ANNALS OF
BOTANY
Founded 1887

Fagus sylvatica trunk epicormics in relation to primary and secondary growth

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• *Background and Aims* European beech epicormics have received far less attention than epicormics of other species, especially sessile oak. However, previous work on beech has demonstrated that there is a negative effect of radial growth on trunk sprouting, while more recent investigations on sessile oak proved a strong positive influence of the presence of epicormics. The aims of this study were, first, to make a general quantification of the epicormics present along beech stems and, secondly, to test the effects of both radial growth and epicormic frequency on sprouting.

• *Methods* In order to test the effect of radial growth, ten forked individuals were sampled, with a dominant and a dominated fork of almost equal length for every individual. To test the effects of primary growth and epicormic frequency, on the last 17 annual shoots of each fork arm, the number of axillary buds, shoot length, ring width profiles, epicormic shoots and other epicormics were carefully recorded.

• *Key Results* The distribution of annual shoot length, radial growth profiles and parallel frequencies of all epicormics are presented. The latter frequencies were parallel to the annual shoot lengths, nearly equivalent for both arms of each tree, and radial growth profiles included very narrow rings in the lowest annual shoots and even missing rings in the dominated arms alone. The location of the latent buds and the epicormics was mainly at branch base, while epicormic shoots, bud clusters and spheroblasts were present mainly in the lowest annual shoots investigated. Using a zero-inflated mixed model, sprouting was shown to depend positively on epicormic frequency and negatively on radial growth.

• *Conclusions* Support for a trade-off between cambial activity and sprouting is put forward. Sprouting mainly depends on the frequency of epicormics. Between- and within-tree variability of the epicormic composition in a given species may thus have fundamental and applied implications.

Key words: European beech, *Fagus sylvatica*, epicormics, ontogeny, mixed ZIP models, sprouting, radial growth.

INTRODUCTION

Epicormic structures (buds, shoots, clusters and burls) have recently gained renewed interest within the fields of ecology (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Clarke *et al.*, 2010), silviculture (Spiecker, 1991, Meadows and Goelz, 1999; Kerr and Harmer, 2001; Colin *et al.*, 2008; O'Hara and Berrill, 2009; Kodani *et al.*, 2010; O'Hara *et al.*, 2008; Takiya *et al.*, 2010), wood properties (Fontaine *et al.*, 2004; Colin *et al.*, 2010b) and botany (Meier *et al.*, 2012). From a botanical viewpoint, foliated axes or sprouts have been shown to contribute to (1) the intrinsic unfolding of the architecture (Lanner, 1995; Barthélémy and Caraglio, 2007; Ishii *et al.*, 2007); (2) the repair of damaged structures (Vesk and Westoby, 2003; Burrows *et al*, 2010); or (3) the adjustment of the architecture to the available resources (Hallé *et al.*, 1978). Over the last decades, identification of epicormic structures from the collar to the crown has been addressed by many authors for a wide range of species (Fink, 1980; Kauppi *et al.*, 1987; Del Tredici, 2001; Fontaine *et al.*, 2004; Colin *et al.*, 2008, 2010a; Burrows *et al.*, 2010). Meanwhile, a framework on epicormic ontogeny has progressively emerged, through the use of stem dissection, bark removal

(Fontaine *et al.*, 1998, 1999, 2004; Burrows *et al.*, 2010) and an X-ray computed tomography (CT) procedure (Colin *et al.*, 2010b; Morisset *et al.*, 2012a). These studies have evidenced the axillary origin of the vast majority of epicormics.

To quantify epicormics, two concepts have been introduced: (1) epicormic potential, defined as the frequency of epicormic buds per metre (Fontaine *et al.*, 2001); and (2) epicormic composition, defined as the proportions and frequencies of the different types of epicormics present on a given species and trunk segment (Colin *et al.*, 2010a). Investigations on sessile oak, *Quercus petraea*, have shown that the epicormic potential decreases by 4–5 % every year (Fontaine *et al.*, 2001). Up to 60 % of the epicormic buds persist at sequential branch bases (Colin *et al.*, 2010c). Sprouting is positively related to the frequency of existing epicormics (Colin *et al.*, 2010c; Morisset *et al.*, 2012a).

Suprisingly, European beech, *Fagus sylvatica*, has received far less attention. While forest disturbances including thinning operations do not induce important epicormic sprouting on dominant trees (Altherr and Unfried, 1984; Holmsgaard, 1985; Klädtke, 1997), beech trees can, however, exhibit trunk, collar, root and crown sprouting (Roloff, 1989). In addition, trunks may bear not only sprouts, but also bud clusters,

bud burls and spheroblasts (Fig. 1) (Fink, 1980), but their quantification has never been completed to date. Cordonnier et al. (2007) suggested that trunk sprouting might occur just below the crown base following exceptionally heavy thinnings, although this has never been thoroughly demonstrated. Interestingly, trunks of suppressed individuals systematically bear a lot of epicormic shoots (Nicolini et al., 2001).

Nicolini et al. (2001) observed for suppressed trees the presence of epicormic shoots in relation to the radial growth recorded in the bearing segment of the trunk. They demonstrated that annual shoots with epicormic shoots also showed a decrease in radial growth, with narrow, and often 'missing', rings. This empirical relationship nevertheless remains to be modelled and generalized to other social ranks. Assuming that low growth (narrow or missing rings) triggers epicormic sprouting, the implications may be of significance, as a major yet isolated environmental stress, such as a drought or an insect infestation, would result in epicormic emergence on dominant trees. An underlying question concerns the possible existence of a growth threshold below which sprouts inevitably emerge regardless of the social status.

This study was undertaken in order: (1) to conduct a systematic quantification of the epicormic potential and composition along beech stems; (2) to test and confirm the negative relationship between sprouting and radial growth as highlighted by Nicolini et al. (2001), using the following hypothesis: sprouting is associated with a decrease in radial growth rate resulting in the formation of very thin and sometimes 'missing' rings in the bearing segment of a fork arm (H1); and (3) to test the positive effect of the total frequency of all types of epicormics on epicormic shoot emergence under the following hypothesis: the more abundant the epicormics on a particular annual shoot, the more frequent the epicormic shoots are (H2).

Hypotheses H1 and H2 were tested using a statistical modelling approach applied to data from ten two-fork-armed trees, originating in a lowland forest in Lorraine, France.

As sessile oak has been the focus of a recent investigation on epicormic ontogeny, the results gained in beech will be compared with those gained in sessile oak.

MATERIALS AND METHODS

Sampled stand

The silvicultural design of the present experiment on epicormics was a 0·35 ha plantation of *Fagus sylvatica* installed in early spring 1981 at spacing of 1·4 m × 1·4 m in the compartment 486 of the Haye forest, Nancy, France (6°9′E, 48°39′N). The soil was a ≥40 cm leached brown soil on a calcareous parent material. Mean annual rainfall is 760 mm and the mean annual temperature is 9·8 °C. Every third row of the plantation was thinned in 1985.

Sampled trees

During winter 2006–2007, ten sample trees with two fork arms of comparable height but different diameter were selected (Fig. 1). The principle of this sampling design was to perform matched comparisons between stems of the same

genotype under the same soil conditions, exhibiting almost equivalent annual height increments but different radial growth. The main attributes of the ten trees and 20 fork arms are provided in Table 1.

Tree description

On each arm, the successive annual shoots (AS) were identified, and ordered from the most recent in 2006 to the oldest (Fig. 1). Eventual multiple growth units within annual shoots (polycyclism) were detected by comparing the number of limits between growth units and the number of rings on wood slices cut at different heights, the difference being positive in the case of polycyclism. The length of each AS was measured to the nearest centimetre. Due to different dates of fork emergence, the number of annual shoots per arm differed
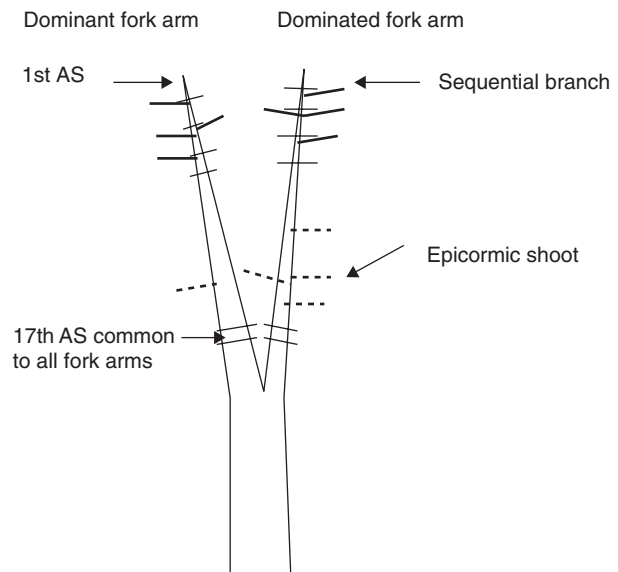

Fig. 1. Diagram of a forked tree where epicormics were recorded on the 17 more recent annual shoots (AS) common to all fork arms. Only the four most recent AS and the 17th common to all fork arms are noted. Among all possible epicormic types, only epicormic shoots are indicated.

TABLE 1. *Tree and fork arm attributes at the beginning of year 2007*

Tree No.	H (m)	DBH (cm)	HF (m)	Dominant arm D (cm)	Dominated arm D (cm)
66	14·3	33·1	2·3	7·8	7·6
82	15·6	59·2	2·4	14·4	12
112	16·1	52·5	4·4	11·2	11
377	16·1	40·7	2·8	10·7	6·4
509	15·5	46·8	2·2	11·0	8·8
535	17·7	64·6	4·5	15·5	11·3
586	17·2	42·0	2·2	11·9	7
669	17·8	46·1	3·9	11·6	7·2
722	17·4	54·4	2·7	12·4	10·8
802	17·0	40·4	3·2	9·9	7·6

D, diameter 10 cm above insertion; DBH, diameter at breast height; HF, height to the fork insertion.

between the trees. However, all fork arms had at least 17 AS. Consequently, we used the last 17 AS on each arm for further analyses. Epicormics were tallied on each AS with their precise location and classified into three classes: at branch base, on the limit between AS, and in lateral positions different from the two previous ones, corresponding to the initial position of isolated latent buds.

On the first AS, i.e. the 2006 AS, we counted the axillary buds together with eventual sequential branches that develop on the first growth unit when a second growth unit occurred within the growing season. On all the other 16 AS per fork arm, we tallied (Fig. 2): (*a*) sequential branches; (*b*) forks; (*c*) latent buds (also known as suppressed or epicormic buds) either in bud clusters or not; (*d*) epicormic shoots (ES); (*e*) burls (BL); and (*f*) spheroblasts (SP).

As the observed latent buds all had an axillary origin, they were initially axillary buds that did not develop into a sequential branch (often referred to as proventituous buds). Also, the distinction between sequential and epicormic branches lies in the duration of bud rest before emergence. Sequential branches

emerged after a bud rest period of ≤ 1 year while epicormic branches emerged after a longer period in which the bud remained latent. In the present study, the scarce burls were pooled with the bud clusters and were henceforth referred to as bud clusters. The epicormic potential per metre was computed as the total number of epicormics on a given AS divided by the length of this AS (ASL).

Wood disks were sampled from each annual shoot along each fork arm in 2007. Radial increments were measured on four radii, two on the largest diameter and two on the perpendicular diameter. The lowest ring width (LRW), the width of the most recent ring in 2006, the average ring width of the radial profile (MRW) and the number of 'missing' rings were measured or computed for each disk. We omitted the first ring because it included the pith, which made the ring width quite variable along a particular annual shoot. When missing rings were suspected in a given AS on the dominated fork arm, we examined the corresponding AS on the dominant arm and evaluated the difference in number of rings in order to confirm the occurrence of missing rings.

Type	Definition (abbreviation)	
Isolated bud	A latent bud not in a cluster (IB)	
Epicormic shoot	Any foliated axis originating from a suppressed bud either isolated or in cluster or burl (ES)	
Bud cluster	A group of less than 6 close latent buds (BD)	
Burl	A group of more than 6 buds, eventually with epicormic shoots or even remnants of sequential branches (BL)	
Spheroblast	Isolated buds progressively engulfed in a small ball of wood generated from the base of the bud on the external side (SP)	

FIG. 2. Beech epicormic classification used in this study.

Preliminary epicormic analysis

A graphical analysis of the data was intended to highlight general trends of ASL, lowest ring width (LRW) and the epicormics present according to the annual shoot age and the location within the annual shoot.

Statistical analysis of sprouting

The tree, the fork arm and the AS hierarchical levels were indexed as i, j and k, respectively, such that $i = 1, 2, \ldots, 10$, $j = 1, 2$ and $k = 1, 2, 3 \ldots .17$. The response variable for the statistical analysis was the number of epicormic shoots per AS (nes_{ijk}). This variable was characterized by an excess of zeros, which made usual distributional assumptions invalid. Consequently, we adopted an approach based on zero-inflated Poisson (ZIP) models, as suggested by Cunningham and Lindermayer (2005). This approach consisted of fitting two sub-models, the first one for the occurrence of epicormic shoots and the second one for their number, being conditional on the occurrence. The first sub-model was a logistic regression, based on a Bernoulli distribution, whereas the second one relied on a classic discrete distribution such as Poisson or negative binomial. For the second sub-model, preliminary trials revealed no departure from a truncated Poisson, which was retained.

Given the repeated measurements on the same tree and the same fork arm within a tree, the assumption of independent observations was not valid. One way to handle these correlations among the observations was to use a mixed-model approach, where random effects accounted for the data structure. Here, we tested two nested random effects in each sub-model: a tree random effect and a fork arm random effect nested in that of the tree. Some preliminary tests showed that both random effect levels were significant. However, when the fork arm social status was included in the model as a fixed effect, the fork arm random effects did not improve the model likelihood. As a consequence, only the tree random effects were kept in the sub-models.

Under their generic forms, the two sub-models could be expressed as

$$Pr(nes_{ijk} > 0) = \frac{e^{\mathbf{x}_{ijk}\boldsymbol{\beta} + u_i}}{1 + e^{\mathbf{x}_{ijk}\boldsymbol{\beta} + u_i}} \qquad (1a)$$

$$Pr(nes_{ijk} = m | m > 0) = \frac{\lambda_{ijk}^m e^{-\lambda_{ijk}}}{m!(1 - e^{-\lambda_{ijk}})} \qquad (1b)$$

with variable

$$\lambda_{ijk} = e^{\mathbf{g}_{ijk}\boldsymbol{\gamma} + v_i} \qquad (1c)$$

where $\mathbf{x}_{ijk}$ and $\mathbf{g}_{ijk}$ were two row vectors of explanatory variables; $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ were two column vectors of unknown parameters; and u_i and v_i were two tree random effects.

Following hypotheses H1 and H2, we tested different variables and interactions in vectors $\mathbf{x}_{ijk}$ and $\mathbf{g}_{ijk}$. Amongst others, in the model we tested the annual shoot age, the number of epicormics, the number of missing rings, the arm social status (dominated or dominant), the minimum ring width and the interactions between these variables. The selection of the explanatory variables was based on their level of significance as well as the Bayesian information criterion (BIC) (cf. Pinheiro and Bates, 2000, p. 84). The goodness of fit was assessed visually by plotting the average observed proportions and the mean predicted probabilities against some explanatory variables. The sub-models were fitted using the GLIMMIX (sub-model 1a) and the NLMIXED (sub-model 1b) procedures available in SAS version 9·2.

RESULTS

Observed patterns in the data

The patterns of most variables against the annual shoot rank or age are presented in Fig. 3. In the graphs, we omitted the 2005 and 2006 annual shoots (1- and 2-year-old) because the 2006 annual shoots bore only axillary buds and a few sequential branches while the 2005 annual shoot bore only sequential branches and 1-year-old suppressed buds; any other type of lateral structures such as sprouts and other epicormics could not be found on these most recently formed annual shoots.

Primary growth of fork arms

Differences in distributions of the length of every AS between dominant and dominated fork arms were quite small (Fig. 3A) in each tree, in accordance with the sampling strategy which aimed to have fork arms of equivalent length within every tree. The distribution of annual shoot lengths that held for both arms was composed of four portions:

(1) AS_2 (AS elongated in 2005) where only sequential branches and 2-year-old suppressed buds were present.
(2) AS_3 to AS_7 (AS elongated between 2004 and 2000 inclusively) making up the group gp_AS_{3-7} where there was a clear increasing trend of ASL.
(3) AS_8 to AS_{12} (AS elongated between 2000 and 1995) making up gp_AS_{8-12} where there was a clear decreasing trend of ASL.
(4) AS_{13} to AS_{17} (AS elongated between 1994 and 1990) making up gp_AS_{13-17} where the trend also decreased but at a higher level than for the previous group.

The latter AS elongated just after fork emergence; the almost equivalent lengths on both fork arms on a tree have ensured their persistence. Maximum ASL was quite large (150 cm) and so was mainly located in the highest k indices of AS. Conversely, minimum length was 20 cm, mainly present between AS_9 and AS_{12}.

Secondary growth. The distribution of LRW according to AS is provided in Fig. 3B. The other two synthetic variables RW06 and MRW were not displayed since they looked like LRW. The decreasing trend of LRW was obvious for both fork arms, as well as null LRW corresponding to missing rings observed only for dominated arms. The difference in LRW between both arms was large and corresponded well to the objective of the sampling.

General features of epicormics. Regarding the total epicormic number per AS profile (Fig. 3C), four segments could be
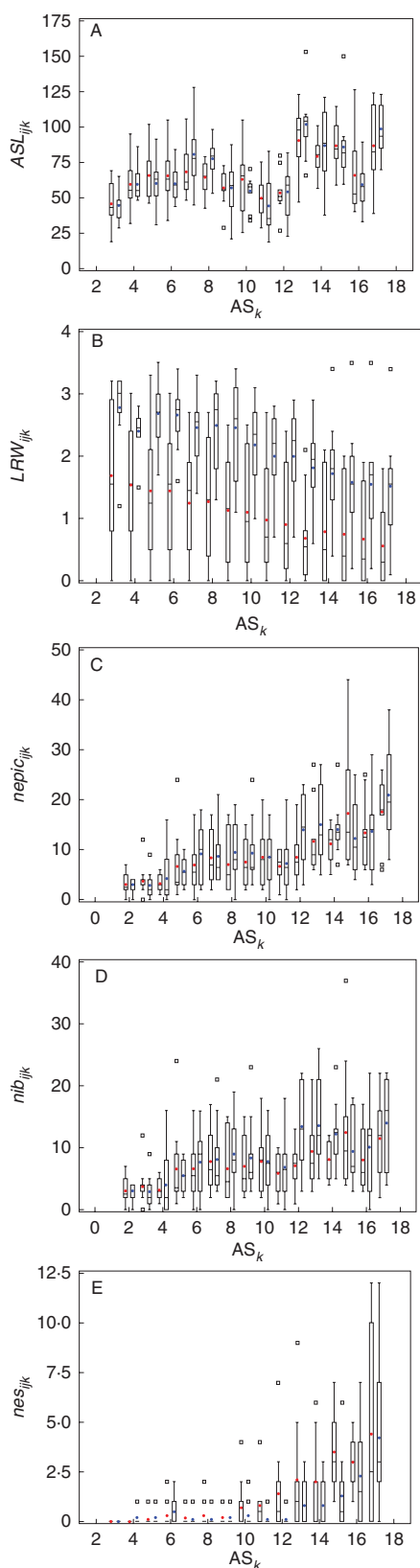
FIG. 3. General patterns of growth and epicormics relative to annual shoot AS_k and fork arm. Annual shoots were ranked with $k = 1$ for AS formed in 2006, $k = 2$ for AS formed in 2005, and so on. Box-plots sum up the distribution of the 20 values observed for every AS. Mean values are shown by red dots for dominated fork arms, and blue dots for dominant fork arms. (A) Annual shoot length. (B) Lowest ring width. (C) Number of epicormics. (D) Number of isolated buds. (E) Number of epicormic shoots.

visually distinguished within the general increasing trend: a plateau for AS_2 to AS_4, an increase for AS_4 to AS_7, a plateau for AS_7 to AS_{11} and a steep increase between AS_{11} and AS_{17}.

The number of suppressed buds per AS (Fig. 3D) was about 15 epicormics m^{-1} on average, with extreme values being 0 and 50. There was a continuous increase of the epicormic potential from AS_4 to AS_{17}, with a noticeable trough for AS_{12}. Conversely, there was a horizontal plateau at a low level between AS_2 and AS_4. This trend paralleled that observed for ASL in Fig. 3A.

As regards the number of epicormic shoots per AS profile (Fig. 3E), there was a clear increasing trend with particularly high values of AS_{16} and AS_{17}. In addition, epicormic shoots were present mostly on the dominated arms.

Relationship between primary growth and number of epicormics. The relationship between ASL1 and number of axillary buds (together with rare sequential branches on the lowest growth units) was quite strong (Fig. 4A). A positive association between the AS length and the number of axillary buds was observed. Attributes of the statistical model are provided in Table 2. The relationship was clearly positive. For this relationship, the effect of the fork arm was not significant.

The relationships between ASL_{ijk} and total frequency of epicormics ($nepic_{ijk}$) appeared weaker and depended strongly on the group of AS (Fig. 4B). The ranking was as follows: $AS_2 < gp\_AS_{3-7} < gp\_AS_{8-12} < gp\_AS_{13-17}$. This ranking suggested an effect of the AS group in addition to the still significant effect of ASL. The main attributes of the statistical analyses are provided in Table 2. Note that AS_2 bore only 2-year-old suppressed buds in addition to the sequential branches not accounted for here. The relationship was clearly positive. For this relationship, the effect of the fork arm was not significant.

Locations of epicormics. The most important locations of epicormic buds were branch bases and lateral locations (Fig. 4C). Branch bases bore the highest proportions from AS_5; these proportions increased continuously, reaching 70 % between AS_{15} and AS_{17}.

The same trend prevailed for the locations of epicormics according to AS (Fig. 4D). Branch bases bore the highest proportions from AS_5; these proportions increased continuously, reaching 65 % from AS_{12}. Complementarily, the proportions of epicormics in lateral positions and in the limits between growth units decreased.

Gradients in the epicormic composition according to AS_k. The epicormic compositions of AS_1 and AS_2 were not considered, since epicormics were not present on AS_1. Although epicormics were still present on AS_2, epicormic shoots could not be present. Group gp_AS_{13-17} bore the highest proportions of epicormic shoots, bud clusters and spheroblasts, and gp_AS_{3-7} bore the lowest proportions (Fig. 4E). Values for gp_AS_{8-12} were intermediate. The proportions of epicormic
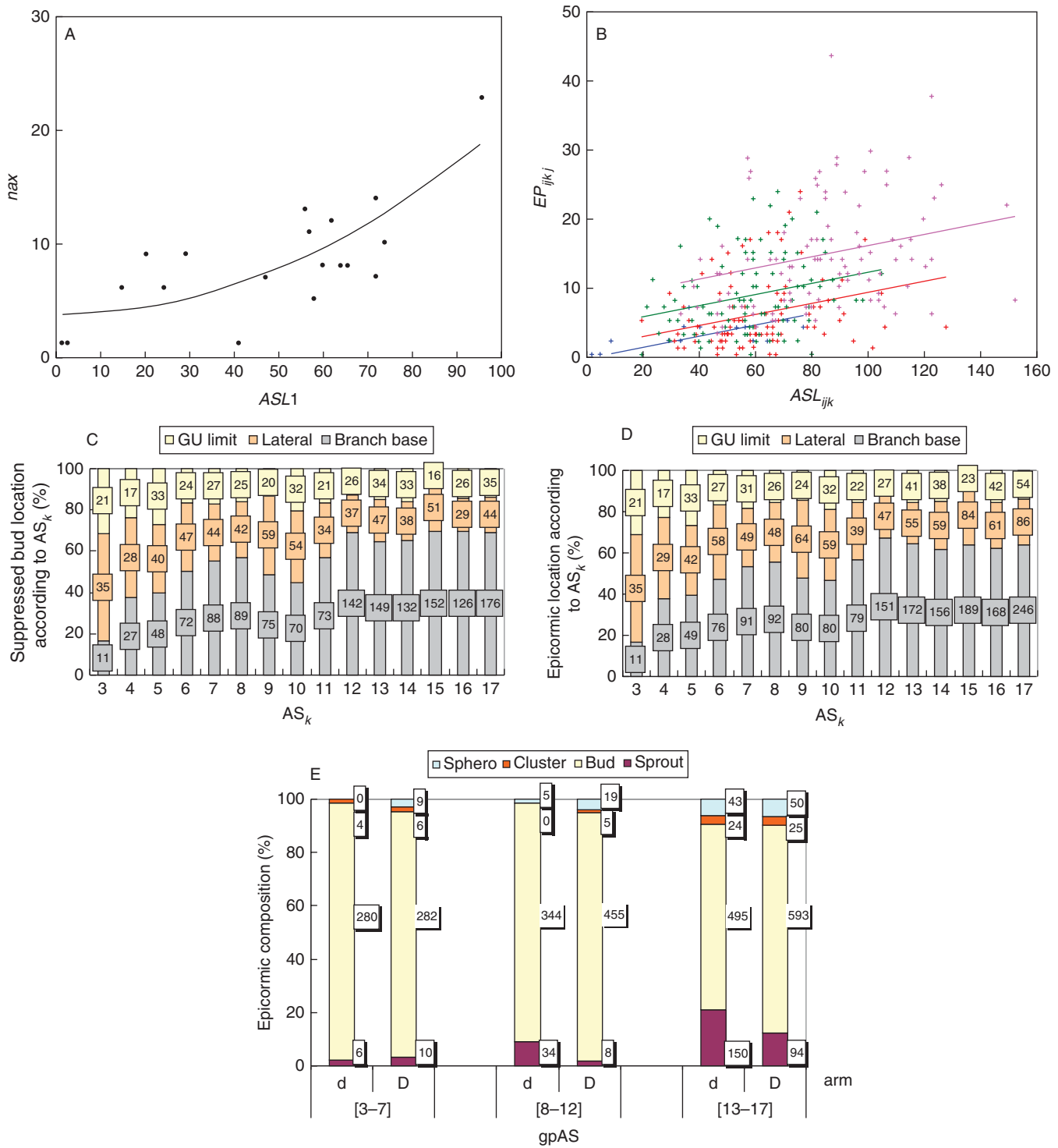
FIG. 4. Number of axillary buds (nax_{ijk}) and epicormics ($nepic_{ijk}$) depending on ASL_{ijk}, in (A) and (B), respectively, and epicormic composition (EP_{ijk}) and sprout proportion depending on groups of AS, in (D) and (E), respectively; locations of suppressed buds in (E) and epicormics in (F) relative to AS_k. Annual shoots were ranked with $k = 1$ for AS formed in 2006, $k = 2$ for AS formed in 2005, and so on. In (A), fork arms are symbolized as: dominated arm in red, dominant arm in blue. In (C), groups of AS are symbolized as follows: in blue: AS # 2; in red: gpAS [3–7], in green: gpAS [8–12]; in magenta: gpAS [13–17].

shoots increased in the three groups up to 20 % and were higher in dominated fork arms in groups gp_AS$_{8–12}$ and gp_AS$_{13–17}$. The proportions of spheroblasts, as well as bud clusters, were higher in dominant arms in gp_AS$_{3–7}$ and gp_AS$_{8–12}$, and were equivalent for both arms in gp_AS$_{13–17}$.

TABLE 2. *Main attributes of the models adjusting the number of axillary buds (*nax_{ij}*) and frequency of epicormics (*nep_{ijk}*)*

$nax_{ij} = f(ASL1_{ij})$	$nep_{ijk} = f(ASL_{ijk}, gAS)$ [$k = 2, 3 \ldots 17$]
Linear model: $P < 0.0001$; $R^2 = 0.67$ (with intercept) 0.90 (without); ASL slope = 0.187	Linear model: $P < 0.0001$; $R^2 = 0.34$ (arm effect non-significant); intercept = 4.007; ASL slope = 0.081 gAS effect: g2 = −4.574; g3−7 = −3.012; g8−12 = 0 (reference); g13−17 = 3.869

TABLE 3. *Frequencies of annual shoots with or without epicormic shoots relative to missing rings and fork arm*

	Annual shoots	With missing rings	Without missing rings
Dominant fork arms	With epicormic shoot(s)	0	41
	Without epicormic shoots	0	109
Dominated fork arms	With epicormic shoot(s)	23	40
	Without epicormic shoot	7	80

Presence of epicormic shoots according to missing rings. From Table 3 we observed that: (1) dominant arms had no annual shoots with missing rings, but several annual shoots bore epicormic shoots; and (2) on dominated arms, several annual shoots lacked rings ('missing' rings) but not all of them bore epicormic shoots, and annual shoots without 'missing' rings could also bear epicormic shoots.

Modelling of sprouting according to secondary growth and number of epicormics

The best fit we obtained was with the following sub-models:

$$Pr(nes_{ijk} > 0) = \frac{nepic_{ijk}e^{\beta_0 + (\beta_1 + \beta_2 s_{ij})age_{ijk} + \beta_3 nmr_{ijk} + u_i}}{1 + nepic_{ijk}e^{\beta_0 + (\beta_1 + \beta_2 s_{ij})age_{ijk} + \beta_3 nmr_{ijk} + u_i}} \quad (2a)$$

$$Pr(nes_{ijk} = m | m > 0) = \frac{\lambda_{ijk}^m e^{-\lambda_{ijk}}}{m!(1 - e^{-\lambda_{ijk}})} \quad (2b1)$$

$$\lambda_{ijk} = e^{\gamma_0 + \gamma_1 age_{ijk} + \gamma_2 \ln(nepic_{ijk}) + v_i} \quad (2b)$$

with $u_i \approx N(0, \sigma_{1,tree}^2)$ and $v_i \approx N(0, \sigma_{2,tree}^2)$

where $nepic_{ijk}$ was the number of epicormics on shoot k of arm j in tree i; s_{ij} was a dummy variable that took the value of 1 if the arm was suppressed or 0 otherwise; age_{ijk} was the cambial age of the annual shoot; and nmr_{ijk} was the number of missing rings. Note that the formulation in 2a was slightly different from the original form in 1a. The current form in 2a was obtained by specifying the natural logarithm of $nepic_{ijk}$ as offset in the sub-model. The maximum likelihood estimates of the model parameters are shown in Table 4.

Some predicted probabilities of epicormic shoot occurrence are shown in Fig. 5. Basically, the probability increased with the social status, the suppressed arm having higher probabilities of epicormic shoot occurrence (Fig. 5A). The probability also increased with the age of the annual shoots and the
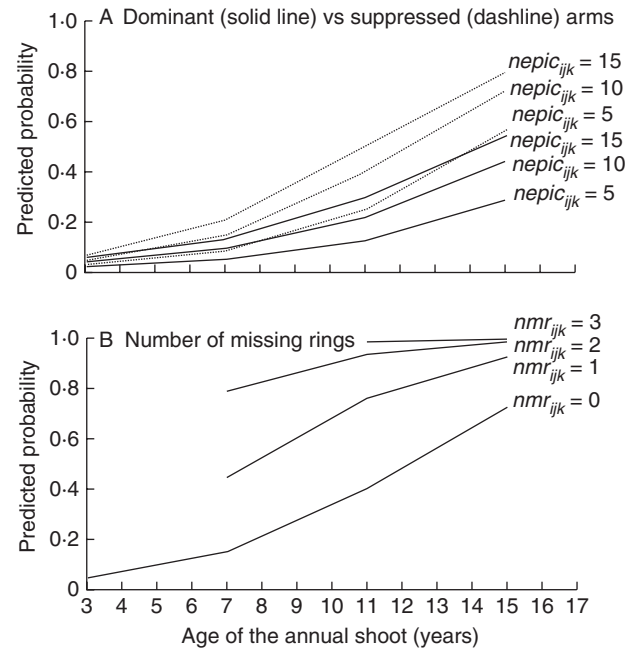
TABLE 4. *Maximum likelihood estimates of the parameters in sub-models 2a and 2b (standard errors are given in parentheses)*

Model and parameter	Estimates
First sub-model (presence/absence)	
β_0	−6.4517** (0.8013)
β_1	0.2603** (0.0535)
β_2	0.0790* (0.0320)
β_3	1.5419** (0.4907)
$\sigma_{1,tree}^2$ (variance of u_i)	1.8928**
Second sub-model (abundance)	
γ_0	−3.5794** (0.5529)
γ_1	0.1909** (0.0322)
γ_2	0.6528** (0.1544)
$\sigma_{2,tree}^2$ (variance of v_i)	0.0849**

*Significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$.

FIG. 5. Predicted probabilities of epicormic shoot occurrence as a function of the age of the annual shoot, the number of epicormics ($nepic_{ijk}$), the social status of the arm and the number of missing rings (nmr_{ijk}): nmr_{ijk} is set to 0 in (A); suppressed arm and $nepic_{ijk}$ set to 10 in (B).

number of epicormics. The probabilities tended toward 0 for a young annual shoot with small numbers of epicormics on the dominant arm, whereas a 15-year-old annual shoot on the suppressed arm with a large number of epicormics had estimated probabilities of epicormic shoot occurrence close to 0.8.

F$_{\text{IG}}$. 6. Predicted number of epicormic shoots (nes_{ijk}) as a function of the age of the annual shoot and the number of epicormics ($nepic_{ijk}$).

The number of missing rings also increased the probability of occurrence (Fig. 5B). For an 11-year-old annual shoot on the suppressed fork arm, the probability of epicormic shoot occurrence ranged from 0·4 when there was no missing ring, to nearly 1 when three rings were missing. None of the other ring descriptors, such as lowest ring width per AS, appeared significant and, consequently, they were not kept in the model.

The predictions of the conditional part of the model are illustrated in Fig. 6. The predicted number of epicormic shoots increased with the number of epicormics and the age of the annual shoot. At 15 years of age, an annual shoot with five epicormics had 1·5 epicormic shoots on average, whereas a similar annual shoot with 15 epicormics tended to have three epicormic shoots.

DISCUSSION

Beech epicormics

Even though epicormic buds originating from suppressed axillary buds have been described anatomically in European beech (Fink, 1980), other epicormic structures have attracted less attention. This paper is the first one in which the full epicormic composition has been thoroughly quantified for beech.

In AS_1, we found that when the annual shoots are longer, they bear more numerous axillary buds. This sounds evident from the widely demonstrated close structural relationship between internode number and annual shoot length, with no accessory buds (Barthélémy and Caraglio, 2007), occurring to our knowledge in *F. sylvatica*. This trend was also confirmed for suppressed buds (Fig. 3B), but the statistical relationships were weaker than for axillary buds (Table 2).

We found between 0·08 and 0·1 epicormics (mostly epicormic buds) cm^{-1}, respectively, in AS_2 and gp_AS_{3-7} (Fig. 3B). Compared with 0·14 axillary buds cm^{-1} previously found on AS_1, this showed a marked initial decreasing trend. In group gp_AS_{13-17}, 0·26 epicormics cm^{-1} were observed, underlining an obvious increase after the initial decrease. This decrease may be linked to a possible more persistent activity of the axillary meristem, which in turn is likely to be consistent with the fairly high ability of beech to produce adventitious structures at least on the stump after felling (F. Colin, pers. obs.). However, this assertion requires further testing. It is more likely that this increase is linked to the high production rate

of suppressed buds at the branch base. In support of this latter hypothesis, we observed that the proportion of either suppressed buds or epicormics emerging at the branch base increased continuously and finally constituted the majority of the epicormics, reaching >50 %.

The general epicormic composition on the entire fork arms (Fig. 3E) mostly included buds and sprouts. Other epicormic types, spheroblasts and clusters, were in negligible proportions. Bud clusters become relatively more numerous on the oldest annual shoots (gp_AS_{13-17}) which also bore lateral axes (sequential or epicormic branches). Death of the latter induced the presence of the former by the development of the lateral meristems present in the basal part of the epicormic shoots remaining in the bark. Spheroblasts (data not shown) reacted in a similar way, confirming Fink's (1980) observations. As they are gradually engulfed by xylem production expanding from their bases, suppressed epicormic buds transform progressively into spheroblasts and may produce epicormic shoots. However, this hypothesis requires further confirmation.

Beech epicormics compared with oak epicormics

If we compare our results with those obtained on sessile oak (Fontaine *et al.*, 2001, 2002), we first observe that the number of axillary buds found on sessile oak was 0·76 cm^{-1} (Fontaine *et al.*, 2002) which is 5·5 times greater. One of the reasons why beech is a less strong sprouter than oak might be because it bears fewer axillary buds per initial metre. This in turn may have a phyllotactic origin (Bell, 1991, p. 218), as beech has alternate–decussate leaves and an axillary bud arrangement, while sessile oak has a spiral arrangement with a 2:5 ratio (Bartels, 1993). The initial dynamics of epicormics also seem to differ between the two species. From the number of axillary buds on AS_1, a first decrease in the number of epicormics is followed by an increase attributed to the high ability of beech to produce buds. The initial dynamics seem to be in contrast to those observed on sessile oak. Indeed Fontaine *et al.* (2001) demonstrated that there was first an increase ascribed to the branch base production of buds and then a regular decrease due to a low rate of bud death. In addition we observed that the proportion of either suppressed buds or epicormics which emerged at the branch base increased continuously and finally constituted the majority of the epicormics, reaching >50 %. In sessile oak this proportion reached 60 % (Colin *et al.*, 2010c). This nearly equivalent trend observed for these two species must now be tested on the most important forest species. Lastly, beech produces a lot of spheroblasts that may sclerose the buds and prevent their burst. These spheroblasts exist on sessile oak but are very rare (F. Colin, pers. obs.).

Epicormic shoot emergence, low radial growth and occurrence of 'missing' rings

From our results, it appeared clear that the number of 'missing' rings was statistically related to epicormic shoot emergence (Fig. 4 and Table 4): the more 'missing' rings an annual shoot has, the more epicormic shoots can emerge. Hypothesis H1 is thus confirmed. However, this relationship is slightly

different from that highlighted by Nicolini *et al.* (2001) in which only the occurrence of 'missing' rings was included. All other descriptors of ring width profiles such as LRW or threshold values of ring width could not be retained in the model. This is probably attributable to the fact that the occurrence of 'missing' rings on a given ring width sequence was closely linked with the earlier occurrence of very thin rings.

An increase in the number of 'missing' rings was associated with increased epicormic shoot emergence, which strongly suggests a trade-off between radial growth and epicormic bud maintenance. This trade-off should be supported by previous results from Fink (1980) gained from a structural point of view. Beech suppressed buds have been qualified by this author as 'high buds' with two 'growth centres'. The first centre occurs at the bud base (Braun, 1960 and Hartig, 1851 in Fink, 1980) and the second one at the bud tip. The former repairs the broken connection due to radial growth which prevents the bud cambium from being disconnected from the bearing stem cambium. It probably involves parenchymatous cells (Fink, 1980). The second leads to bud elongation by adding minute pairs of scaly leaves, and leaves a bud trace. Bud traces contain living cells (Fink, 1980; Fontaine, 1999) that probably allow radial–transversal water flow. Low or no radial growth means low or no wood and bark production. Assuming that the bud is still supplied by inner water flow thanks to its bud trace, the two growth centres contribute to putting the bud tip far away from the bark surface. The buds can then take advantage of external irradiance which is at its highest when the upper canopy is just starting to be leafed and when endo-dormance is at its lowest (Mauget, 1984; Wignall *et al.*, 1987; Ricaud *et al.*, 1995).

This trade-off can also be related to local competition for carbohydrates between buds and close cambium. Inactive cambium may consume few carbohydrates coming either from carbon storage (Barbaroux *et al.*, 2003) or from newly formed and phloem-translocated soluble carbohydrates. This carbon availability may favour the burst of suppressed buds.

From Table 3 it is obvious that epicormic sprouting was not only linked with the presence of 'missing' rings. Indeed on dominant arms as well as on dominated ones, some annual shoots that had no 'missing' rings bore epicormic shoots, a fact scarcely observed in dominant trees (Nicolini, 1997). Conversely, some dominated arms with missing rings (seven occurrences) did not bear epicormic sprouts.

A major limitation of our experimental design is the dependence between the annual shoot location and its cambial age. The older the annual shoot, the lower it is in the canopy. Consequently, we cannot distinguish the effect of the location from the cambial age. Actually, both sub-models rely on the cambial age as a predictor because it provided the best fit. However, there is no certainty that this effect is truly a cambial age effect and not a location effect or at least an interaction between these. This has to be further investigated.

Finally, it must be mentioned that our study focused on fork arms for which ring width profiles had thinner rings which, on dominated arms alone, led to the occurrence of missing rings. Consequently it could not be inferred how sprouting might be in the case of a very transient growth decrease or ring disappearance followed by increasing growth. This requires further investigations.

Ontogenetic constraints on epicormic sprouting

On *F. sylvatica*, epicormic sprouting is not perfectly associated with the occurrence of 'missing' rings, and could be partly explained by an 'ontogenic constraint', quantified by the number of epicormics currently available and illustrated by specifying the natural logarithm of *nepic*$_{ijk}$ as offset in sub-model 2a. This 'ontogenic constraint' has already been demonstrated in oak (Wignall and Browning, 1988; Morisset *et al.*, 2012a) and *Prunus* (Gordon *et al.*, 2006). Specifically, Wignall and Browning (1988), when using a generalized linear model with bud numbers included in the linear predictor in addition to the thinning treatment, did not find any thinning effect. All these results, including our own results, confirm hypothesis H2.

The network of trade-offs between the different traits observed can be synthesized as follows for *F. sylvatica* at least. First, there are structural relationships between annual shoot age, ring width distribution and occurrence of 'missing' rings. Secondly, current total frequency of all epicormics is related to annual shoot length. The second relationship is a result of the epicormic ontogenesis, initially including a quite strong relationship between annual shoot lengths and axillary bud frequency. Then epicormics disappear through death and engulfment. This is offset by the renewal of epicormics, probably through persistent axillary meristem activity and the emergence of secondary buds, mainly at branch bases. In turn the emergence of epicormic shoots is strongly constrained by the number of epicormics available. From this network it can be stated more precisely that the epicormic ontogeny is controlled by four phenomena: (1) the initial availability of axillary buds originating from the leaf arrangement, node number and annual shoot length leading to a certain frequency of buds per metre; (2) the proportion of axillary buds that become suppressed or produce sequential branches, the latter producing secondary suppressed buds; (3) the renewal capacity of meristematic axillary territories; and (4) the transformation of an unknown proportion of suppressed buds into spheroblasts which are not expected to be able to develop into epicormic shoots.

Silvicultural and ecological implications

In the current context of increasing beech forest productivity (Bontemps *et al.*, 2010; Charru *et al.*, 2010), latitudinal shift of the natural area due to increasing drought periods (Kramer *et al.*, 2010) and the even more evident mechanical vulnerability of mature beech stands to strong winds (Colin *et al.*, 2009), several alternative forest management strategies have been conceived, leading to very different situations for beech individuals. In situations where trees are far apart (Bock *et al.*, 2007), increased radial growth and probably less sprouting are expected. Conversely, in mixed and/or uneven-aged stands where individuals may remain in the understorey for a large part of their life span, this will probably result in stems with narrow rings and emerging sprouts. Once formed, these sprouts may induce secondary epicormics which may increase the epicormic composition even more (Morisset *et al.*, 2012a). Moreover the results of the present study suggest that biotic or abiotic stress events that reduce radial growth may also favour

sprouting. This is particularly true at development stages where epicormics other than spheroblasts are still present on the trunk, i.e. at young stages. This study revealed overall that sprouting is statistically related to the frequency of epicormics and to the number of 'missing' rings, but more to the former. This clearly suggests that a strong tree effect controls sprouting. Consequently crop trees must be selected from those individuals that bear very few suppressed buds and other epicormics, whatever their subsequent radial growth.

That epicormic buds are mainly produced at branch bases results in the more frequent location of burls (which are 'old' epicormic types) at branch bases. Finally, pruning success will be linked to the presence of suppressed buds (O'Hara and Berril, 2009; Springmann *et al.*, 2011). In fact these buds may burst vigorously when the branch above is pruned, due to the release of internal physiological correlations. Consequently, in horticulture, forestry or urban forestry, care must be taken either to prune individuals without suppressed buds at branch bases or to remove suppressed buds present at branch bases when performing a pruning operation.

All the presented results are complementary to those recently gained by Morisset *et al.* (2012*b*). These latter authors evidenced an influential tree effect on sprouting due to the frequency of epicormics fixed very early in the tree life span, either small or large depending on the tree. This ontogenic point must be taken into account in ecological studies dealing with sprouting in frequently disturbed forest ecosystems.

Conclusions

We confirmed that epicormic sprouting is associated with radial growth and the number of epicormics present. We demonstrated that the second factor is the most influential. These factors are related to cambial activity for the first, and primary growth and budding for the second. Obvious arguments supporting a trade-off between cambial activity and sprouting have been put forward. Thanks to the thorough tally of all epicormic types related to the annual shoot, we have laid the foundations for an accurate quantification of beech epicormic ontogeny similar to that which is already underway for sessile oak (Morisset *et al.*, 2012*b*). This paves the way towards precise ecological studies, taking the between-tree variability and the effects of age and location into account, either at the tree or even at the annual shoot scales.

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