Hydraulic architecture correlates with bud organogenesis and primary shoot growth in beech (*Fagus sylvatica*)

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Summary   In beech (*Fagus sylvatica* L.), the number of leaf primordia preformed in the buds determines the length and the type (long versus short) of annual growth units, and thus, branch growth and architecture. We analyzed the correlation between the number of leaf primordia and the hydraulic conductance of the vascular system connected to the buds. Terminal buds of short growth units and axillary buds of long growth units on lower branches of mature trees were examined. Buds with less than four and more than five leaf primordia formed short and long growth units, respectively. Irrespective of the type of growth unit the bud was formed on, the occurrence of a large number of leaf primordia was associated with high xylem hydraulic conductance. Xylem conductance was correlated to the area of the outermost annual ring. These results suggest that organogenesis and primary growth in buds correlates with secondary growth of the growth units and thus with their hydraulic architecture. Possible causal relationships between the variables are discussed.

Keywords: development, hydraulic conductance, leaf primordia, meristem, xylem.

Introduction

Branches of beech (*Fagus sylvatica* L.) trees are composed of different types of annual growth units that differ in morphology, branching patterns and primary and secondary growth (Daniel 1910). The spatial and temporal organization of these growth units are highly specific and define the architectural development of the species (Thiébaut 1982, Roloff 1988, Thiébaut et al. 1990*b*, Nicolini 1997, 1998). Annual growth units located near branch apices are known as "long shoots" because they bear many leaves, separated by elongated internodes, and thus form axes from several cm to several dm in length (Figure 1e). The long growth units are characterized by

substantial primary meristematic (Roloff 1985) and secondary cambial growth, and hence, these long growth units are mainly responsible for dry matter accumulation in the crown (Renard 1971) and for the characteristic growth habit of beech trees. The second type of annual growth unit is much shorter (< 1 cm), with few and barely visible internodes (Figure 1c). These "short shoots" remain slender and never branch. They typically form on the lower part of a 1-year-old long shoot. Most of the leaf area of a beech crown is associated with short growth units because most of the axilliary buds initiate short shoots that survive for many years (Renard 1971). Thus, short growth units are the primary assimilate-exporters, whereas long growth units are the primary users of assimilates in the production of wood. Hence, the relative production of long versus short growth units is likely to determine tree leaf area and wood production. Understanding how beech architecture and crown structure are elaborated is thus a decisive step in understanding beech physiology and how its productivity will respond to climatic changes.

Approaches to such studies have so far relied on architectural analysis (Thiébaut 1982, Thiébaut and Puech 1984, Roloff 1988, Nicolini 1998). These descriptive and statistical studies help identify the rules governing the morphological development of a tree. However, during its life, a given meristem can successively produce short and long annual growth units. Similarly, periods of soil drought or changes in light regime can affect the relative production of short and long annual growth units (Collet et al. 2001, 2002, Lemoine et al. 2002). Architectural and stochastic modeling does not correctly render these modifications, which occur on a small temporal and spatial scale. A functional explanation for this phenomenon is still lacking.

The objective of this study was to unravel some of the physiological mechanisms associated with the formation of short and long annual growth units in beech. We developed a new

approach that combines morphological, anatomical and eco-physiological observations. We measured both the hydraulic efficiency of the sap pathway supplying water to the buds and the carbon (C) isotope composition (δ^{13}C) of leaf primordia in the buds, a parameter determined by the intrinsic water-use efficiency of the leaves that synthesized the C in the buds (Farquhar et al. 1982). We focused our analysis on bud organogenesis. The rationale for this choice being that, in beech, leaves that expand in a given year were preformed in the bud during the growing season of the previous year (Roloff 1985, Druelle 1996); i.e., the number of leaf primordia present in a bud at the end of a summer corresponds to the number of leaves present on a growth unit the following spring (Roloff 1985, Druelle 1996). Thus, the fate of a beech bud (i.e., production of short shoots with few leaves versus long shoots with many leaves) is predetermined 1 year in advance by the meristematic activity of the buds. There is increasing evidence that hydraulic efficiency of trees may modulate shoot growth (Koch et al. 2004, Woodruff et al. 2004). Hence, we hypothesized that there is a positive correlation between bud growth activity and the hydraulic conductance (k_x) of the underlying vascular tissue. To test this hypothesis, we compared k_x of the vasculature supplying the different buds on a growth unit to their anatomical characteristics. We also measured the δ^{13}C of buds to obtain information on the microclimatological conditions under which their C was assimilated (Farquhar et al. 1982). The δ^{13}C of leaf photosynthates has been shown to be positively related to the light availability at the site of C fixation within the crown (Collet et al. 1993). This information enabled us to assess whether contrasting bud types differ in their constitutive C origins and, ultimately, in their C sink strength within the tree.

Materials and methods

Plant material

Experiments were conducted on beech trees (*Fagus sylvatica* L.) more than 100 years old from the Allagnat forest, near the Puy-de-Dome volcano in central France (45°45.23′ N, 2°56.26′ E, 1000 m a.s.l.). Trees were located along the northern edge of an east–west oriented forest road. Basal, south- oriented branches were sampled. These branches were partly exposed to direct sunlight during the day. Branches were sampled during the winter, in December 2000 and February 2001, when they were leafless and buds dormant. Branches sampled in the field were immediately brought to the laboratory for analysis.

Hydraulic measurements

Our objective was to compare the hydraulic efficiency of the xylem tissue connected to the meristematic tissues in the different buds on a shoot. A critical concern in this study was to ensure hydraulic values were comparable. The relevant hydraulic parameter determining the water supply available to the different buds is the k_x of the entire sap pathway, from branch base to bud base (Tyree 1988). This value correlates with the total xylem pressure drop along the sap pathway and, unlike hydraulic conductivity data, it takes account of the effect of path length on hydraulic efficiency. We measured the hydraulic efficiency of both whole branches (Figure 1a) and unbranched annual growth units (Figure 1c). In the first case, we measured the whole sap pathway conductance, from the branch proximal end to the different terminal ends. In the second case, we compared k_x values for annual growth units having the same architecture (e.g., 4-year-old short axes, 1-year-old long axes).

Values of k_x were derived from pressure–flow relationships obtained with a XYL'EM apparatus (Bronkhorst France, Montigny les Cormeilles, France). The proximal (basal) end of one sample was connected to the XYL'EM water tank containing deionized and filtered water (0.22 μm). The water pressure (*P*; MPa) in the tank was adjusted to between 0 and 0.5 MPa. Water entering the sample dripped rapidly from the distal (terminal) cut ends. The water pressure at these distal cut ends was thus nil (relative to atmospheric pressure) and the total pressure drop along the path length was thus equal to *P*. Water-filled tubing was firmly attached to each cut end and connected to the XYL'EM flow meter (5 g h^{-1} full scale) and the rate of water exudation through the cut end (F_i; mmol s^{-1}) was determined. We then computed k_x as the slope of F_i versus *P*. Thus, we did not measure whole-branch hydraulic conductance with this technique, but rather the hydraulic conductance of the individual sap pathways from the cut basal end to the different distal cut ends. In preliminary experiments with shoots having more than one bud (sets a and e below), we noticed that F_i for a given bud was slightly decreased when other buds were removed. This occurred because the hydraulic conductance of individual sap pathways to a given cut end is not independent of the water pathways to different cut ends. Therefore, it was decided that all buds on a shoot would be removed at the beginning of an experiment, with water flowing to all the cut ends simultaneously. We presumed that this situation was qualitatively equivalent to water flow in an intact shoot. Six sets of measurements were performed (see Figures 1a–f).

(a) On two large branches, we measured k_x of the xylem sap pathway from the proximal cut end to all the terminal buds of different axes (Figure 1a). The branches were 7 and 12 years old, and were 1.4 and 2.2 m long, respectively. We first removed the buds belonging to different axes just below the first bud scars and then successively connected the terminal ends to a XYL'EM apparatus. A total of 95 pathways were measured this way.

(b) On 14 segments composed of a long annual growth unit followed by a short annual growth unit, we measured k_x between the base of the last internode of the long annual growth unit and the base of the terminal bud (Figure 1b).

(c) On 101 short axes, we measured k_x of the sap pathway from the base of the segment to the base of the terminal bud (Figure 1c, black arrow). The mean length of a short growth unit was 0.02 m. The base of the segment was cut just below the bud scales scar of the short annual growth unit formed dur-
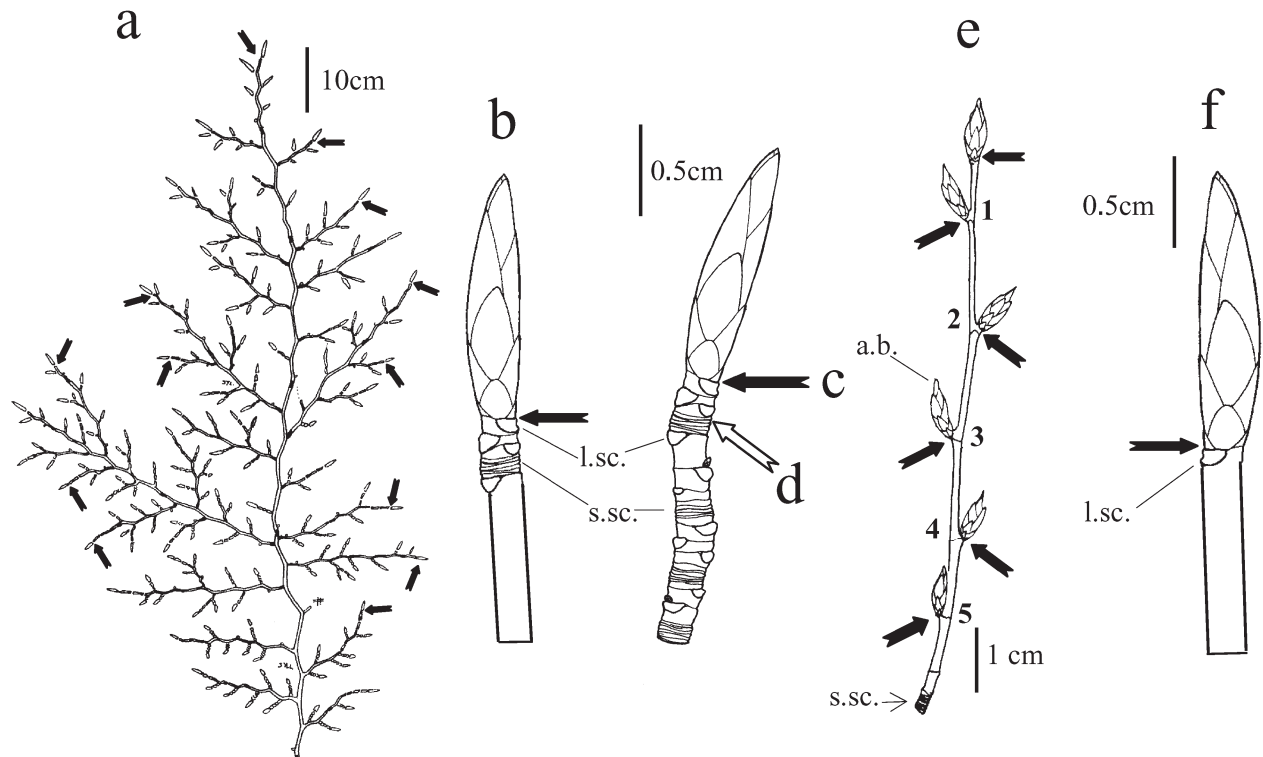
Figure 1. Morphological characteristics of different shoot types analyzed during winter 2000–2001. The arrows indicate where samples were cut and where water flow was measured when a positive pressure was applied at the base of the sample. (a) An old ramified branch; (b) a 2-year-old shoot comprising a 1999 long annual growth unit followed by a 2000 short annual growth unit; (c and d) a short shoot comprising four successive annual short growth units (1997–2000), (e) a 2000 long growth unit; (f) a terminal internode of a 2000 long growth unit. The bud scale scars (s.sc.) delimit each annual growth unit. On the growth units, the number of leaves is determined by counting the number of leaf scars (l.sc.); in (e), the axillary buds (a.b.) are labeled from the top to the base of the long growth unit.

ing the 1997 growing season, so that the segments comprised four successive short annual growth units.

(d) On 84 more segments similar to the ones described in (c), we measured k_x between the base of the 1997 short growth unit and the base of the first leaf scar of the 2000 short growth unit (Figure 1d, open arrow).

(e) On 11 long growth units, we measured k_x of the sap pathway from the base of the growth unit to the base of each bud (one terminal bud and up to five axillary buds) (Figure 1e). The mean growth unit length was 0.22 m. The base of the segment was cut just below the scales of the previous year terminal bud. Again, all buds were cut at the beginning of the experiment below their first scale. A watertight collar was successively clamped around the axillary buds to determine F_i. A total of 50 pathways were measured this way.

(f) On 30 annual long growth units, we determined k_x between the base of the last terminal internode and the base of the bud (Figure 1f).

When distal cuts corresponded to the bud base (sets a, b, c, e and f), we measured k_x of the sap pathway supplying leaf primordia in the bud during its formation. When the distal cut was located at the base of the terminal growth unit (set d), we measured the sap pathway supplying the leaves connected to the shoot.

Morphological observations

Morphological markers, which were determined immediately after the hydraulic measurements, included growth unit length, number of leaf scars and bud fresh mass. Bud fresh mass (FM; mg) was measured with a digital balance (resolution 0.0001 g) immediately after bud excision. Bud dry mass was obtained after drying for 2 days at 70 °C. Bud fresh mass provided an estimate of the dry mass of leaf primordia (DM; mg) with DM = 0.208FM – 3.76 ($r^2 = 0.94$, $n = 50$, $P < 0.001$). Bud fresh mass was also highly correlated with the number of leaf primordia in the bud (n) ($n = 0.04$FM + 0.72; $r^2 = 0.91$, $n = 50$, $P < 0.001$).

Anatomical observations

Samples stored in 95% alcohol in individual vials were used for anatomical observations and δ^{13}C analysis. Growth unit anatomy was assessed in cross sections obtained from a sub-sample of the short growth units used for the set c hydraulic measurements. In 88 samples, a thin cross section was made at the base of the first leaf scar of the year 2000 short growth unit and mounted on a microscope slide. High-resolution digital images were obtained for each cross section and the xylem area was determined with standard image analysis software. In

a few samples, cross sections were obtained from the different annual short growth units of the segment, and ring width and vessel size were assessed. The minimum and maximum diameters of each vessel were determined with the aid of an optical microscope equipped with a light chamber and a digital tablet (resolution 0.1 μm).

Carbon isotopic composition

A subsample of the short growth units collected for k_x determination (set c above) was used for $\delta^{13}C$ (‰) analysis. We measured $\delta^{13}C$ on the leaf primordia of the terminal buds. Because samples were kept in alcohol, molecules soluble in alcohol were partially solubilized. As this may have biased the $\delta^{13}C$ values, we first completed the extraction of soluble compounds by placing the leaf primordia in vials containing 0.5 ml of alcohol. Although the extraction of compounds in alcohol probably modified the bulk $\delta^{13}C$ values, the relative differences between treatments remain valid. The vials were heated at 55 °C for 4 h. The samples were then rinsed with distilled water, finely ground, centrifuged and dried at 60 °C for 48 h. A subsample of about 1 mg of powdered material was placed in a tin capsule, combusted and analyzed for ^{13}C composition with an isotope ratio mass spectrometer (Delta S, Finnigan MAT, Bremen, Germany) at the INRA Nancy stable isotope facility. Measurements were made on buds containing 2–6 leaf primordia, with five replicates for each type.

Results

Morphological markers

Morphological analysis of the sampled branches revealed two distinct groups of terminal annual growth units. Growth units that contained less than five leaf scars were less than 1 cm long, whereas growth units with more than 5 leaf scars had elongated internodes (Figure 2): hereafter, we refer to these two groups as "short" (Figure 1c) and "long" (Figure 1e) annual growth units, respectively. Within each group, there was a significant linear relationship between unit length and number of leaf scars. Because beech leaves are preformed in the dormant buds, the number of leaf primordia was thus a marker of the type of growth unit produced the following spring. We have used this morphological marker to identify traits that best correlate with the fate of a bud.

The morphology of the terminal annual growth unit was not a good predictor of the type of growth unit to be formed by the terminal bud. For instance, the number of leaf scars on the terminal growth unit (Year 2000) was poorly correlated with the number of leaf primordia in the dormant terminal bud ($r^2 = 0.74$; Figure 3), indicating that long growth units can initiate short growth units and vice versa.

Xylem anatomy

Xylem area at the base of the first leaf scar of the Year 2000 short growth units was linearly and positively correlated to the number of leaf primordia in the buds ($r^2 = 0.97$; Figure 4). When short annual growth units were bearing a terminal bud
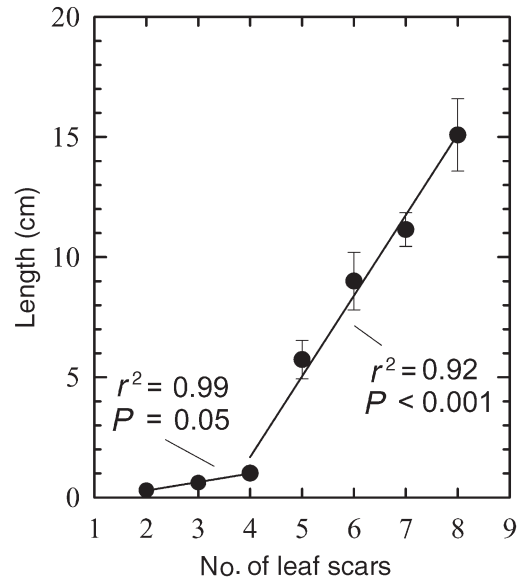

Figure 2. Length of an annual growth unit versus the number of leaf scars present on the growth unit. The relationship was established for all the terminal growth units of two large branches ($n = 95$). The error bars represent 1 SE. Lines are linear regressions. Only annual growth units having more than four leaves exhibited elongated internodes.

with more than five leaf primordia, we noticed the occurrence of a wide annual ring on all the different annual growth units. Wider rings were accompanied by wider xylem lumens. For instance, at the base of a short growth unit having buds with two and five primordia, vessel diameter averaged 7.9 μm (SE = 0.05, $n = 30$) and 14.8 μm (SE = 0.07, $n = 30$), respectively.
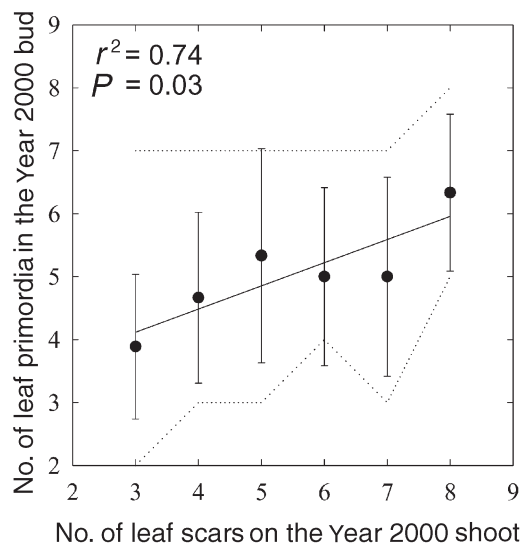

Figure 3. Number of leaf scars on the Year 2000 growth units versus the number of leaf primordia in the terminal buds of these growth units. The relationship was established for all the terminal growth units of one large vegetative branch ($n = 54$). Dashed lines indicate the minimum and maximum values. Error bars represent 1 SD.
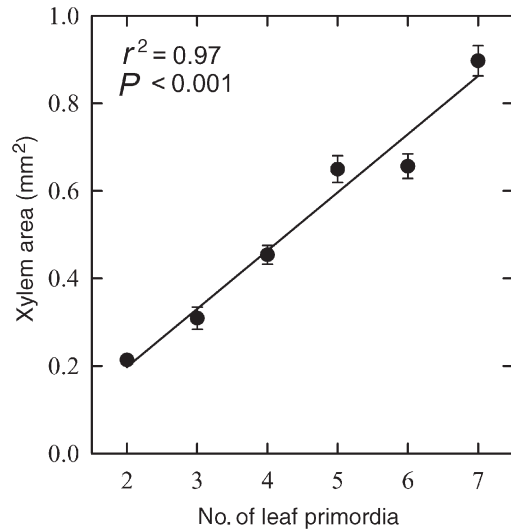
Figure 4. Xylem area at the base of the first leaf scar of the Year 2000 annual short growth units versus the number of leaf scars present on the growth units. The error bars represent 1 SE. The line was fit by linear regression.

Hydraulic conductances

Figure 5 provides a summary of all the hydraulic measurements made on the different types of branch material. Whatever the material, a positive and significant relationship was found between xylem conductance of the whole sap pathway and the number of leaf primordia in the dormant buds. A similar relationship was obtained when k_x was measured between the base of the 1997 bud scales and the base of the first leaf scar on the 2001 short growth unit (set d, Figure 5d), although the k_x values were more than 10 times higher. For long annual growth units, the occurrence of a large bud containing more than four leaf primordia (which will give birth to a long growth unit) was always associated with high k_x values, whatever the position of the bud on a branch (Figure 5e). Buds containing flowers (mature structures) exhibited a significantly more conductive sap pathway (open symbols; Figure 5a) than sterile structures. The relationships in Figure 5 tended to be nonlinear, with k_x increasing for buds with more numerous primordia.

Carbon isotopic composition

Dormant buds containing more than four leaf primordia exhibited significantly higher (less negative) $\delta^{13}C$ values than buds containing fewer leaf primordia ($r^2 = 0.87$; Figure 6A). A linear relationship was found between $\delta^{13}C$ and FW ($r^2 = 0.99$; Figure 6B).

Discussion

The objective of our study was to identify physiological traits associated with beech branch development, with an emphasis on the formation of short versus long annual growth units. Short and long annual growth units were clearly segregated by

leaf number, with short annual growth units forming only from dormant buds having less than five leaf primordia. Because all leaves were preformed in the buds, the number of leaf primordia present in a dormant bud was a simple, yet effective, marker of the type of growth unit to be initiated, making it possible to identify morphological and physiological traits associated with the formation of each bud type.

We found that preformation of a long or short growth unit in a terminal bud was poorly correlated to the type of the current annual growth unit (Figure 3). For instance, terminal buds with preformed short growth units were present on both short and long current growth units, although there was a greater chance of a short growth unit succeeding a short growth unit. This suggests that the type of growth units produced by a meristem is not an intrinsic property of the tissue, but may vary from year to year according to internal and external factors.

We identified highly significant statistical correlations between the number of leaf primordia in the bud and the hydraulic conductance of the sap pathway connected to the bud when hydraulic conductances were measured in the winter on leafless branches. Branches were perfused with water under high pressure, which probably minimized the effect of embolisms that may have formed in xylem vessels following drought or freeze–thaw events (Lemoine et al. 1999). Therefore, the variations in hydraulic conductance that we measured reflect the variations in xylem sap pathway conductance that the plant would have experienced under the best possible conditions. The variations in xylem conductance were clearly associated with differences in xylem anatomy. The conductance of a xylem vessel is a function of the fourth power of its diameter (Tyree et al. 1994). Thus, a small increase in mean vessel diameter has a large effect on xylem conductance. Most of the resistance of the sap pathway was located in the most distal portion, which explains why the hydraulic conductance values were largely independent of path length. This was particularly evident from our counterintuitive results for axillary buds located on long terminal growth units where hydraulic conductances increased with the path length. The nonlinearity of the relationships between hydraulic conductance of the sap pathway and the number of leaf primordia in the buds suggests that the water supply per primordium increased with the number of primordia; however, this relationship may reflect the increase in leaf primordium size with increases in the number of primordia.

We found that the primary meristematic growth of a bud was correlated with the secondary cambial activity of the growth unit to which it gave rise. The formation of a bud containing more than four leaf primordia on a short terminal growth unit was concomitant with the formation of a large and highly conductive ring with large vessels (Figure 4). The mechanism underlying this relationship was not examined in this study, but probably involves hormonal control (Roberts et al. 1988). These observed relationships reflect either a correlation of no biological significance or a more causal link between bud growth and hydraulic conductance. For example, it is plausible that variations in the hydraulic conductance of the sap pathway substantially alter the water potential of the primary meristem
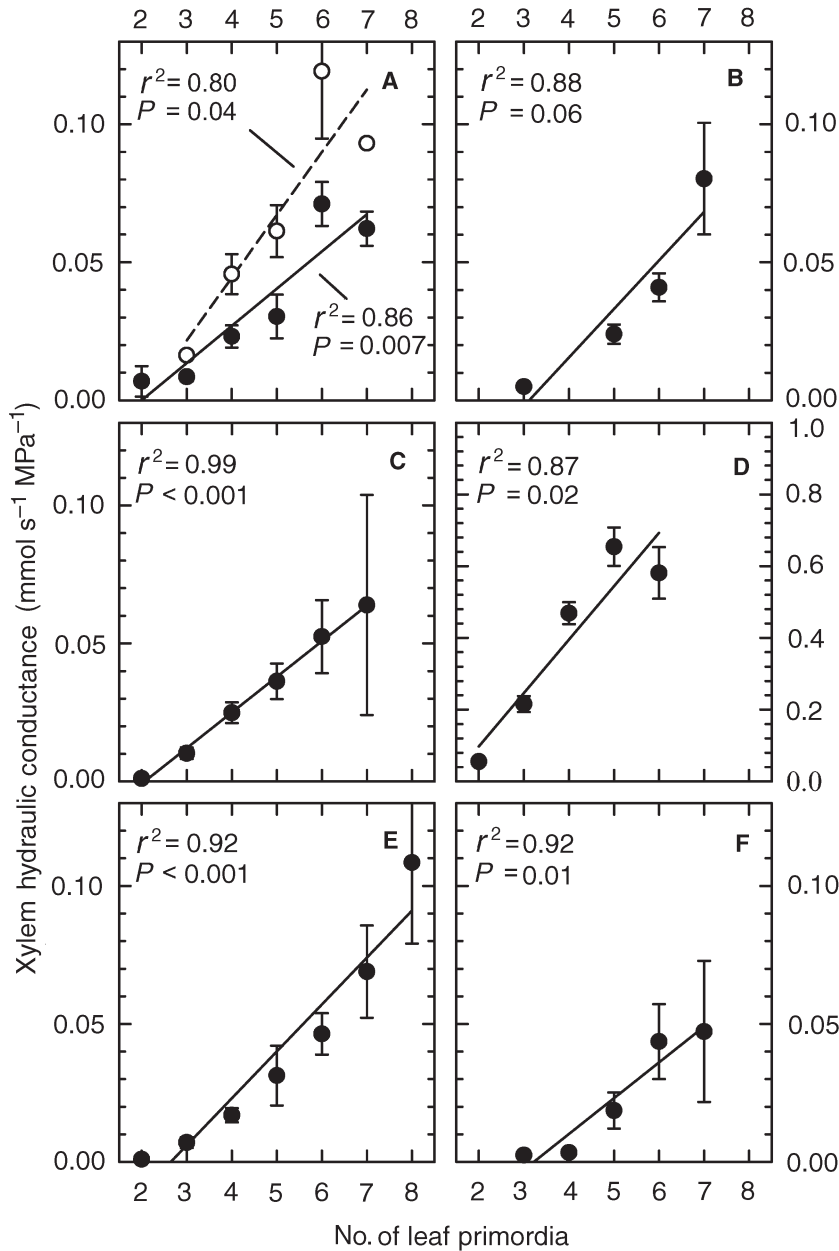
Figure 5. Hydraulic conductance (k_x) of the xylem sap pathway versus the number of leaf primordia in the buds. Samples were perfused at their proximal cut ends and water flow was measured at the arrow locations indicated in Figure 1. (A) The value of k_x measured between the cut base of large branches and the terminal buds of all annual growth units on the branch (see Figure 1a). Symbols: ○ = reproductive buds; and ● = vegetative buds. (B) k_x measured between the last internode of the previous year's long growth unit and the current year's short growth unit (see Figure 1b); (C) k_x measured from four successive annual short growth units (see Figure 1c); (D) k_x measured from four successive annual short growth units, as in (C), but with the distal segment end at the base of the first leaf scar on the year 2000 annual growth unit (see Figure 1d); (E) k_x measured between the base of long terminal growth units and the base of each bud along the growth unit (see Figure 1e); (F) k_x measured in a segment consisting only of the last internode of the terminal long growth units (see Figure 1f). Note the different scale on the y-axis in D. The error bars represent 1 SE.

and, possibly, its activity. Cell growth in the meristem is partly influenced by cell turgor pressure according to Lockhart (Lockhart 1967). Thus, any change in the hydraulic conductance of the sap pathway to the bud is likely to alter bud turgor pressure and growth potential (Hsiao and Xu 2000, Nardini 2002). To substantiate this hypothesis, we need to quantify the potential drop in turgor pressure resulting from variations in k_x. This calculation requires an estimate of water flow through the xylem growth unit and the flow entering the bud, but there was no information available for flow into the bud. With our data set, we could compute only a change in xylem pressure at the base of the terminal growth unit. The k_x of a 4-year-old short growth unit with three leaves is about 0.2 mmol MPa^{-1} s^{-1} (Figure 5d). Assuming a total distal leaf area of 0.0075 m^2

and a mean transpiration rate of 2 mmol m^{-2} s^{-1}, the pressure drop across the shoot is about 0.075 MPa during the day. At night, this pressure drop will be much less. If k_x increases to 0.65 mmol MPa^{-1} s^{-1}, the pressure drop decreases to 0.023 MPa, a difference of close to 0.05 MPa. Short axes often contained more than eight successive short annual growth units, so the variation in pressure drop along a whole short axis might be as large as 0.1 MPa. This is a minimum estimate of the pressure change at the base of the bud consequent to the formation of a more conductive annual ring on a short growth unit. The contrasted pressure drop in the most distal sap pathway may further enhance the difference. Therefore, on the basis of this calculation, we cannot reject the hypothesis of a direct effect of xylem conductance on meristematic growth
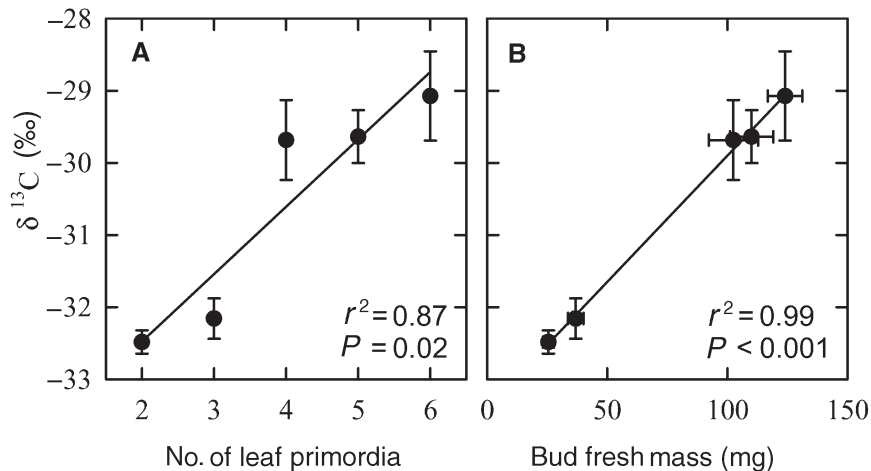
Figure 6. Carbon isotopic ($\delta^{13}C$) composition of leaf primordia versus the number of leaf primordia (a) and the fresh mass (b) of the terminal buds of short growth units. The error bars represent one SE. Lines are linear regressions.

mediated through a change in xylem pressure. Furthermore, this hypothesis is consistent with the recent findings of Koch et al. (2004) and Woodruff et al. (2004), indicating that changes in turgor pressure with tree height may limit tree growth. However, the hypothesis awaits experimental testing.

Beech growth units can exhibit drastic morphological changes from one year to another. We found instances of short growth units with only two leaves giving birth to long growth units with six or more leaves the following year. We have documented that these morphological transitions were preceded by anatomical and physiological modifications at the xylem level. The reason for these sudden modifications remains hypothetical, but it is complex and many phenomena are likely involved. For example, it is well known that auxin concentrations control xylem conduit diameters and are probably involved (Roberts et al. 1988); however, there is not simply a threshold conductance that, once reached, results in the production of long shoot instead of short shoots. Although our carbon isotopic data were restricted to 4-year-old short shoots (measurement set c) and may not be representative of all situations, they provided some insight into the mechanisms underlying the morphological transitions. Leaf primordia in the two bud types had distinct isotopic signatures. Carbon isotope composition is an integrative marker of intrinsic water-use efficiency (WUE) of the leaves that produced the carbohydrates fixed in the primordia (Farquhar et al. 1982), and is defined at the leaf level as the ratio between assimilation rate (A) and vapor water stomatal conductance (g_{H_2O}). Therefore, an increase in WUE might be caused by an increase in A or a decrease in g_{H_2O}. Because it seems unlikely that low g_{H_2O} could be related to high growth rate, we hypothesize that differences in A were responsible for the higher $\delta^{13}C$ found in buds containing an embryonic long growth unit compared with buds containing an embryonic short growth unit. The high WUE of buds containing an embryonic long growth unit might be explained by two phenomena. First, the carbohydrates incorporated in the buds may have come from branches in the upper crown. Leaves on upper-crown branches have higher assimilation rates because of the higher irradiance they receive compared with lower-

crown branches. This hypothesis implies an increase in the carbon sink strength of the meristematic cells. The sink strength might have been modulated by a hormonal signal or by meristem water status. A second hypothesis is that carbohydrates in the buds may have been synthesized by the leaves attached to the same short shoots. Again, this may have been caused by a local increase in irradiance, and hence, a higher assimilation rate. Both hypotheses highlight the significance of light availability. This is consistent with the empirical results of Collet et al. (2001, 2002), who found that shaded beech saplings formed only short growth units, but when the stand was thinned (winter year n) they first noticed an increase in the annual secondary growth of the main stem (summer year n), and then formation of long growth units the following year (summer year $n + 1$).

Based on our data and the literature, we propose the following scheme for inter-annual shoot growth in beech. In spring of year n, buds expand to form long or short growth units depending on the number of preformed leaf primordia they contain. Leaf primordia are initiated in terminal or axillary buds during the growing season (May to September) (Roloff 1986). Secondary cambium is activated synchronously with primary bud growth (Lachaud and Bonnemain 1981) and its activity during the n growing season determines the anatomy and hydraulic efficiency of the sap pathway to the buds. Primary meristematic activity determines the number of leaf primordia and is positively correlated to the hydraulic conductance of the xylem sap pathway. The morphology of the growth units that develop in year $n + 1$ is correlated to the number of leaf primordia preformed in the buds. From this scheme, it is clear that shoot morphology (i.e., long versus short growth units) is determined one year in advance, probably by cambial activity. This may explain why leaf area in beech stands is correlated to the soil water deficit during the growing period of the previous year (N. Bréda, INRA Nancy, France, unpublished data). Soil water deficit may reduce both secondary cambial growth in the new growth units and primary meristematic activity in the apical bud, and hence reduce the number of leaf primordia in subsequent growth units, increasing the proportion of short

growth units. This scheme also accounts for the 1-year time lag noticed by Collet et al. (2001, 2002) between shoot diameter growth and main stem elongation following stand thinning.

Our data suggest that organogenesis and primary growth in the buds are correlated with secondary growth of the growth units. We do not know if, beyond this correlation, a causal relationship exists between the phenomena. We hypothesize that enhanced secondary growth facilitates water availability and thus primary bud growth. Our results highlight the remarkable coordination between bud activity and cambium growth in a given year, and its functional implications for the following year, with bud activity determining leaf area and water loss, and cambial activity determining xylem water transport efficiency. This may explain why shoot leaf specific conductance (xylem conductance per unit leaf area) is remarkably stable in some species (Cochard et al. 1997). Tree hydraulic architecture may thus help in understanding how plant architecture is elaborated (Leigh 1999, Tyree and Zimmermann 2002).

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