 2-m-tall (1.45 ± 0.37 m, mean ± SD) A. mono trees in the Ogawa Forest and six 0.5 to 3-m-tall (1.56 ± 0.86 m) A. rufinerve trees in the Ashu Experimental Forest were selected from various light environments. The trees were between 3 and 15 years old and appeared free of mechanical injury. About 150 and 350 current-year shoots were examined for A. mono and A. rufinerve, respectively. Data were collected in 1997 for A. mono and in 1998 for A. rufinerve.

Acer rufinerve is a pioneer species and A. mono is a sub-climax species. Both are deciduous, broad-leaved, semi-shade-tolerant trees that often reach the forest canopy at maturity. Their phyllotaxis is decussate and their branching pattern is monopodial (Sakai 1990). In both species, leaf expansion and secondary growth of stems started in early May. Secondary growth finished between mid-August and mid-September in A. mono and in early September in A. rufinerve (Komiyama et al. 1987, 1989). Both species have diffuse-porous wood.

Measurement of light environment of current-year shoots

We assessed the light environments of all 500 current-year shoots in the field before leaf shedding. The relative irradiance of a given current-year shoot (RI<sub>k</sub>), which is the ratio of irra-
distance measured just above the shoot to that measured at an open site, was obtained in diffuse light, and \( RI_S \) was used as an index of the shoot light environment.

For \( A. \ mono \), \( RI_S \) was estimated from hemispherical photographs (Pearcy 1989) analyzed with HEMIPHOT software (ter Steege 1994). We took hemispherical photographs just above each current-year shoot with a film camera (Nikomat, Nikon, Tokyo, Japan) fitted with a fish-eye lens (Fisheye, Nikon). The photographs were taken on cloudy days in October 1997 with the lens held horizontal. Where current-year shoots were too close to one another to be photographed separately, we photographed several shoots from just above the center of the group. From the hemispherical photographs, we calculated an indirect diffuse site factor (ISF) with HEMIPHOT, based on the assumption that the sky was uniformly overcast. We used ISF above each current-year shoot (ISF\(_{\text{CS}}\)) as an index of \( RI_S \). The highest values of \( RI_S \) for the three \( A. \ mono \) trees were 0.052, 0.142 and 0.189.

For \( A. \ rufinerve \), we measured photosynthetically active photon flux (PPF; \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) with quantum sensors (LI-190SB, Li-Cor, Lincoln, NE) in addition to the analysis with hemispherical photographs. These measurements were carried out on cloudy days in September 1998 with two sensors. One sensor was connected to a data logger (Thermodac-E, Eto Denki, Tokyo, Japan) and placed horizontally at a relatively open site on a forest road. Data were recorded every 5 s. The second sensor was kept horizontally just above the current-year shoot, and PPF incident on the shoot (PPF\(_S\)) was measured. The measurements with the two sensors were performed concurrently, and the ratio of PPF above the shoot to that at the open site (RPPF\(_S\)) was calculated (Messier and Puttonen 1995, Parent and Messier 1996). We also took a hemispherical photograph at the same open site where the first quantum sensor was placed, and calculated the ISF of the open site (ISF\(_{\text{CS}}\)) with HEMIPHOT. We used ISF\(_{\text{CS}}\) to correct \( RI_S \) for each current-year shoot. The highest values of \( RI_S \) for the six \( A. \ rufinerve \) trees were 0.855, 0.722, 0.570, 0.299, 0.056 and 0.045.

For RPPF < 0.7, instantaneous RPPF under an overcast sky is strongly correlated with mean daily RPPF under a clear sky \( (r^2 = 0.872) \) as well as with mean daily RPPF under an overcast sky \( (r^2 = 0.969) \) (Messier and Puttonen 1995, Parent and Messier 1996). Therefore, we did not take into account the effects of direct light.

**Measurement of leaf attributes**

We collected all leaves and measured the total leaf area on each current-year shoot \( (Af_S) \). For \( A. \ mono \), we measured leaf area with a leaf area meter (AAM-7, Hayashi Denko, Tokyo, Japan). For \( A. \ rufinerve \), we photocopied the leaves from each current-year shoot, digitized the images with a scanner (JX-250, Sharp, Osaka, Japan) and measured their areas with NIH-Image v. 1.55 software (US National Institutes of Health, Bethesda, MD). The product of \( Af_S \) and \( RI_S \) was regarded as the light interception by the current-year shoot \( (If_S = Af_S \times RI_S) \). The leaves were then dried at 80 °C for 2 to 3 days and total leaf mass of the current-year shoot \( (Wf_S) \) was determined. These leaf attributes \( (Wf_S, Af_S, If_S) \) are collectively referred to as \( F_s \).

We estimated three leaf attributes for each branch: \( Wf, Af \) and \( If \). Each tree was considered as a series of segments separated at every branching point and regarded as a fractal-like structure consisting of branch modules. Each large branch module included many small branch modules, and the largest branch module in a tree was the tree itself. The weighted relative irradiance of a branch \( (RI) \) was calculated as \( If/Af \).

We also counted the number of the current-year leaves per branch \( (Nf) \) and the number of leaf scars on the 1-year-old branches of the whole branch. The latter equals the previous-year leaf number on the branch \( (Nf_{\text{-1}}) \). We then estimated the current-year increment in leaf number as \( \Delta Nf = Nf - Nf_{\text{-1}} \).

We estimated \( Nf, \Delta Nf \), leaf attributes \( (F) \) and \( RI \) for all branch modules in all trees.

**Measurement of stem attributes**

After collecting the leaves, the trees were felled and transported to the laboratory. Lengths of all current-year shoots and of the branch segments between neighboring branching points were measured.

The greatest diameter \( (D) \) perpendicular to the length was measured at the base of each current-year shoot and at the middle point of each branch segment with digital calipers. Trunk diameters at the base of the crown and at the stem base were also measured. From these diameters, we calculated the cross-sectional areas of the current-year shoots \( (A_s) \) and of the branch segments and trunk \( (A) \): \( A \) or \( A_s = \pi D^2/4 \). For \( A \) of the branch, \( A \) of the most basal branch segment within the branch or of the trunk just below the crown was used. Areas were estimated for all branches of all sample trees. All branch and trunk cross sections were wet and had a similar whitish color, indicating no heartwood in the samples.

Current-year growth in cross-sectional area was estimated for each branch, by cutting branch segments or trunks at the position where the diameter was measured. At the greatest diameter of the section, we measured the diameter of the current-year annual ring, excluding the bark and phloem, and that of the previous-year annual ring. The annual rings boundaries were identified with a magnifying glass. The difference between the areas enclosed by the current- and previous-year annual rings was regarded as the current-year’s growth in cross-sectional area of the branch segment or trunk \( (\Delta A) \). For each branch, \( \Delta A \) of the most basal branch segment within the branch or \( \Delta A \) of the trunk just below the crown base was used. In some branch segments with dense annual rings, the current-year \( \Delta A \) values were not estimated.

**Status of each branch**

The length of each current-year shoot was measured, and the mean length of the current-year shoot \( (\bar{L}_S) \) was obtained for each branch. The vigor index \( (VI) \) was calculated according to Goulet et al. (2000).

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Statistical analyses

Statistical analyses were performed with StatView J-4.5 software (Abacus Concepts, Berkeley, CA). Relationships between leaf attributes and stem attributes were assessed by linear regression. We used multiple regression and partial correlation to test the dependency of diameter growth of a branch on solar irradiance (RI), $L_S$ and VI of the branch.

Results

Cross-sectional branch area and area growth versus leaf attributes

We analyzed the relationships between cross-sectional area ($A$) and leaf attributes ($F$) for all branch modules within the crown (Figure 1). As leaf mass ($W_f$) or leaf area ($A_f$) increased, $A$ increased proportionally in both species ($r^2 = 0.90–0.95$). The coefficients of determination for the relationships between light interception ($I_f$) and $A$ ($r^2 = 0.78$ and 0.87) were smaller than those for $W_f$ and $A_f$. The slopes of the relationships between $A$ and $I_f$ varied depending on the relative irradiances experienced by the trees. Trees growing in environments with a high relative irradiance had smaller slopes for these relationships than trees growing in a low relative irradiance (regression lines for respective irradiances are not shown).

When the current-year growth of a branch ($\Delta A$) was plotted against $F$, the data points were more scattered than those in Figure 1 ($r^2 = 0.45–0.87$) (Figure 2). However, in contrast to the results of the relationships between $A$ and $F$ (Figure 1), the coefficients of determination were greater for $I_f$ ($r^2 = 0.75$ and 0.87) than for $W_f$ ($r^2 = 0.66$ and 0.70) and $A_f$ ($r^2 = 0.45$ and 0.67).

Branch cross-sectional area growth versus leaf increment

If $A$ is always proportional to $F$ and there is no heartwood formation, current-year growth of the cross-sectional area of a branch should be proportional to the annual increments in leaf attributes (Valentine 1985, Mäkelä 1986). In Scots pine, Nikinmaa (1992) observed that the difference in cross-sec-
tional area growth of the trunks between just below and above a given whorl was correlated with growth of the needle mass for the whorl. This observation implies that the amount of newly formed wood is correlated with the quantity of new leaves.

We examined the relationships between $\Delta A$ and the annual increment in leaf number ($\Delta N_f$) (Figure 3). In $A. \text{rufinerve}$, the correlation between $\Delta A$ and $\Delta N_f$ was stronger ($r^2 = 0.86$) than the correlation between $\Delta A$ and $N_f$ ($r^2 = 0.54$). In $A. \text{mono}$, the correlation was slightly stronger between $\Delta A$ and $\Delta N_f$ ($r^2 = 0.67$) than between $\Delta A$ and $N_f$ ($r^2 = 0.61$).

Patterns of carbon allocation from branch tip to trunk base

The pipe model assumes that the cross-sectional area of a branch is equal to the cumulative cross-sectional area of its daughter branches (Shinozaki et al. 1964a, Richter 1970, Nikinmaa 1992, Yamamoto and Kobayashi 1993). Therefore, we analyzed the relationships between $A$ and $\Sigma A$ and between $\Delta A$ and $\Sigma \Delta A$ for every branching point. For each branching point, $A$ or $\Delta A$ of a branch segment just below the branching point and $\Sigma A$ or $\Sigma \Delta A$ of all the branch segments just above the branching point were measured and plotted (Figure 4). For the branching points within the crowns, $A$ was almost identical to $\Sigma A$ of the daughter branches in both species (slope = 0.96 and 1.0, $r^2 = 0.96$ and 0.97). However, $A$ values obtained at the trunk base tended to be larger than $\Sigma A$. In contrast, $\Delta A$ for the branching points within the crowns was smaller than $\Sigma \Delta A$ for the daughter branches in most cases (slope = 0.78 and 0.61), although the coefficient of determination for $A. \text{mono}$ was not large ($r^2 = 0.93$ in $A. \text{rufinerve}$ and 0.60 in $A. \text{mono}$). However, again, $\Delta A$ values for basal trunks were larger than $\Sigma \Delta A$ for the daughter branches.

Dependency of branch diameter growth on light availability and shoot elongation

We analyzed the dependency of branch diameter growth on the branch light environment, measured as relative irradiance, and branch relative status. The relative status of a branch was indicated by the $L_S$ on the branch and the VI of the branch. We tested the effects of these parameters on branch growth in
Figure 3. Relationships between current-year growth of branch cross-sectional area (ΔA) and current-year leaf number (Nf); and between ΔA and annual increment in leaf number (ΔNf) within the crown. Symbols: □ = 20–40%; ○ = 5–20%; and △ = < 5% of relative irradiance for the trees.

Figure 4. Relationships between branch cross-sectional area (A) and the sum of branch cross-sectional areas of daughter branches (ΣA) (left panels); and between branch cross-sectional area growth (ΔA) and the sum of branch cross-sectional area growth of daughter branches (ΣΔA) (right panels). We measured and plotted A and ΔA in the branch-segment immediately below each branching point and ΣA and ΣΔA of the daughter branch segments immediately above the branching point. Data for six A. rufinerve trees and three A. mono trees are shown. The regression lines were obtained for the branches within the crowns excluding the trunk parts below the crowns (○). Squares (□) indicate the data for the basal trunk parts below the crowns.
cross-sectional area per unit of leaf area ($\Delta A/Af$) by partial correlation and multiple regression analyses, with the multiple regression model: $\Delta A/Af = b_0 + b_1(RI) + b_2(L_S) + b_3(VI)$, where $b_0$ is a constant and $b_1$, $b_2$ and $b_3$ are partial regression coefficients.

In both species, $\Delta A/Af$ was correlated with $\bar{L}_S$ (Table 1). Although $\Delta A/Af$ was correlated with $RI$ in $A. rufinerve$, the correlation was not significant in $A. mono$. There was no effect of VI on $\Delta A/Af$ in either species. There were no significant or strong partial correlations among $L_S$, RI and VI (Table 1). The coefficient of determination ($R^2$) for $A. rufinerve$ was larger than for $A. mono$ (Table 2). In both species, $\bar{L}_S$ was a significant determinant, RI was significant only for $A. rufinerve$ and VI was not significant in either species.

### Discussion

Two assumptions of the pipe model are that there is a proportional relationship between branch cross-sectional area (or sapwood area) and leaf mass (or area), and that the sum of branch area just above a branching point equals the branch area just below the branching point. The results of this study indicate that these assumptions are generally valid (Figure 1 and left panels of Figure 4). Although it was reported for Scots pine (Nikinmaa 1992) and Cryptomeria japonica (L.f.) D. Don (Yamamoto and Kobayashi 1993) that the cross-sectional area of the trunk at the crown base was smaller than the sum of branch cross-sectional area, these trees were large (diameter > 10 cm) and the stems included heartwood.

We found, however, that these two assumptions were invalid for the current-year growth in cross-sectional area. For the branches within the crowns, $\Delta A/\Sigma A\Delta A$ was markedly less than 1, and $\Delta A/F$ gradually decreased with increasing branch size (Figure 2 and the right panels of Figure 4). These trends indicate that diameter growth per unit of leaf area decreased toward the base. In other words, carbon allocation decreased in the basal direction within the crown.

The proportion of current-year cross-sectional area growth to cross-sectional area ($\Delta A/A$) generally decreases with increasing branch size and age. This fact and the constant $A/\Sigma A$ and $A/F$ ratios explain why the slopes in the right panels of Figure 4 are less than 1. However, for the basal parts of the trunks, $A$ was larger than $\Sigma A$ (left panels of Figure 4). Shinozaki et al. (1964a) obtained a similar finding and suggested that swelling of the trunk base is a result of the accumulation of disused pipes (i.e., of heartwood) that were connected to old branches that died back. However, we found that $\Delta A$ was larger than $\Sigma A\Delta A$ at the trunk base (right panels of Figure 4), indicating that biomass allocation increased toward the trunk base and that this also contributes to swelling of the trunk base. Several researchers have suggested that, when stems develop heartwood and leaf turnover is faster than heartwood formation, newly formed sapwood area per unit of new leaf area decreases (Kershaw and Maguire 2000, Vanninen and Mäkelä 2000, Valentine 2001, Mäkelä 2002), which might explain the decrease in $\Delta A/\Sigma A\Delta A$ with crown depth. However, there was no heartwood in our samples. If the age of the sapwood is greater than the leaf age, the leaves are connected to the older xylem as well as to the current-year xylem, which is always the case in deciduous *Acer* species having sapwood of multiple ages. This would at least partly explain the trend we observed, in which $\Delta A/\Sigma A\Delta A$ was less than 1 within the crown. The swelling at the trunk base would also contribute to mechanical support (Oohata and Shinozaki 1979) and to the increment of sapwood area per area, number or weight of leaves (Mäkelä et al. 1995). It is probable that the inner xylem at the trunk base gradually dies back and has low water conductivity.

The coefficients of determination between $A$ and $I_f$ were smaller than those for $W_f$ and $A_f$ (Figure 1). Values of $A/I_f$ were larger in shaded parts than in sunlit parts. It has been reported that sap flow rate is higher in the outer xylem than in the inner xylem (Kozlowski and Pallardy 1997, Domec and Gartner 2003). Sapwood may show a steeper radial gradient of water conductivity in older stems in shaded sites than stems in

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**Table 1. Partial correlation coefficients for the relationships between cross-sectional area growth per unit of leaf area ($\Delta A/Af$), relative irradiance ($RI$), mean current-year shoot length ($\bar{L}_S$) and vigor index (VI) of branches of *A. rufinerve* and *A. mono*. Values of $P < 0.05$ were considered significant.**

<table>
<thead>
<tr>
<th>Relationship</th>
<th>$A. rufinerve$ ($n = 193$)</th>
<th>$A. mono$ ($n = 77$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Delta A/Af$ versus $RI$</td>
<td>$0.575$</td>
<td>$0.194$</td>
</tr>
<tr>
<td>$\Delta A/Af$ versus $\bar{L}_S$</td>
<td>$0.482$</td>
<td>$0.601$</td>
</tr>
<tr>
<td>$\Delta A/Af$ versus VI</td>
<td>$0.051$</td>
<td>$-0.137$</td>
</tr>
<tr>
<td>RI versus $\bar{L}_S$</td>
<td>$0.185$</td>
<td>$0.151$</td>
</tr>
<tr>
<td>RI versus VI</td>
<td>$0.050$</td>
<td>$0.229$</td>
</tr>
<tr>
<td>$\bar{L}_S$ versus VI</td>
<td>$0.123$</td>
<td>$0.149$</td>
</tr>
</tbody>
</table>

**Table 2. Partial and standardized regression coefficients for the multiple regression analysis of cross-sectional area growth per leaf area ($\Delta A/Af$) as a function of relative irradiance ($RI$), mean shoot length ($\bar{L}_S$; mm) and vigor index (VI) of branches of *A. rufinerve* and *A. mono*. The regression model is $\Delta A/Af = b_0 + b_1(RI) + b_2(L_S) + b_3(VI)$, where $b_0$ is a constant, $b_1$ are partial regression coefficients. Values of $P < 0.05$ were considered significant.**

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Partial regression coefficients</th>
<th>Standardized partial regression coefficients</th>
<th>$P$ values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A. rufinerve$ ($n = 193$, $R^2 = 0.710$, $P &lt; 0.0001$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RI</td>
<td>$1.766 \times 10^{-4}$</td>
<td>$0.229$</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>$\bar{L}_S$</td>
<td>$3.332 \times 10^{-7}$</td>
<td>$0.404$</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>VI</td>
<td>$3.040 \times 10^{-6}$</td>
<td>$0.017$</td>
<td>$0.673$</td>
</tr>
<tr>
<td>Intercept</td>
<td>$1.236 \times 10^{-5}$</td>
<td>$1.236 \times 10^{-5}$</td>
<td>$0.017$</td>
</tr>
<tr>
<td>$A. mono$ ($n = 77$, $R^2 = 0.445$, $P &lt; 0.0001$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RI</td>
<td>$1.392 \times 10^{-4}$</td>
<td>$0.162$</td>
<td>$0.095$</td>
</tr>
<tr>
<td>$\bar{L}_S$</td>
<td>$5.835 \times 10^{-7}$</td>
<td>$0.605$</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>VI</td>
<td>$-7.668 \times 10^{-6}$</td>
<td>$-0.107$</td>
<td>$0.241$</td>
</tr>
<tr>
<td>Intercept</td>
<td>$2.420 \times 10^{-5}$</td>
<td>$2.420 \times 10^{-5}$</td>
<td>$0.0004$</td>
</tr>
</tbody>
</table>
well-lit sites. In contrast, If was a better determinant of $\Delta A$ than $Wf$ or $Af$ (Figure 2), indicating that light interception is a more important determinant of branch diameter growth than of leaf area or leaf mass. The strong relationships between $\Delta A$ and If imply that the xylem produced in the current year is a major pathway for sap flow in these maple species.

The value of $\Delta A$ was strongly dependent on leaf number increment ($\Delta N_f$) in A. rufinerve (Figure 3), whereas in A. mono, this relationship was no stronger than that between $\Delta A$ and Nf, and the plot patterns were similar to each other. These findings indicate that $\Delta N_f$ is proportional to Nf. This may occur in cases where: (1) sample trees are young and small and $\Delta N_f$ is a major portion of Nf; and (2) sample trees are old or located in shaded sites, where shoot elongation is negligible and leaf increment is small and constant. In the second scenario, sink strength is homogeneous among the branches within a tree. The first scenario probably accounts for the relationships observed in the A. mono trees. The strong relationship between $\Delta A$ and $\Delta N_f$ is consistent with theoretical predictions (Valentine 1985, Mäkelä 1986). Our findings raise two questions: Which factor determines stem diameter growth, light interception or leaf increment, and what is the physiological mechanism?

Branch diameter growth per leaf area ($\Delta A/\Delta f$) depended on RI in A. rufinerve, but not in A. mono (Tables 1 and 2). The reason for the limited dependency in A. mono could be a result of the much smaller variation in RI in this species ($RI = 0.007–0.189$) compared with A. rufinerve ($RI = 0.011–0.855$). Hanba et al. (2002) showed that leaf mass per area and photosynthetic capacity on a leaf-area basis increases with site irradiance in both Acer species. Thus, RI probably affected photosynthetic production in both A. mono and A. rufinerve.

In both species, $\Delta A/\Delta f$ depended on the mean length of current-year shoots in the branch ($L_s$) (Tables 1 and 2), indicating that the elongation rate of the whole branch was important for branch diameter growth. Elongation of the current-year shoot enhances the annual increment in leaf number because long shoots generally have more leaves. Auxin, synthesized in active shoot apices and young leaves, is transported basipetally from the tips and activates branch elongation and cambial growth (Mohr and Schopfer 1995). It is probable that branch diameter growth is enhanced by auxin synthesized by many long shoots or leaders. On the other hand, many short shoots receiving strong light would be net producers (i.e., sources rather than sinks) of photosynthates and probably contributed to the growth of trunk parts, in particular swelling of the trunk base and growth of the root system.

Goulet et al. (2000) and Nikinmaa et al. (2003) showed that shoot elongation depends on light availability and the VI of the VI of the shoot (VIs). We found that the partial correlations among $L_s$, RI and VI of the branch were slight or insignificant (Table 1). Moreover, VI of the branch was a poor determinant of $\Delta A$ of the branch, probably because the elongation and VIs of shoots showed large variation even within a branch. Moreover, elongation of each shoot within branches with similar RI or VI differed considerably (data not shown). Some individual branches contained both long and short shoots, and both a leader and lateral daughter branches.

We conclude that the major factor responsible for leaf increment is shoot elongation, with branch diameter growth within the crown being determined by the balance between supply of photosynthates, which depends on light conditions (RI), and the demand for photosynthates created by the high cambial activity associated with vigorous shoot elongation ($L_s$ or $\Delta N_f$).

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