

Effect of branch position and light availability on shoot growth of understory sugar maple and yellow birch saplings

Julie Goulet, Christian Messier, and Eero Nikinmaa

Abstract: Phenotypic plasticity enables tree saplings to change their morphology according to their environment to grow toward a better light micro-habitat. Therefore, processes of crown development could be expected to vary as a function of light. The objectives of this study were to (i) evaluate the effects of position and light availability on shoot growth within the crowns of understory saplings of sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton.); (ii) develop a new vigour index for shoots; and (iii) evaluate the possible factors relating to branch mortality in the crown of sugar maple saplings. The results revealed that there is a clear branch position effect on shoot growth in the crown for yellow birch saplings and that it is partly related to the presence of two types of shoots. Dead branches were located at the bottom of the crown of sugar maple saplings; they were smaller in size, had wider angles and had lower indexes of vigour than live branches found nearby. Preliminary results obtained on the vigour index indicate that it is a potentially useful tool for predicting the growth and vigour status of a branch.

Key words: shoot growth, branch position, light availability, branch mortality, sugar maple, yellow birch.

Résumé : Les caractéristiques architecturales sont le reflet des particularités de chaque espèce et elles varient selon leur degré de tolérance à l'ombre. Les objectifs de cette étude étaient (i) d'analyser les effets du positionnement des branches et de la disponibilité en lumière sur la croissance des pousses dans la couronne de gaulis d'érables à sucre (*Acer saccharum* Marsh.) et de bouleaux jaunes (*Betula alleghaniensis* Britton.) poussant sous couvert forestier; (ii) de développer un nouvel indice de vigueur des branches et (iii) d'analyser les facteurs affectant la mortalité des branches chez l'érable à sucre. Les résultats obtenus démontrent qu'il y a un effet de position marquée sur la croissance des pousses dans la couronne des gaulis de bouleau jaune en partie dû à la présence de deux types de rameaux. Les branches mortes sont localisées dans le bas de la couronne des gaulis d'érable à sucre, elles sont de plus petites tailles, elles sont moins vigoureuses et ont des angles plus grands que les branches saines. Les travaux préliminaires sur le développement de l'indice de vigueur indiquent qu'associé à la lumière, il prédit de façon satisfaisante la croissance et la vitalité des branches.

Mots clés : accroissement des branches, position des branches, disponibilité de la lumière, mortalité des branches, érable à sucre, bouleau jaune.

Introduction

The architecture of a tree determines the location of photosynthetic surfaces and is the most important determinant of light interception. Crown development is the result of endogenous growth processes that are genetically programmed for each species and the effect of the environment on these growth processes (Barthélémy et al. 1989). A sympodial or monopodial shoot system, plagiotropic or orthotropic branches, and simple or compound leaves are some of the features that

discriminate one species from another. Branch arrangement, leaf display, and the degree of overlap are characteristics that can help associate a species with the habitat in which it has evolved. Species can modify their architecture according to light availability, and the degree of plasticity is believed to be related to shade tolerance status (Canham 1988; Steingraeber et al. 1979; Steingraeber 1982a, 1982b). Late successional species are believed to have greater morphological plasticity than early successional species (Canham 1988). Tree architecture also varies with the ontogenic development stage and the age of the tree (Hallé and Oldeman 1970; Millet 1998).

For tree saplings growing in a shaded environment, light interception is a strong determinant of survival. Some species extend their crown horizontally by developing an umbrella shape (i.e., by increasing their ratio of lateral to height growth), which improves light interception. This is especially true for shade-tolerant conifers such as fir and spruce (O'Connell and Kelty 1994) as well as shade-tolerant deciduous species such as maple (Beaudet and Messier 1998; Aubin 1999).

Received November 26, 1999.

J. Goulet and C. Messier.¹ Groupe de recherche en écologie forestière interuniversitaire (GREFi), Université du Québec à Montréal, C. P. 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

E. Nikinmaa. Department of Forest Ecology, University of Helsinki, P.O. Box 24, 00014 Helsinki, Finland.

¹Author to whom all correspondence should be addressed (e-mail: messier.christian@uqam.ca).

Table 1. Sample size per light availability classes (% available PPFD).

Species	Light classes				Total
	<5%	6–10%	11–20%	>21%	
Sugar maple	11	11	13	5	38
Yellow birch	1	11	10	2	24

Crown architecture and the degree of lateral spreading can be quantified by the measurement of the ratio of lateral to height growth (Kohyama 1980), by the efficiency of leaf display (Canham 1988), or by the extension growth index (Lei and Lechowicz 1990). The ratio of crown length to crown diameter (Beaudet and Messier 1998) can also indicate how the crown development responds to light availability. All these crown-level morphological indices provide a way to measure plasticity in terms of light interception, but they do not provide any precise information on how this is achieved within the crown.

Hallé and Oldeman (1970) and Hallé et al. (1978) have studied tree architecture in the tropics based on the development of meristem growth. They identified 23 architectural models with which each species, tropical or temperate, can be associated. These models are based on the structure of trees, not on any functional attributes such as light interception. Tree architecture can be evaluated in terms of light interception through computer simulation. Such modelling is now being undertaken by several groups (De Reffye and Houllier 1997; Perttunen et al. 1996, 1998; Mech and Prusinkiewicz 1996; Takenaka 1994; Pearcy and Yang 1996).

Few studies have investigated how individual shoots within a tree grow in relation to light or position within a tree crown. Schoettle and Smith (1991) found that annual shoot length increment and integrated daily photosynthetically active radiation (DPAR) at shoot tips increased with increasing height in the crown of *Pinus contorta* ssp. *latifolia*. In conifers, apical control is pronounced and branching pattern, as well as shoot growth, is well regulated (Bollmark et al. 1995). Deciduous species have a more complex overall crown architecture that is not as well regulated.

The complex crown of broad-leaved trees makes the determination of branch position not so obvious. While there is not always a clear main stem, the branching system of trees has a clear topology. There are different branch classification systems that describe branch position within such topology. Although informative, these systems fail to consider that the difference in sizes of branches that has a strong influence on shoot functions. It has been suggested that the position of the shoot in the hydraulic pathway system will influence its performance (Zimmerman 1983). Shoots that are most proximal to the main stem are also best supplied with water and nutrients. On the other hand, shoot size and pathway thickness reflects vigorous growth, probable apical dominance, and thus a preferred position within the topology. The relative position of a growing meristem influences its growth, most likely through hormonal signalling (Staftstrom 1995).

Crown shape is an important determinant of tree sapling performance especially in the understory environment. Shoot growth and mortality have key roles in determining crown shape dynamics in different environments. The objectives of

this study were to (i) analyse the effect of position and light on shoot growth of understory yellow birch and sugar maple with heights of 201–300 cm, (ii) develop a new branch vigour index that could describe the response of shoot growth to light in different positions in the crown, and (iii) analyse the factors affecting branch mortality in sugar maple saplings with heights of 201–300 cm.

Material and methods

Study area

The study area is located at the Duchesnay Experimental Forest near Québec City, Canada, in a sugar maple – yellow birch – beech stand. In this region, mean annual precipitation is 1220 mm. Mean temperature is -12°C in January and 28°C in July. The study area is located in the northwestern part of the experimental forest ($46^{\circ}55'\text{N}$ and $71^{\circ}40'\text{W}$) at an altitude of 200–300 m with a slope range of 2–20%. The moder humus covers a podzol humo-ferric orthic soil that is underlain by a well-drained undifferentiated glacial till. A selection cut was performed in 1989 at the site of the study area removing approximately 30% of the basal area and creating gaps of different sizes.

Sampling

Field work was performed in the summer of 1997, between May 15 and September 15. Four 100-m transects, 20 m apart, with sampling plots at every 10 m were established on the site. Five sugar maple saplings with heights between 201 and 300 cm were randomly sampled in a 1-m radius circle in every plot. Since yellow birch saplings were much less abundant than sugar maple, we selected every birch sapling with a height between 201 and 300 cm encountered within 2 m of the transect lines. Care was taken that every selected sapling was undamaged.

Light availability was measured above each sapling to characterise the light conditions in which they were growing. Individuals were then subsampled randomly within each light class (% available photosynthetic photon flux density (PPFD)) to obtain a good light gradient (Table 1). A total of 36 sugar maple and 19 yellow birch were sampled the first year. A second sampling was performed in the summer of 1998 to obtain more trees in environments with greater light levels. A total of five yellow birch and two sugar maple with heights between 201 and 300 cm were selected randomly in gaps in July of the second year. All individuals were classified into one of four light environment classes.

Light measurements

Light availability was measured, using the technique described by Parent and Messier (1996), in late July and early August. This technique consists of measuring the diffuse radiation reaching the forest understory. A sensor connected to a datalogger (LI-1000, LI-COR, Lincoln, Nebr.) was installed in an open area to record the PPFD (in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) available over the forest canopy (PPFD₀). A hand-held sensor (LI-189, LI-COR) was used simultaneously under the forest canopy (PPFD_x) to measure the light availability in different locations. The percentage of light available under the canopy was obtained by dividing the value measured under the forest canopy by the value obtained in the open area (PPFD_x/PPFD₀ × 100). Light availability was measured above the terminal leader, above the upper branch, a randomly chosen middle branch and the lowest living branch for all saplings of both species. In addition, light was also measured above dead branches in the crown of sugar maple saplings. The branches were tagged to ensure that the architectural measurements would be taken on the same branches for which the light was measured.

Sapling measurements

Shoot growth increment was measured at the end of the growing season from the same branches above which the light was measured.

For all the measurements, the order 0 was attributed to the main stem. First order branches are those directly attached to the main stem, second order branches are attached to first order branches, and so on. The height of attachment of first order branches on the main stem was measured from the ground. The length was also measured for all first order branches and the age was determined from bud scale scars when visible. The diameter at the base of the branches and at the base of the growth increments was measured to the nearest 0.1 mm on all branches using a caliper. For sugar maple saplings, dead branches were measured using the same procedure as for living branches.

To study the possible influence of the position of shoots and to describe the shoot position within a tree crown in a more functionally justifiable manner, we calculated a vigour index (VI) and determined if it correlated favourably with growth. The VI value of the axis below the branching point by v_0 is denoted. Then the equation for VI values of axes i ($i = 1, \dots, n$) that fulfils the above requirements can be specified as:

$$[1] \quad v_i = \left(\frac{d_i}{d_M} \right)^2 v_0$$

where d_i is the diameter of axis i and d_M is the maximum thickness of axes forking away towards the apex ($d_M = \max(d_i \mid i = 1, \dots, n)$) (Fig. 1). The value of VI for the shoot at the end of a stem or branch axis is the product of consecutive VI's at each branching point from the base of the stem to the branch tip in question. The VI value for the thickest branch leaving the branching point is thus 1 (equal to the main stem). Since the values for the main stem are always one by definition, the VI of the shoot at the end of the main stem is one. The higher the branching order, the smaller the value since each time a minor branch forks away from the main branch the accumulated product up to that point is multiplied by a value that is smaller than one.

The diameters over the branch junctions on the main stem were not measured directly but were estimated from the diameters of branches located above the branch junction. This estimation is based on the Pipe Model Theory (Shinozaki et al. 1964) assuming that the branches and stem of these fairly small saplings consists of sapwood only. Earlier studies have shown that under such conditions, the sum of the branch area is a fairly good estimator of the stem diameter (Hari et al. 1986).

Statistical analysis

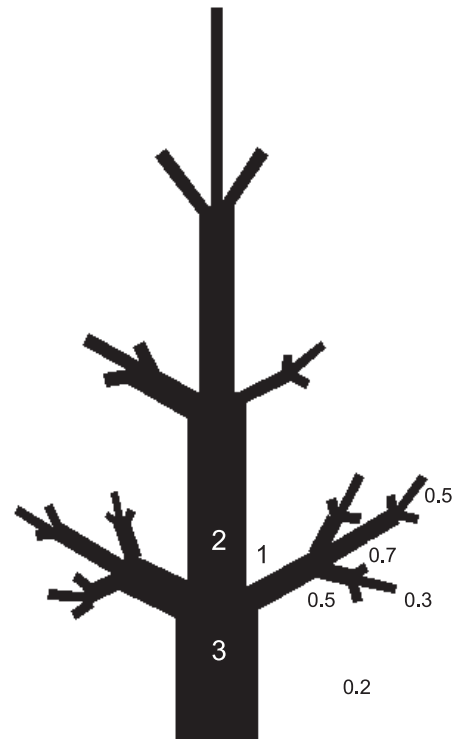
ANCOVA analyses were used to verify if the relationships between the growth increment and light were the same for every branch position for each species. Residuals normality was tested using a non-parametric Kolmogorov–Smirnov one-sample test with Lilliefors option. A t test was used to compare differences between dead and live branches for sugar maple. Finally, multiple regression analyses were used to test if the growth increment can be predicted by the VI associated with light availability. The significance level used was $P < 0.05$ for every analysis. Version 7.0 of SYSTAT was used for every analysis (SPSS 1997).

Results

The effect of branch position and light on shoot growth

Covariance analyses were made between the shoot growth increment (GI) and the percentage of light for four positions in the crown of sugar maple saplings. This analysis revealed that the relation between GI and light did not vary between

Fig. 1. An example of the vigour index calculation. VI is a product of consecutive values that is obtained when the woody pathway from base to tip is followed (see text for explanation). For example, the VI of the shoot marked with an arrow is $1/2 \times (0.5/0.7) \times (0.2/0.3) = 0.24$.



positions in the crown (i.e., the interaction factor between branch position and percent PPFD was not significant) (Fig. 2; Table 2). In other words, the slopes were similar and there was no branch position effect. Light and branch position together explained 55% of the variation observed around shoot growth in the ANOVA model for sugar maple saplings. Branch position alone was not significant in the model.

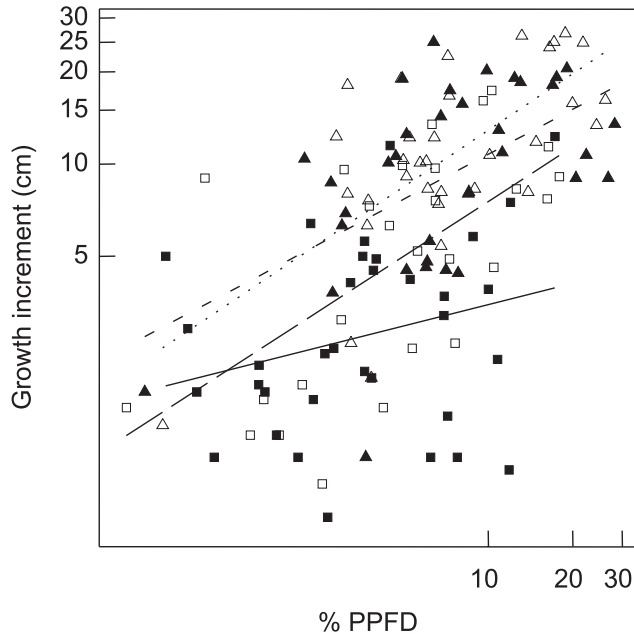
The covariance analysis performed for yellow birch between shoot GI and percentage of light for the four positions gave significant results. The interaction factor between percentage of light and branch position was significant (Fig. 3, Table 2), indicating a difference in slopes. There is a clear branch position effect for this species. The bottom and middle branches did not respond to an increase in light availability compared with the terminal leader and the upper branch position (Fig. 3). Light and branch position together explained 64% of the variability observed for growth in the ANOVA model.

The comparison of shoot GI by branch position between species revealed that there was a significant difference between the bottom branch, upper branch, and terminal leader GI (Fig. 4, Table 3). The GI for the terminal leader and upper branch positions was more pronounced in yellow birch than in sugar maple, but sugar maple has a larger GI for the bottom part of the crown than yellow birch.

The effect of vigour and light on branch shoot growth

Multiple regression analyses carried out for both species separately for branch GI, light, and the vigour index re-

Fig. 2. The logarithm of the shoot growth increment as a function of the logarithm of percent PPFD for branches from four positions in the crown of sugar maple saplings. ■, bottom branch; □, middle branch; ▲, upper branch; △, terminal leader. Lines are limited to data range. ANCOVA statistics are provided in Table 2.



vealed that the relation between growth and light did not vary with an increase in the vigour index (i.e., the interaction factor was not significant for both species) (Figs. 5 and 6, Table 4). Light and vigour alone were significant factors in the ANOVA models for sugar maple and yellow birch, and they explained 62 and 57% of the total variation observed in growth for each of these two species, respectively.

Sugar maple branch mortality

The height of the attachment of dead branches on the main stem was significantly lower than that of live branches ($P < 0.000$; 152 ± 43.4 cm for live branches and 95.3 ± 37.2 cm for dead branches). Therefore, a subsample of live branches located in the bottom of the crown and at a comparable height to that of the dead branches ($P = 0.130$) was used for further analysis. Light availability measured above the apex of dead branches was not significantly different from that measured above live branches located in the same locations in the lower part of the crown (Table 5). The mean age of dead branches was not significantly different from that of the live branches. Dead branches had significantly larger angles than live branches. Both diameter and total length of the dead branches were significantly lower than those of live branches. Dead branches had significantly lower vigour indexes than live branches (Table 5).

Discussion

Growth patterns and shade tolerance

Shoot growth in the crown of sugar maple saplings seems to be well-regulated by light availability and much less or not at all by position within the crown. Only branches in the

lower part of the crown seem to show less growth than branches in other positions, but the differences were not significant. These results suggest that there is very little apical control from the terminal leader over the lower branches. As Millet (1997) discussed, forking in the crown of sugar maple saplings causes apical dominance to be shared between multiple axes. Forking delays the establishment of a true main axis, at least temporarily, and can be beneficial in a shaded environment (Millet 1997; Nicolini and Caraglio 1994). The fact that growth seemed to be significantly correlated with light and vigour index would support Millet's conclusion about apical control of shoot growth.

Yellow birch shoot growth was also well-regulated by light availability, but this was true only for the terminal leader and upper branch. Lower branches did not show much growth, and growth was not related to light availability. This lack of response to light by lower branches can be explained, in part, by the presence of short shoots in the lower part of the crown. Short shoots are characterised by a lack of elongation and are usually located in the lower part of the crown in the more shaded environments (Maillette 1982; MacDonald and Mothersill 1983). On the other hand, long shoots are characterised by a pronounced elongation and are usually located in environments with more light (i.e., in the upper part of the crown) (Maillette 1982; MacDonald and Mothersill 1983). Our results suggest that short shoot formation in yellow birch is not only the result of a low light environment, but mainly of the position within the branch and the crown since short shoots received as much as 14% PPFD. The presence of these two types of shoots in the crown of yellow birch saplings is believed to contribute to the multi-layered morphology (*sensu* Horn 1971) of this species according to White (1983). It is also not clear if this species is showing a strong apical dominance since both terminal and upper lateral shoots responded similarly to the light gradient investigated. The shoot system of yellow birch, with short and long shoots, is believed to maximize height growth while minimizing energy expenditure on less efficient supportive woody structure (Sakai 1987). Such a system is regarded as advantageous in competitive environments like canopy gaps where rapid height growth might be rewarded with increased light availability (Sakai 1987). Kozłowski and Clausen (1966) observed the same type of growth pattern for *Populus tremuloides* and *Populus grandidentata*, two species also possessing the long and short shoot system.

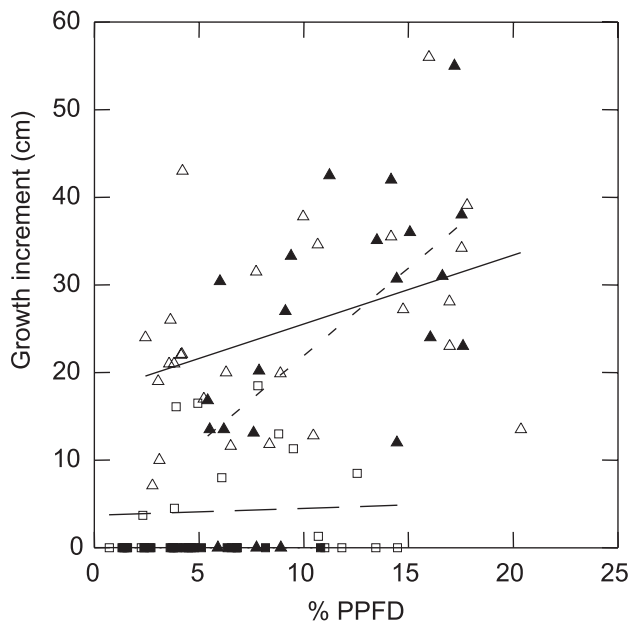
A comparison of overall shoot growth between sugar maple and yellow birch showed some clear differences in growth strategies. Yellow birch seemed to allocate more resources to the shoots in the upper crown receiving more light to maximize light capture where light is more available. Furthermore, the indeterminate growth of yellow birch saplings and the maintenance of numerous short shoots in the lower part of the crown may enable this species to respond well to any sudden increase in light availability as found in gaps (Sakai 1987). According to King (1994), height growth is important for the response of saplings to gaps because it determines the amount of time that a sapling will survive in the gap environment before the gap closes. These results agree with those reported by Beaudet and Messier (1998) showing that understory yellow birch had a better capacity for height and lateral growth than understory sugar maple.

Table 2. A summary table of the ANCOVA used to test the effect of light on the shoot growth increment (GI) of branches at four positions (BP) in the crown of sugar maple and yellow birch saplings.

Source	Sugar maple				Yellow birch			
	df	MS	F ratio	P	df	MS	F ratio	P
%PPFD	1	19.527	48.363	<0.000	1	1125.6	13.290	<0.000
BP	3	0.535	1.326	0.269	3	478.79	5.653	0.001
%PPFD × BP	3	0.668	1.656	0.180	3	252.74	2.984	0.036
Error	121	0.404			88	84.699		

Note: R^2 is 0.55 for sugar maple and 0.64 for yellow birch. The ANCOVA model is $GI = \text{constant} + \%PPFD + BP + (\%PPFD \times BP)$. GI and percent PPFD were transformed with the natural logarithm to have normally distributed residuals in the sugar maple model. $P < 0.05$ were considered significant. The light gradient was from 1 to 30%.

Fig. 3. Shoot growth increment as a function of %PPFD for branches from four positions in the crown of yellow birch saplings. ■, bottom branch; □, middle branch; ▲, upper branch; △, terminal leader. Lines are limited to the data range. ANCOVA statistics are provided in Table 2.

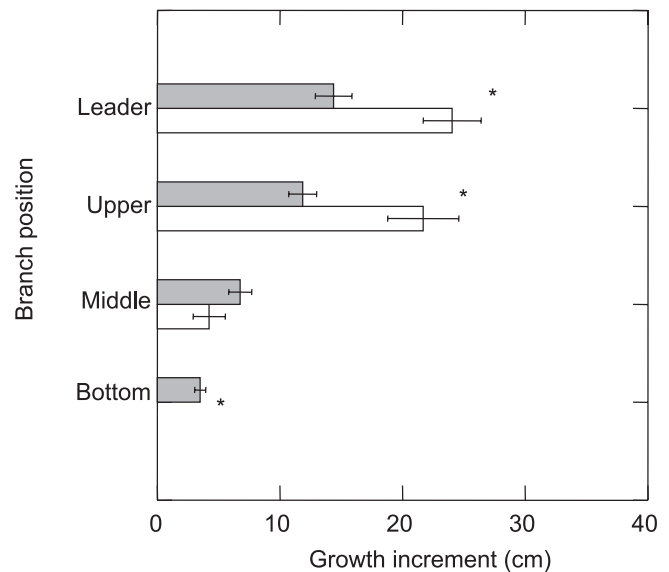


Branch mortality

Very few dead branches were found on understory yellow birch saplings. The reason for this is unclear, but it might be related to the ability of yellow birch to stop shoot growth by producing short shoots when the branch becomes less vigorous. Sugar maple, on the other hand, had numerous dead branches, mainly in the lower section of the crown. These dead branches were not receiving less light, but they were smaller, had a wider angle and had a much lower vigour index than live branches of similar position.

The vigour index was a good parameter for explaining branch mortality, presumably because it includes the growth history of the branch, the size, and the relative position in the crown in the calculation. Older branches located in the bottom of the crown are thought to be mostly autonomous in their carbon balance. Therefore, branches with a low vigour index may not receive the water and nutrients they need to continue to grow, even if they receive enough light (Sprugel et al. 1991). This difficulty of obtaining water and nutrients

Fig. 4. Comparison of the growth increment by branch position between yellow birch (empty bars) and sugar maple (dotted bars) saplings. *, significant differences in growth increment between species. ANOVA statistics are provided in Table 3.



by branches with a lower vigour index could explain why they tended to be much smaller than adjacent live branches.

Dead branches also had wider angles than live branches. This result agrees with other studies that found that branches located at the bottom of the crown were wider, partly to avoid self-shading and because of self-weight (Bozzuto and Wilson 1988; Veres and Pickett 1982; Pickett and Kempf 1980); however, it does not explain why they were wider than the live ones that were in the same position. As Bozzuto and Wilson (1988) mentioned, it is difficult to associate branch angle with branch dimensions, age, or status because actual branch angle is the result of branch angle at the time of branch formation and growth history of the branch. Further investigation would be necessary to explain the cause of the wider angles of dead branches.

Vigour index

Most of the vigour indices for branches that exist in the literature are based on visual observation. Ouellet and Zarnovican (1988) used the IUFRO classification criteria to classify trees in a young yellow birch stand to provide a new tool for the selection of trees that would form a future stand. Coursolle (1996) used a branch classification that is based

Table 3. A summary of the ANOVA used to test the effect of branch position on shoot growth increment (GI) in the crown of sugar maple and yellow birch saplings.

Branch position	Dependant factor	MS	F ratio	df	P
Leader	GI	1733.270	15.041	1,55	<0.000
Topmost	GI	2421.399	21.952	1,58	<0.000
Middle	GI	87.437	2.703	1,54	0.106
Bottom	GI	112.889	56.598	1,52	<0.000

Note: $P < 0.05$ indicated a significant difference in GI.

Fig. 5. Logarithm of branch growth increment as a function of the logarithm of %PPFD for branches of sugar maple saplings. Symbol size is the logarithm of the vigour index (VI) value. Multiple regression statistics are provided in Table 4.

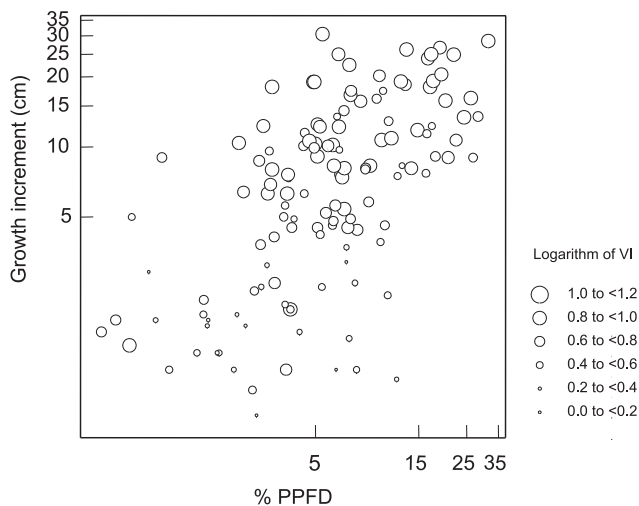
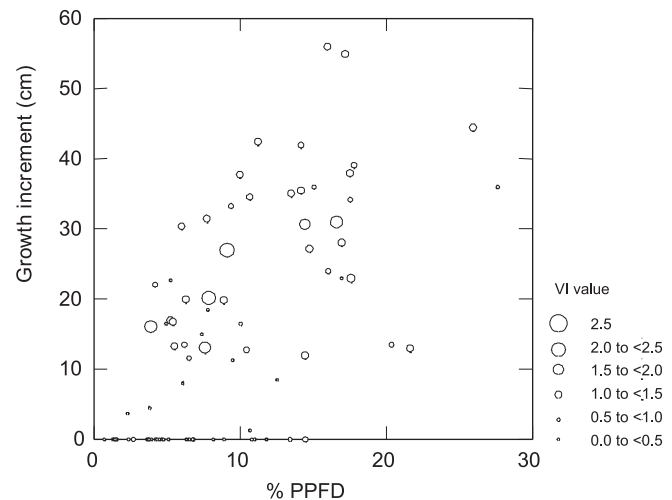


Fig. 6. Branch growth increment as a function of %PPFD for branches of yellow birch saplings. Symbol size is the vigour index (VI) value. Multiple regression statistics are provided in Table 4.



on a visual classification of tree vigour for European beech. This classification is based on the degree of damage caused by stress and considered to cause die back. The interpretation of vigour is based on the observation of the number of long shoots that a branch can produce. Coursolle (1996) found that leaf morphology and spectral properties of leaves differed with the vitality class of the supporting branch. Also, Coursolle (1996) suggested that the vitality of the supporting branch was associated with relative growth of the branch or leaves. She found that vigour was associated with length of the supporting branch and light quantity, but she could not confirm that light availability and the relative position of the branch in the crown was associated with vigour.

Our formulation of branch vigour index is a readily measurable value. It takes into consideration the topology of the branch (i.e., the relative position in the crown). With the use of the cross-sectional area ratios, the index includes the growth history of the branch in the measurement. When used with light availability, it was found to be a good predictor of the growth increment of branches. Coursolle (1996) could not confirm that branch vitality was associated with the relative position in the tree crown or with growth. Also, the classification used by Coursolle (1996) was developed for trees with long and short shoots in their crown and could not have been used for sugar maple.

The vigour index is similar to branch classification systems such as gravelius order (MacDonald and Mothersill 1983), which states that major change takes place at forking.

In our case, the index value is multiplied with a number smaller than or equal to one. Therefore, as branching proceeds, the index yields gradually smaller values. This is similar, for example, to the branching order increases in the gravelius classification. Unique to our vigour index is that the difference is proportional to the size of the branch. When looking along an axis, the branches close to the leader yield comparable, if somewhat smaller values, since they are very similar in size. However, in the lower part of the crown, similar size branches near the end of the axis have much lower values since they are compared to the thickness of the main axis at the same forking point.

The results for sugar maple show that vigour and light are not necessarily autocorrelated. The index is very good at describing and quantifying the autocorrelative nature of branch growth, i.e., big branches tend to grow faster whereas small ones grow gradually less and less. It is often observed that among branches growing close together, some grow well and some do not or die, even if there are no obvious difference in light climate (Staftstrom 1995). As we observed in this study, vigour index was very highly correlated with mortality. Our vigour index could therefore be used to predict which branches are more likely to die.

The presence of short shoots in yellow birch makes the use of the VI more problematic since they may support branches for a long time without any observable growth, thus leading to very low VI values. In fact, the relationship was not as good for yellow birch compared with sugar ma-

Table 4. A summary of statistics for the multiple regression using growth increment (GI), vigour index (VI), and %PPFD for sugar maple and yellow birch saplings.

Source	Sugar maple			Yellow birch		
	Slope	<i>P</i>	<i>R</i> ²	Slope	<i>P</i>	<i>R</i> ²
%PPFD	0.549	<0.000	0.624	0.966	0.021	0.565
VI	0.359	0.001		10.120	0.046	
%PPFD × VI	0.092	0.130		0.396	0.459	

Note: The regression model is $GI = \text{constant} + \%PPFD + VI + (\%PPFD \times VI)$. GI, percent light, and VI for sugar maple were transformed with the natural logarithm. $P < 0.05$ was considered significant.

Table 5. Differences between live and dead first-order branches for sugar maple saplings using a *t* test.

Variables	Branch state	<i>n</i>	Mean ± SD	df	<i>P</i>
Light above branch apex	Live	63	5.0 ± 4.1	93	0.233
	Dead	32	4.0 ± 2.7		
Age	Live	60	7.6 ± 3.1	87	0.640
	Dead	29	7.9 ± 3.6		
Angle (°)	Live	63	57 ± 22	93	0.001
	Dead	32	72 ± 19		
Diameter (cm)	Live	63	5.08 ± 1.86	93	0.008
	Dead	32	3.95 ± 2.00		
Length (cm)	Live	63	60.1 ± 35.5	93	0.042
	Dead	32	44.2 ± 36.0		
Vigour	Live	63	0.209 ± 0.202	93	0.001
	Dead	32	0.088 ± 0.071		

Note: $P < 0.05$ indicated a significant difference between the two types of branches.

ple. Also, some vigour values were higher than one, particularly for branches in the crown of yellow birch saplings. As mentioned earlier, we found that apical dominance is not well differentiated between the terminal leader and the upper lateral branch in the crown of yellow birch saplings. Lateral branches were often found to be bigger and more vigorous than terminal leaders. The calculations of the vigour index were done using the main axis from a developmental point of view, which sometimes differs from the thickest pathway. This could have contributed to the lower relationship observed for yellow birch.

Changes that take place in wood properties as wood axes age (Gartner 1995) may also influence the generalisation of the results. We estimated the stem area above each branching point with the sum of the branch cross-sectional area above that point. In small trees this estimation is most likely fairly good, since there is hardly any heartwood present, but as trees grow and age heartwood proportion will start to vary (e.g., Sievänen et al. 1997). In such a case, our estimation would not be a very good estimator of the stem thickness and it is questionable whether or not the vigour index would work for such branches. The hypothesis of hydraulic architecture of trees proposes that the leaf specific conductivity of the main axes would be larger than that of the distal ones (Zimmermann 1983). Then shoots that are at the end of the thickest pathways would be hydraulically preferred and thus could maintain higher photosynthetic rates than side branches in similar light. In cases where much of the cross-section is heartwood, this argumentation does not work. A large branch with a high proportion of heartwood is more likely to be a declining branch with low vigour than a vigor-

ous one as the index would suggest. To calculate the vigour index in such a situation, sapwood areas instead of total areas or thickness of different axes should be used. The sum of the sapwood cross-sectional areas of side branches is a much better predictor of the “active wood” than total diameter. Based on the pipe model (Shinozaki et al. 1964), the total sapwood area of all side branches has often been shown to be highly correlated to that of the main stem measured at crown base (e.g., Hari et al. 1986; Nikinmaa 1992; Berninger et al. 1995).

Furthermore, wood permeability changes that take place with developing trees may also influence the vigour index estimates, so that the relationship between our vigour index and shoot growth would not remain the same in different size trees. Whitehead et al. (1984) and Pothier et al. (1989) showed that in conifers considerable permeability changes may be present in wood and that these could influence the wood–foliage relationship. Wood structural properties vary vertically and as a function of tree ring depth in conifers (Gartner 1995). Berninger and Nikinmaa (1994) also noted that the foliage area – sapwood area relationship was changing within the crown of Scots pines. If the basic reason for the relationship between vigour index and axis length growth is due to hydraulic considerations, then these types of changes would influence the usability of our vigour index to predict shoot growth.

Overall, we think our vigour index is a promising tool for describing the vigour status of various branches within a tree and that it offers quantitative measurements of vigour that are more precise than visual observations. Because it is easy to measure, it can be used to parameterise 3-D tree models

and improve the realism of simulations of tree crown development. However, more work is still needed to evaluate wider usability of the method for predicting shoot dynamics within tree crowns, especially larger ones. This is connected to better understanding of the underlying mechanisms that cause formation of such structural relationship.

Acknowledgements

Financial support was provided by an NSERC strategic grant to C. Messier and by a GREFi and PAFARC (UQAM) scholarship to J. Goulet. We wish to thank E. Duplessis and S. Hamel for their valuable assistance with the field work and especially M. Beaudet for her support and comments on an earlier version of the paper. An earlier version of this paper was reviewed by M. Lechowicz and E. Lo.

References

- Aubin, I. 1999. Végétation de sous-bois et disponibilité de la lumière dans la forêt boréale du sud-ouest québécois. M.Sc. thesis, Département des sciences biologiques, Université du Québec à Montréal. Montréal, Qué.
- Barthélémy, D., Édelin, C., and Hallé, F. 1989. Architectural concepts for tropical trees. *In* Tropical forests. Edited by L.B. Holm-Nielsen, I.C. Nielson, and H. Balslev. Botanical dynamics, speciation and diversity. Academic Press, London, pp. 89–100.
- Beaudet, M., and Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* **28**: 1007–1015.
- Berninger, F., and Nikinmaa, E. 1994. Geographical variation in the foliage mass-wood cross-sectional area ratios in young Scots pine stands. *Can. J. For. Res.* **24**: 2263–2268.
- Berninger, F., Mencuccini, M., Nikinmaa, E., Grace, J., and Hari, P. 1995. A relationship between the characteristics of woody structure of scots pine and climate; an analysis from hydraulic point of view. *Oecologia*, **102**: 164–168.
- Bollmark, M., Chen, H.J., Moritz, T., and Eliasson, L. 1995. Relations between cytokinin level, bud development and apical control in Norway spruce, *Picea abies*. *Physiol. Plant.* **95**: 563–568.
- Bozzuto, L.M., and Wilson, B.F. 1988. Branch angle in red maple trees. *Can. J. For. Res.* **18**: 643–646.
- Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, **69**: 786–795.
- Coursolle, C. 1996. Variations morphologiques et spectrales des feuilles du bouleau jaune (*Betula alleghaniensis* Britton.) en fonction du développement de la cime et du rayonnement solaire. Doctorat thesis, Université Laval, Québec, Qué.
- De Reffye, P., and Houllier, F. 1997. Modelling plant-growth and architecture—some recent advances and applications to agronomy and forestry. *Curr. Sci.* **73**: 984–992.
- Gartner, B.L. 1995. Plant stems physiology and functional morphology. Academic Press, San Diego, Calif.
- Hallé, F., and Oldeman, R.A.A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Masson et Cie, Paris.
- Hallé, F., Oldeman, R.A.A., and Tomlison, P.B. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin..
- Hari, P., Heikinheimo, P., Mäkelä, A., Kaipainen, L., Korpilahti, E., and Salmela, J. 1986. Trees as a water transport system. *Silva Fenn.* **20**: 205–210.
- Horn, H.S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, N.J.
- King, D.A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. *Am. J. Bot.* **81**: 948–957.
- Kohyama, T. 1980. Growth pattern of *Abies mariessi* saplings under conditions of open-growth and suppression. *Bot. Mag. Tokyo*, **93**: 13–24.
- Kozlowski, T.T., and Clausen, J.J. 1966. Shoot growth characteristics of heterophyllous woody plants. *Can. J. Bot.* **44**: 827–843.
- Lei, T.T., and Lechowicz, M.J. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. *Oecologia*, **84**: 224–228.
- LI-COR 1986. LI-COR Radiation Sensors Inc. Lincoln, Nebr.
- MacDonald, A.D., and Mothersill, D.H. 1983. Shoot development in *Betula papyrifera*. I. Short-shoot organogenesis. *Can. J. Bot.* **61**: 3049–3065.
- Maillette, L. 1982. Structural dynamics of silver birch. I. The fates of buds. *J. Appl. Ecol.* **19**: 203–218.
- Mech, R., and Prusinkiewicz, P. 1996. Visual models of plants interacting with their environment. *Comp. Graph. Proc.* **96**: 397–410.
- Millet, J. 1997. Rapports entre le mode de développement architectural des arbres et le statut successional des espèces en forêts feuillue tempérée. *In* Rapports entre le mode de développement architectural des arbres et le statut successional des espèces dans le Québec méridional. *Édité par* J. Millet. Doctorat thesis, Université de Montréal. Montréal, Qué. pp. 93–140.
- Millet, J. 1998. Plant succession and tree architecture: an attempt at reconciling two scales of analysis of vegetation dynamics. *Acta Biotheor.* **46**: 1–22.
- Nicolini, E., and Caraglio, Y. 1994. L'influence de divers caractères architecturaux sur l'apparition de la fourche chez le *Fagus sylvatica*, en fonction de l'absence ou de la présence d'un couvert. *Can. J. Bot.* **72**: 1723–1734.
- Nikinmaa, E. 1992. Analyses of the growth of Scots pine; matching structure with function. *Acta For. Fenn.* **235**: 1–68.
- O'Connell, B.M., and Kelty, M.J. 1994. Crown architecture of understory and open-grown white pine (*Pinus strobus* L.) saplings. *Tree Physiol.* **14**: 89–102.
- Ouellet, D., and Zarnovican, R. 1988. La conduite des jeunes peuplements de bouleaux jaunes (*Betula alleghaniensis* Britton.): caractéristiques morphologiques. *Can. J. For. Res.* **19**: 992–996.
- Parent, S., and Messier, C. 1996. A simple and efficient method to estimate microsite light availability under forest canopy. *Can. J. For. Res.* **26**: 151–154.
- Pearcy, R.W., and Yang, W. 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia*, **108**: 1–12.
- Perttunen, J., Sievänen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., and Väkevä, J. 1996. LIGNUM: A tree model based on simple structural units. *Ann. Bot.* **77**: 87–98.
- Perttunen, J., Sievänen, R., and Nikinmaa, E. 1998. LIGNUM: a model combining the structure and the functioning of trees. *Ecol. Model.* **108**: 189–198.
- Pickett, S.T.A., and Kempf, J.S. 1980. Branching patterns in forest shrubs and understory trees in relation to habitat. *New Phytol.* **86**: 219–228.
- Pothier, D., Margolis H.A., Poliquin J., and Waring, R.H. 1989. Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. J. For. Res.* **19**: 1564–1570.
- Sakai, S. 1987. Patterns of branching and extension growth of vigorous saplings of Japanese *Acer* species in relation to their regeneration strategies. *Can. J. Bot.* **65**: 1578–1585.

- Schoettle, A.W., and Smith, W.K. 1991. Interrelation between shoot characteristics and solar irradiance in the crown of *Pinus contorta* ssp. *latifolia*. *Tree Physiol.* **9**: 245–254.
- Shinozaki, K., Yoda, K., Hozumi, Z., and Kira, T. 1964. A quantitative analysis of plant form—the Pipe model theory. I. Basic analyses. *Jap. J. Ecol.* **14**(3): 97–105.
- Sievänen, R., Nikinmaa, E., and Perttunen, J. 1997. Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. *Silva Fenn.* **31**: 329–340.
- Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The theory and practice of branch autonomy. *Ann. Rev. Ecol. Syst.* **22**: 309–334.
- SPSS 1997. SYSTAT 7.0 for Windows. SPSS Inc., Chicago, Ill..
- Staftstrom, J.P. 1995. Developmental potential of shoot buds. *In* Plant stems physiology and functional morphology. *Edited by* B.L. Gartner. Academic Press, San Diego, Calif. pp. 257–279.
- Steingraeber, D.A. 1982a. Phenotypic plasticity of branching pattern in sugar maple (*Acer saccharum*). *Am. J. Bot.* **69**: 638–640.
- Steingraeber, D.A. 1982b. Heterophylly and neof ormation of leaves in sugar maple (*Acer saccharum*). *Am. J. Bot.* **69**: 1277–1282.
- Steingraeber, D.A., Kascht, L.J., and Franck, D.H. 1979. Variation of shoot morphology and bifurcation ratio in sugar maple (*Acer saccharum*) saplings. *Am. J. Bot.* **66**: 441–445.
- Takenaka, A. 1994. A simulation model of tree architecture development based on growth response to local light environment. *J. Plant Res.* **107**: 321–330.
- Veres, J.S., and Pickett, S.T.A. 1982. Branching patterns of *Lindera benzoin* beneath gaps and closed canopies. *New Phytol.* **91**: 767–772.
- White, P.S. 1983. Corner's rules in eastern deciduous trees: Allometry and its implications for the adaptive architecture of trees. *Bull. Torrey Bot. Club.* **110**: 203–212.
- Whitehead, D., Edwards, W.R.N., and Jarvis, P.G. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can. J. For. Res.* **14**: 940–947.
- Zimmerman, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.