

Does past emergence of epicormic shoots control current composition of epicormic types?

Jean-Baptiste Morisset · Frédéric Mothe ·
Bruno Chopard · Didier François · Florence Fontaine ·
Francis Colin

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Abstract

- **Context** While past studies on epicormics in oak (*Quercus* sp.) have focused on the effect of thinning on epicormic shoots emergence, the consequences of this emergence on the epicormic ontogeny and future wood quality have rarely been asked.
- **Aims** This paper aims at quantifying the relationship between past emergence and current composition of epicormics.
- **Methods** Three thinning experiments with *Quercus petraea* (Matt.) Liebl. or *Quercus robur* L. were investigated. Epicormic shoots were regularly tallied and epicormic composition recorded recently. Some logs were scanned using X-ray computed tomography (CT).
- **Results** Past tallies on both species were mainly and positively related to the current frequency of bud

clusters and burls. This was due to the production of buds by epicormic shoots for only certain trees, as evidenced by CT, and mainly to correlated numbers of current epicormic shoots, bud clusters and burls, all originating from a past common set of buds and bud clusters.

- **Conclusion** The important tree effect on both species suggests that oak silviculture can be optimized by the early selection of crop trees with few epicormics and/or eventually a first and heavy thinning that helps in spotting remaining individuals being prone to the development of multiple epicormics.

Keywords Sprouts · *Quercus petraea* · *Quercus robur* · Secondary buds · Bud clusters

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J.-B. Morisset · F. Mothe · F. Colin (✉)
LERFoB (Forest and Wood Resource) UMR 1092 INRA/
AgroParisTech-ENGREF, Centre INRA de Nancy,
54280 Champenoux, France
e-mail: colin@nancy.inra.fr

J.-B. Morisset
e-mail: morisset@nancy.inra.fr

F. Mothe
e-mail: mothe@nancy.inra.fr

B. Chopard
ONF Département R&D 10,
Rue Pasteur,
51470 Saint Memmie, France
e-mail: bruno.chopard@onf.fr

D. François
ONF-Département R&D,
21 Rue du Muguet,
39100 Dole, France
e-mail: didier.francois@onf.fr

F. Fontaine
UFR Sciences, Laboratoire SDRP, Université de Reims
Champagne-Ardenne,
Moulin de la Housse, B.P. 1039, 51 687 Reims Cedex 2, France
e-mail: florence.fontaine@univ-reims.fr

1 Introduction

The term epicormic refers to branching where a suppressed bud gives birth to a branch with a pith not directly connected to the pith of the bearing axis but indirectly through the trace of the suppressed bud. In addition to branches, bud clusters, burls and picots may also originate from suppressed buds (Colin et al. 2010a). All of these are named epicormic structures, including suppressed buds, epicormic being in this case an adjective. By extension, the noun epicormic designates any epicormic structure. Ontogeny of epicormic shoots and other types of epicormics on sessile oak trunks has been an important topic during the past decade (Fontaine et al. 1998, 1999, 2001, 2004; Colin et al. 2010a; Morisset et al. 2011). This recent impetus was motivated by the essential practical and economical need to improve the cultivation of oak and produce larger proportions of high-quality timber than in the past, in addition to a general market situation of decreasing wood prices (Jarret 2004; Sardin 2008). Crown recession, driven by the progressive shedding of sequential branches, has been modelled in several studies, enabling the prediction of the length of the trunk and its sequential knotty core (Spiecker 1991; Hasenauer and Monserud 1996; Nutto 1999; Dhôte et al. 2000). Once formed, oak trunks respond to silvicultural operations by eventually producing epicormic shoots. This production depends decisively on the suppressed buds present either in isolation or in different epicormic types: bud clusters, epicormic shoots, picots and burls (Colin et al. 2010a, c). Indeed, while isolated buds are the most frequent epicormic types present on recently elongated annual shoots and are quantified by the epicormic potential (Fontaine et al. 2001; Colin et al. 2010b), later they become a minority and are replaced by the other epicormic types which are better quantified by the epicormic composition (Colin et al. 2010a). Most studies on epicormics have focused on emergence of epicormic shoots on trunks (Spiecker 1991; Colin et al. 2008), as epicormic shoots were thought to induce the most serious epicormic defects in the trunk wood, namely the epicormic knots. We have examined epicormic ontogeny ourselves as a prerequisite for studying epicormic shoot emergence resulting from thinning (Colin et al. 2010a) or the removal of accompanying vegetation (Morisset et al. 2011). However, the consequences of epicormic shoot emergence itself on epicormic production and epicormic ontogeny have never been considered precisely; it has been rather under-estimated and even ignored. Nevertheless, it has been known for decades (Hahne 1926; Fontaine 1999), that every epicormic shoot, like any foliated shoot, bears axillary buds (Bell 1991; Barthélémy and Caraglio 1997) of which a certain proportion becomes suppressed, especially those at its base. The risk thus exists that epicormics develop from these suppressed buds of secondary origin (Fontaine 1999). Consequently, we assume that emergence of epicormic

shoots may promote new epicormics from secondary suppressed buds which adjusts the epicormic ontogeny. Epicormics originating from epicormic shoots could persist after shedding of the shoots and knot engulfment.

This paper aims firstly to test the following hypotheses:

- Hypothesis 1: emergence of epicormic shoots on the trunk gives rise to the production of secondary buds in a similar way to sequential branching; these buds may in turn develop into various epicormics.
- Hypothesis 2: trees on which epicormic shoots have emerged the most in the past, are those which currently bear the most numerous epicormics.

Secondly, this paper aims to complete oak epicormic ontogeny (Fontaine et al. 1998, 1999, 2001, 2004; Colin et al. 2010a, c) by including the eventual emergence of new epicormics as a consequence of past emergence of epicormic shoots.

To test the different assumptions, we took advantage of the opportunity that epicormic shoots were regularly tallied by the French Forest Service (ONF) in some of its silvicultural experiments. It must be made clear that what is basically analysed in this paper is not the thinning effect on the emergence of epicormic shoots but rather the effect of the emergence of epicormic shoots on the subsequent epicormic composition.

2 Materials and methods

The three ONF stands selected for the present study belong to two state forests in Larivour (LA) and Longchamp (LO) and one private forest in Grand Orient (GO) (Table 1). These three experimental stands were sampled because of the equivalent treatments that had been applied and their very good site indices. The oak species are sessile oak in GO and LO and pedunculate oak in LA. The LO and GO experiments are located respectively on the Eastern and Western sides of the lake of “Forêt d’Orient”. The water level of the lake is at its highest between April and the end of June and the lowest in November and December (DREAL Champagne-Ardenne 2010). This water regime provides a good water supply and large annual fluctuations of the water table. The LO experiment is located on a drier site.

Four treatments were applied to each stand (Table 1): the control treatment abbreviated by CO (without any thinning) and three treatments with different thinning intensities quantified by the number of expected crop trees per hectare: 42, 49, 70, 91 or 98 trees/ha. Treatments were designated by forest abbreviation (GO, LA or LO) and treatment (e.g. LA49).

Epicormic shoots were tallied regularly between 1992 and 2008 at different dates before or after thinning (Table 1), according to a specific ONF protocol consisted of counting

Table 1 Main features of the forests, treatments and trees sampled in the present study

| Experiment (<i>oak species</i>) | Grand Orient | Larivour | Longchamp |
|---|---|---|---|
| Oak species | <i>Quercus petraea</i> | <i>Quercus robur</i> | <i>Quercus petraea</i> |
| Geographic coordinates | 751567, 2368199 | 745643, 2373733 | 824589, 2255911 |
| Ownership | Private | State | State |
| Regeneration (main acorn mast year) | Natural (1966) | Natural (1960) | Natural (1949 and 1960) |
| Compartments | 37 | 3 | 55 |
| Elevation (m) | 110 | 110 | 200 |
| Soil | 60-cm-deep leached brown soil on sandy clay | 35-cm-deep leached soil with iron spots due to fluctuating water on Brienne clay | >60-cm-deep silty brown soil weakly leached with water table at depth 50 cm |
| Climate | $R=650$; $T=10$ | $R=650$; $T=10$ | $R=800$; $T=9$ |
| Treatments, abbreviation (no. of crop trees) | Control, GOCO (18) N91, GO91 (18) ^a N70, GO70 (18) N49, GO49 (18) | Control, LACO (17) N91, LA91 (18) N70, LA70 (17) N49, LA49 (18) | Control, LOCO (14) N98, LO98 (15) N70, LO70 (14) N42, LO42 (14) |
| Installation in winter | 1988/1989 | 1988/1989 | 1987/1988 |
| Age at installation (years) | 23 | 29 | 27 and 38 |
| Thinning in winters | 1988/1989, 1992/1993, 1996/1997, 2001/2002, 2006/2007 | 1988/1989, 1992/1993, 1996/1997, 2001/2002, 2006/2007 or 2007/08 (last thinning made during 2 winters) | 1987/1988, 1992/1993, 1997/1998, 2002/2003, 2007/2008 |
| in italic are mentioned the common campaigns | <i>1992, 1994, 1996,</i> <i>1997, 2001, 2002,</i> <i>2004, 2006</i> | <i>1992, 1994, 1996,</i> <i>1997, 2001, 2002,</i> <i>2004, 2006</i> | <i>1992, 1994, 1996, 1997,</i> <i>1998, 2002, 2003, 2005,</i> <i>2007</i> |
| Epicormic composition measured in | July 2007 | July 2007 | July 2008 |

Geographic coordinates are Lambert II coordinates

R annual rainfall in mm, T average annual temperature (°C). $N70$ for instance, means 70 crop trees expected at commercial maturity (according to Pardé 1978)

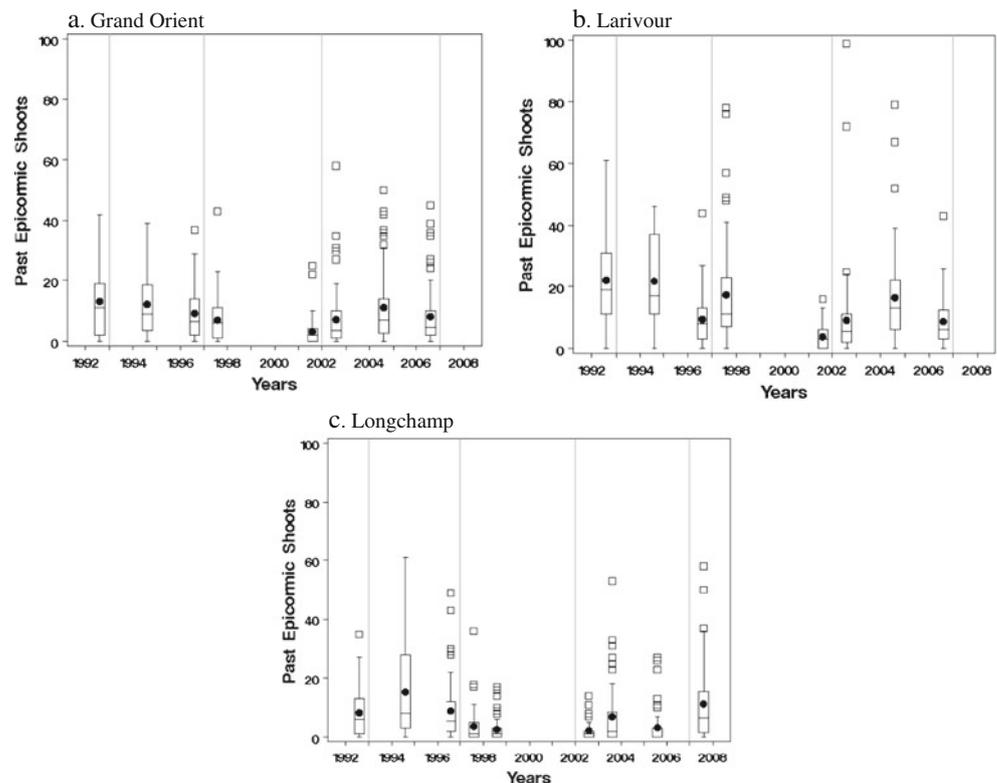
^a The epicormic composition was not described in this treatment in 2007

from the soil level short (<75 cm) and long (≥ 75 cm) living epicormic shoots in 2-m-long trunk segments up to 4 m. When several shoots belonged to the same burl, they were counted separately. Figure 1 displays the successive tallies made in the three experiments, all treatments included. It is obvious that the 2002–2003 campaigns gave the lowest values; the LO tallies had the smallest values; and the LA tallies had the largest values.

These tallies were not used directly but were synthesized into several variables. We retained the variable $S4m$ which was the total frequency of epicormic shoots recorded at the two trunk segments 0–2 and 2–4 m during the eight to nine campaigns, and averaged by dividing by the relevant number of campaigns. Figure 2 shows the $S4m$ distribution according to treatments. Treatments were compared with a Poisson model which is a generalized linear model relevant for adjusting counting data and with the contrast methodology (McCullagh and Nelder 1989). Treatments GO49, LA49, LACO, LO42, LO70, LO98 and LOCO appeared

not different. Treatments GO70, LA70 and LA91 had significantly larger $S4m$ values but were not different to each other. It must be remembered that treatments LA70 and LA91 were applied on the oak species *Quercus robur*. Treatments GO91 and GOCO had significantly smaller $S4m$ values but were not different to each other. Control treatments had amongst the smallest $S4m$ values. In the LA experiment (with *Q. robur*) with the exception of the control treatment LACO, we observed that the more severe the thinning, the weaker the emergence of epicormic shoots: LA49 < LA70 < LA91. In the GO experiment, the same trend occurred for only two treatments: GO49 < GO70. This trend was not discernible in the LO experiment. The effect of the treatments on the emergence of epicormic shoots will not be analysed any further since this analysis is not the objective of this paper. But the past emergence of epicormic shoots as presented above represents the effect that we aim to test on the current epicormic composition.

Fig. 1 Boxplot of past epicormic shoot emergence per tree and measurement campaign in Grand Orient (a), Larivour (b) and Longchamp (c) experiments



In 2007 or 2008, the crop trees were described in all treatments (except GO91, see Table 1). The main characteristics of the measured crop trees are summarized in Table 2. We quantified the epicormic composition from 0 to 4 m after Colin et al. (2010a) by counting the following five epicormic types: buds, bud clusters, epicormic shoots (alive or dead), picots and burls (see Fig. 3). Numbers of the five classes from 0 to 4 m were summed to form the total from 0 to 4 m (*Total*) and the total per metre when divided by 4 (*Total/m*). The numbers corresponding to the five types were complemented by the numbers of three epicormic classes. Buds and bud clusters which had only bud traces without any impairing effect on the wood quality were pooled to compose the “suppressed epicormics” class; their number was the variable *Suppressed*. All the other epicormics, which were the most detrimental to the wood quality were classified as “developed epicormics”; their number was the variable *Developed*. An additional class was made: “Bud clusters and burls” pooling both of these epicormic classes together. Their number was the variable *Bud clusters + burls*.

2.1 X-ray computed tomography

A four-slice medical X-ray scanner (BrightSpeed Excel by GE Healthcare) provided images with grey levels related to X-ray attenuation of trunk logs, depending both on internal

dry density and moisture content. Based on botanical standards (Barthélémy and Caraglio 1997), a homemade plug-in “gourmand” was added to the free ImageJ software (Rasband 1997–2009) and allows to manually describe and quantify the network of traces of buds and shoots (Colin et al. 2010c). Various files of quantitative data were created. A 3D viewer of the scanned log interior named Bil3D displays the following traces: vertical stem pith; oblique

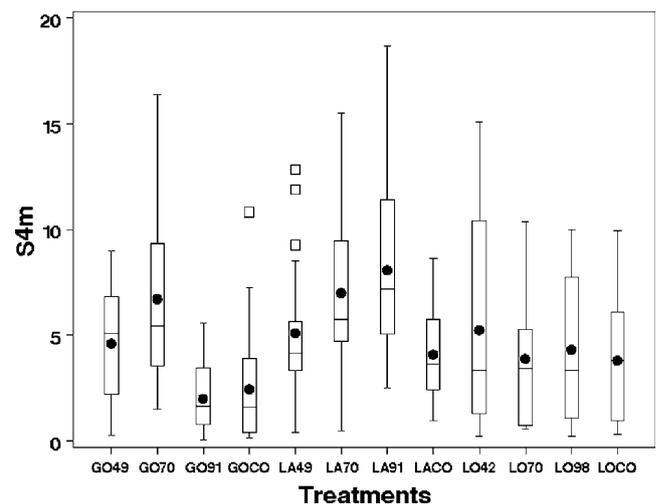


Fig. 2 Box plot of past epicormic shoot emergence averaged per treatment by summing the measurements of all campaigns and dividing the sum by the number of campaigns; eight or nine

Table 2 Usual tree measurements of the crop trees at the end of 2006 (in Grand Orient and Larivour) or 2007 (in Longchamp) with height to the lowest living branch (HBC) and standard deviation (SD)

| Experiment | Treatment | HBC (m) | | Girth (cm) | | H (m) | |
|--------------|-----------|---------|------|------------|------|-------|-----|
| | | Mean | SD | Mean | SD | Mean | SD |
| Grand Orient | GOCO | 10.4 | 1.4 | 67.4 | 7.1 | 19.5 | 0.9 |
| | GO70 | 8.7 | 1.75 | 80.5 | 8.1 | 19.2 | 1.0 |
| | GO49 | 8.4 | 1.3 | 86.8 | 9.0 | 20.0 | 1.0 |
| Larivour | LACO | 11.8 | 1.4 | 74.7 | 8.3 | 21.1 | 0.9 |
| | LA91 | 9.5 | 1.0 | 79.4 | 5.3 | 20.1 | 1.2 |
| | LA70 | 10.2 | 1.2 | 84.4 | 8.9 | 21.3 | 0.7 |
| | LA49 | 8.6 | 0.8 | 95.1 | 8.3 | 20.3 | 0.9 |
| Longchamp | LOCO | 13.4 | 1.8 | 72.7 | 11.3 | 22.8 | 1.3 |
| | LO98 | 11.7 | 1.3 | 84.8 | 25.9 | 22.1 | 0.9 |
| | LO70 | 11.3 | 0.9 | 94.3 | 8.3 | 22.3 | 1.0 |
| | LO42 | 9.4 | 1.2 | 101.2 | 13.1 | 22.2 | 1.2 |

knots of sequential branches directly attached to the pith; transversal-horizontal traces of suppressed buds that are persistent axillary buds also directly attached to the pith; transversal-horizontal traces of suppressed buds of secondary origin, originating from the base of either a suppressed bud of primary origin, a sequential branch or an epicormic shoot; and transversal-horizontal knots laid down by epicormic shoots. Complex epicormic structures such as picots and clusters of suppressed buds were identified on the stem surface. A series of traces, all originating either from a sequential branch or from a primary suppressed bud, was referred to a rameal sequence. Quantitative variables are provided in Table 2.

Only trees from the LO experiment were available for scanning. These trees did not belong to the crop tree class (with three exceptions) but to the class of other dominant trees in which trees were regularly selected to be felled during successive thinnings. The nine trees belonging to the three non-control treatments had various levels of external quality as detailed in Table 3. This external quality was estimated approximately using a rapid count of visible “developed” epicormics. For every tree, five 1-m-long logs were then recovered, of which only two were considered to be closely related to our 4-m-long lower log: L2 between 1.5 and 2.5 m and L4 between 3.5 and 4.5 m.

The files of quantitative data made it possible to provide general features of the epicormic ontogeny within the 18 L2 and L4 logs and particularly the relationships between the number of epicormics present at 2 cm around the trunk pith (*epic_pith*), which means a few years after the bearing annual shoots have elongated, and the epicormics present at the trunk surface (*epic_bark*). Epicormics counted at the pith were buds only (of primary or secondary origin) while epicormics counted at the bark were epicormic shoots and suppressed buds, either in isolation, in bud clusters or burls. No picots were detected.

2.2 Statistical analysis

Statistical analysis was performed with SAS software version 9.2. Frequencies of epicormic classes were adjusted on $S4m$ with a linear model using the procedures PROC GLM. We did that for epicormic classes or types for which the numbers of epicormics were more than 30. If the numbers would have been less than 30, Poisson models would have been more relevant (McCullagh and Nelder 1989). Independent variables and factors tested were: $S4m$, $S4m^2$ ($=S4m*S4m$), experiment, $S4m*experiment$ and $S4m^2*experiment$, with $S4m*experiment$ for instance being the interaction between $S4m$ and experiment. Non-significant effects were removed with a manual backward procedure.

The relationship between *epic_pith* and *epic_bark* was fitted with a linear mixed model accounting for the dependence of the observations made on the two logs L2 and L4 of each tree, with the help of the PROC MIXED procedure.

3 Results

3.1 External observations

Figure 4 shows that total frequency of epicormics tallied in 2007 or 2008, standardized per tree and per metre, was not very different from one experiment to another and fluctuated around ten epicormics per metre. Treatments LA49, LACO and LO70 had the smallest values and treatment LO42 had the largest between-tree variability.

Figure 5 illustrates the epicormic composition assessed at the treatment level. Percentages of the different epicormic classes are provided in Table 4. Treatments in LO are characterized by small percentages of buds, bud

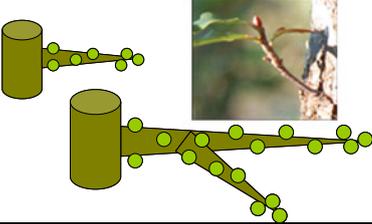
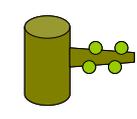
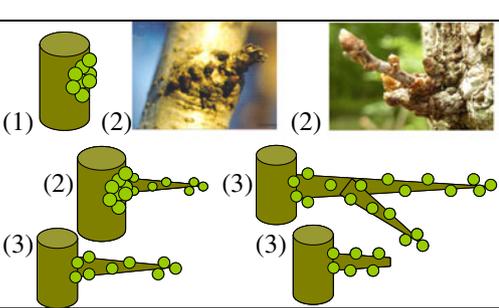
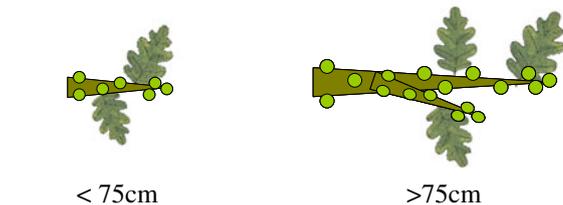
| Type | Definition | Drawings and photos | Class |
|--|--|--|-----------------------|
| Isolated bud | Suppressed bud |  | Suppressed epicormics |
| Bud cluster | Two to 5 buds gathered with less than 3mm of distance between closest ones |  | |
| Epicormic shoot | Living shoot with leaves or not issuing from a suppressed bud without bud at its insertion |  | Developed epicormics |
| Picot | Short axis with superimposed buds and originating from a thin shoot which has lost its proximal end |  | |
| Burl | (1) cluster of more than 5 suppressed buds, (2) with eventual short epicormic shoots or picots or even remnants of branch or (3) epic. shoot or picot with buds at its insertion |  | |
| Epicormic shoots according to the ONF protocol | Foliated green epicormic shoot with no particular information on eventual buds at insertion (some leaves only are drawn) |  | |

Fig. 3 Epicormic classes distinguished in 2007 and 2008 in the INRA protocol and sprout classes distinguished in the ONF protocol (*last row*). Buds are represented in *light green*

Table 3 Main attributes of Longchamp trees sampled for scanning

| Treatment | Tree no. | Girth ₂₀₀₇ (cm) | H ₂₀₀₇ (m) | Quality |
|-----------|----------|----------------------------|-----------------------|---------|
| N98 | 09 | 73 | 21.5 | Low |
| | 15 | 99 | 21.3 | Medium |
| | 16 | 76.2 | 22.8 | High |
| N70 | 18 | 96 | 21.5 | High |
| | 28 | 86.4 | 21.4 | Medium |
| | 42 | 105.4 | 23.0 | Low |
| N42 | 19 | 97.2 | 20.9 | High |
| | 43 | 90.5 | 19.8 | Low |
| | 55 | 87.8 | 22.8 | Medium |

clusters (less than 38.5%) and thus suppressed (buds+bud clusters less than 53%) as opposed to treatments in GO and LA where the proportions are larger: over 38.2% for bud clusters and over 64% for suppressed. Percentages of epicormic shoots are variable and below 20%. Picots are the most numerous in LO and especially in treatment LO98.

The statistical relationships between frequencies of various epicormic classes as dependent variables related to the experiment factor are provided in Table 5. We obtained the following general ranking of the different epicormic types and classes with a decreasing determination coefficient (R^2): Developed>burls>bud clusters+burls>Total>bud clusters>Suppressed>epicormic shoots>buds.

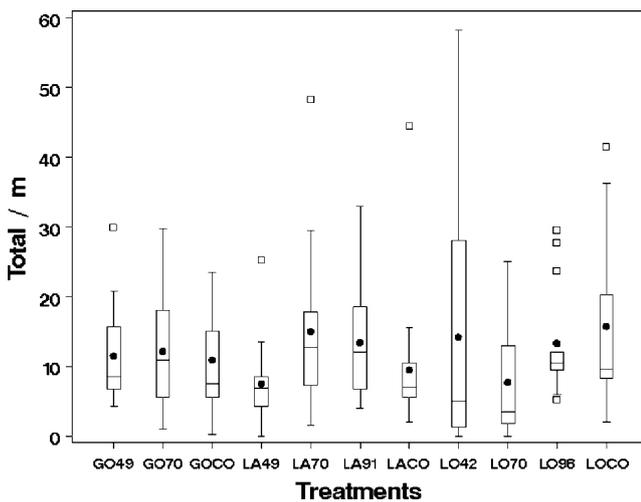


Fig. 4 Box plot of total frequency of epicormics per metre per individual tree as observed in 2007 or 2008 on the lowest 4-m-long trunk section

Figure 6 provides the plot of the frequencies of epicormic types and classes that are the most numerous versus $S4m$. The relationships depend on the experiment factor except for bud clusters and “suppressed” epicormics. For most relationships, observations of LO trees are above the other observations while observations of the experiment GO are slightly above observations of the experiment LA. This is not the case for buds and epicormic shoots; the former exhibiting no relationship with $S4m$ and the latter only a weak relationship. This latter relationship demonstrates that current epicormic shoots are not especially related to past emergence of epicormic shoots, demonstrating the turnover and instability of epicormic shoots already shown by Colin et al. (2008).

Figure 7 provides an illustration of the highly significant linear model ($R^2=0.40$) adjusting the number of epicormic

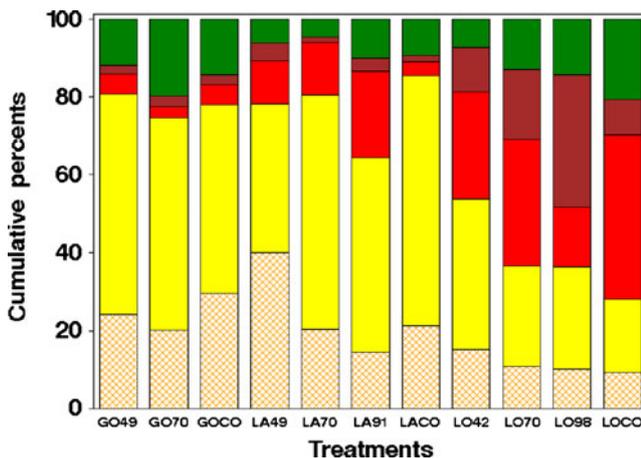


Fig. 5 Chart of percentages of each of the five epicormic types as recorded on 4 m of all trees of each treatment. From the bottom to the top of the chart: suppressed buds (cream), bud clusters (yellow), burls (red), picots (purple) and sprouts (green)

shoots to the retained variables and factors: $Total$, $Total^2$, $Total \times \text{experiment}$, $Total^2 \times \text{experiment}$.

3.2 X-ray computed tomography

Figure 8 provides virtual 3D views of the interior of four L2 logs as interpreted from computed tomography (CT) images. From these views, it can be clearly observed that trees 09 and 18 bear more rameal sequences than trees 19 and 55. Trees 09 and 55 only bear epicormic knots. This depicts the two tree level effects: (1) on the number of rameal sequences and (2) on the responsiveness of the buds occurring in the rameal sequences present. More precisely, the displayed logs have the following features.

- The log from tree 09 which was of low external quality bears 57 rameal sequences, 17 epicormic knots and one bud cluster originating from an epicormic shoot among three bud clusters.
- The log from tree 19 had high external quality due to the low frequency of rameal sequences and buds had neither gathered to form bud clusters nor developed into epicormic shoots; the log bears 21 rameal sequences, 0 epicormic knot and 0 bud cluster.
- The log of tree 18 bears 57 rameal sequences, 0 epicormic knot and 0 bud cluster. In this case, the high external quality was not due to a small number of rameal sequences, but to the fact that this tree had produced neither bud clusters nor epicormic shoots up to now.
- Lastly, tree 55 was of medium quality, due to the emergence of epicormic shoots mainly from a medium frequency of rameal sequences; the log bears 32 rameal sequences, 12 epicormic knots and zero bud cluster.

Figure 9 provides a detailed image of the origin of most epicormic classes. All suppressed buds either of primary origin (Fig. 9a) or of secondary origins are oriented according to a clear radial-transversal direction. The latter buds may originate from primary buds that have branched (Fig. 9b), from sequential branches (Fig. 9c) or from sprouts (Fig. 9d). Bud clusters at the trunk surface are symbolized by green circles (Fig. 9e, f). Rameal sequences originate either from a primary suppressed bud (Fig. 9a, b, d, e and h) or from a sequential branch (Fig. 9c, f, g (except for cases 9L2), i and j).

Table 6 provides variables computed from data recorded in logs L2 and L4 (2 m of trunk) assumed to be representative of the first 4 m of the trunk. No picots produced by epicormic shoot were detected. It can be deduced that:

- Number of rameal sequences per metre was fairly variable from 45 to 114;
- Number of clusters and sprout-originating clusters was larger for lower-external-quality trees, but

Table 4 Percentage of different epicormic classes calculated on all trees of each treatment

| Experiment | Treatment | Developed (picots+epicormic shoot+burls) | Suppressed (buds+bud clusters) | Bud clusters+burls | Bud clusters |
|------------|-----------|--|--------------------------------|--------------------|--------------|
| GO | G049 | 19.25 | 80.75 | 61.62 | 56.54 |
| | G070 | 25.46 | 74.54 | 57.31 | 54.34 |
| | GOCO | 22.04 | 78.03 | 53.63 | 48.41 |
| LA | LA49 | 21.71 | 78.29 | 49.35 | 38.22 |
| | LA70 | 19.51 | 80.49 | 73.73 | 60.10 |
| | LA91 | 35.55 | 64.45 | 72.14 | 49.90 |
| | LACO | 14.44 | 85.56 | 67.86 | 64.29 |
| LO | LO42 | 46.29 | 53.71 | 66.29 | 38.49 |
| | LO70 | 63.34 | 36.66 | 58.35 | 25.81 |
| | LO98 | 63.64 | 36.36 | 41.71 | 26.34 |
| | LOCO | 72.05 | 27.95 | 61.10 | 18.64 |

clusters were too few to confirm this assumption statistically;

- The emergence of epicormic shoots has led to the production of 40 buds (21 on tree 09), seven bud clusters (four on tree 09), one epicormic shoot (on tree 55), no picot and it was impossible to detect burls;
- Of 13 bud clusters, seven originated from epicormic shoots; all of these cases are illustrated in Fig. 9;
- The majority of epicormic shoots did not give birth to secondary suppressed buds, and epicormic shoots giving birth to more than one bud were the least frequent. They were present on trees 09, 15, 43 and 55.

Figure 10 emphasizes the strong statistical relationships between initial epicormics present in the first 2 cm around the pith (*epic_pith*) and current epicormics present near the bark (*epic_bark*). The model attributes are the following: model P value < 0.0001; slope estimate, 1.1444; no intercept. It can be seen that around the general trend, which is slightly above the 1:1 line (meaning that they were as many sequences at the pith as at the bark) trees 28, 43 and 55 have few rameal sequences at the pith and even fewer at the bark for one or two of their scanned logs while trees 09, 15 and 16 have numerous sequences at the pith and many

more at the bark. Other trees have a few sequences at the pith and more at the bark.

4 Discussion

Methodologies XT procedures helped to interpret the statistical results by providing virtual internal views of rameal traces. At the current stage of progress, bud clusters can only be identified at the trunk surface with a threshold distance between the closest buds of 5 mm, which allows the relationship between epicormic shoots and resulting bud clusters to be illustrated (see Fig. 8). Since bud clusters have not been identified within the trunk up to now, the quantification and illustration of the reverse relationships between bud clusters present at any time in the past, and the resulting epicormic shoots, are not yet available.

Only very preliminary elements can be put forward about the comparison between sessile and pedunculate oaks concerning the effect of the past emergence of epicormic shoots on the current epicormic composition. From data shown in Table 5 and Fig. 6, linking current frequencies of different epicormic types and classes and past epicormic

Table 5 Determination coefficient R^2 and variables and factor retained in the general linear models fitted on the different epicormic classes

Developed=sprouts+burls+picots. Suppressed=buds+bud clusters

| Frequencies of: | R^2 | Variables and factor retained |
|--------------------|-------|--|
| Total 4 m | 0.52 | S4m, S4m*experiment |
| Suppressed | 0.38 | S4m |
| Developed | 0.64 | S4m, S4m*experiment, S4m ² *experiment |
| Bud clusters+burls | 0.55 | S4m, S4m*experiment |
| Bud clusters | 0.46 | S4m |
| Burls | 0.57 | S4m, S4m*experiment |
| Buds | 0.09 | experiment |
| Epicormic shoots | 0.31 | S4m, S4m ² , S4m*experiment, s4m ² *experiment |

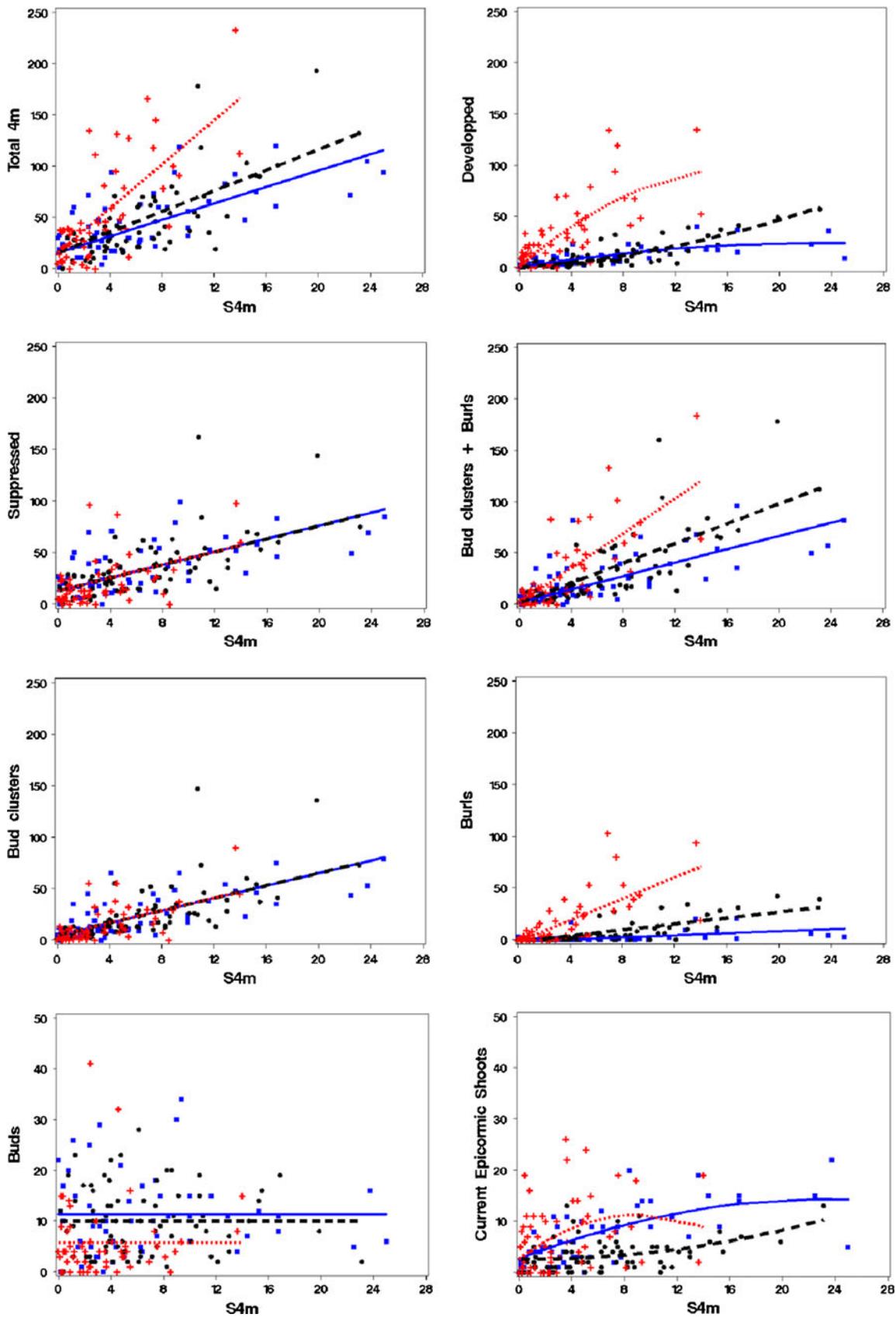


Fig. 6 Statistical relationships between developed epicormics, burls and bud cluster frequencies depending on experiment in (a), (b) and (c), respectively. Symbols are the following: *blue* GO experiment (*line* for predicted values), *black* LA experiment and *red* LO experiment

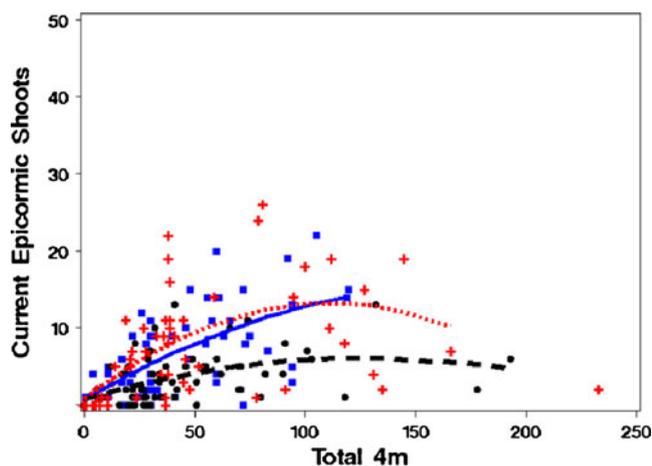


Fig. 7 Relationship between number of current epicormic shoots and total number, depending on the experiment: *blue* GO experiment (*line* for predicted values), *black* LA experiment and *red* LO experiment

shoot emergence quantified by $S4m$, it was demonstrated that the difference between the GO and LA experiments (respectively with sessile and pedunculate oak) was smaller than the difference between these experiments and the LO experiment (sessile oak). Therefore, the two species do not appear to behave differently. This would mean that once epicormic shoots have emerged, the consequences on the future epicormic composition are equivalent. This result obtained on a limited sample of pedunculate oak requires further confirmation. In general, such investigation on an expanded sampled would contribute to increasing the limited knowledge about epicormics on pedunculate oak (Courraud 1987; Spiecker 1991; Lemaire 1992; Fournier et al. 2003).

Hypothesis 1 Once epicormic shoots have emerged, it is essential to know what the ontogenic consequences are. From CT results, it has been demonstrated that some epicormic shoots may produce buds, especially for certain trees (no. 09, 55, 43 and to a lesser extent 15), but these epicormic shoots were generally in the minority. Epicormic shoots may also produce bud clusters. This is structurally relatively straightforward since secondary suppressed buds are all emitted in a transversal-radial direction, increasing the chance of forming clusters of buds in the generated plane. But this occurred for only a small proportion of epicormic shoots and again for trees 09, 43 and 55. Burls or picots originating from epicormic shoots were not detected. Because of the small number of bud clusters originating from epicormic shoots we can assume that burls might be less frequent, or even missing. Hypothesis 1 is thus confirmed: the emergence of epicormic shoots may promote production of buds and bud clusters, but this promotion does not seem to be of great quantitative importance. If most epicormic shoots result in null bud

production, the idea that the emergence of epicormic shoots might exhaust epicormic potential cannot be rejected. Indeed, once an epicormic shoot has emerged from a bud and is later shed, it means that this bud has disappeared and there is one bud less which might subsequently transform into a bud cluster, a sprout with basal buds, or burls. Moreover, the promotion of bud and bud cluster production was obviously specific to a few trees, in our sample, trees 09, 55, 43 and 15. This specificity was not necessarily related to large frequency of epicormics; we observed tree 09 bore 57 rameal sequences per metre while trees 43 and 55 had about half of that number.

Epicormic ontogeny Epicormic ontogeny can be now updated to include the above results and previous ones (Colin et al. 2010a, b, c). For oak, all epicormics originate from axillary buds laid down during annual shoot elongation. Some of these buds fail, some develop into sequential branches and others become suppressed buds of primary origin (Fontaine et al. 2001). This gives birth to the two types of rameal sequences as shown in the 3D views of the interior of the trunk (Fig. 8); sequences originating from suppressed buds or originating from sequential knots. After shoot elongation, for instance approximately 3 to 5 years later, the epicormic composition includes a great majority of buds and a few thin epicormic shoots developed from some of these buds. Trunks with transient shoots are characteristic of young dense stands. Approximately 10 years later, bud clusters emerge either from branched buds or from thin epicormic shoots which have died. These eventually formed thin epicormic shoots again, which died in their turn and are shed, finally leaving residual basal buds. At approximately 20–30 years, bud clusters may represent the majority of epicormic types as shown in Tronçais by Colin et al. (2010a) and in the present study in GO and LO. A few thin epicormic shoots may form once again from buds, but also from buds composing bud clusters. A few thin epicormic shoots may be partially shed to become picots. Burls may have appeared as well. In the case of heavy thinning at this stage, more epicormic shoots may emerge from buds, either in isolation, in bud clusters or even on picots. In the present study, we showed that a few epicormic shoots, belonging to a few trees, may produce buds of secondary origin and even bud clusters. It is evident that depending on the initial frequency of epicormics, the frequency of the different epicormic types may have different values, and transitions from one type to another can be of different magnitudes. The total frequency might even progressively increase as for trees 09, 15 and 16.

Relationships between epicormic at the trunk and epicormics at the pith $Epic_bark$ and $epic_pith$ observed on 18 1-m-long logs were strongly related: overall, the more epicor-

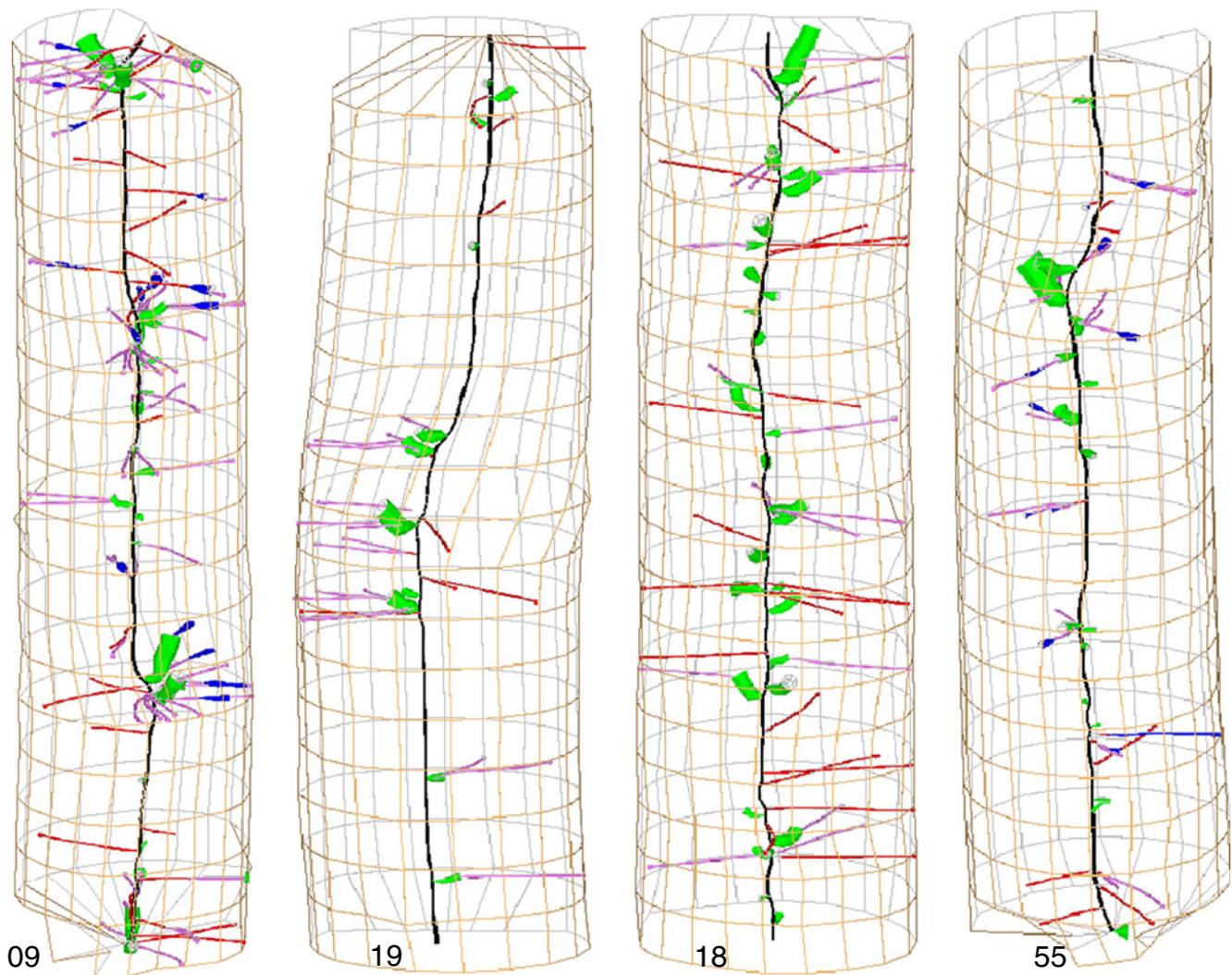


Fig. 8 Rameal sequences of four representative L2 logs (see Table 3 for quantitative data). Symbols are the following. Vertical stem pith (*black*); oblique sequential knots laid down by sequential branches (*blue*); clusters of suppressed buds (less than 6) are identified on the stem surface by green circles, while picots are identified on the stem surface by yellow discs. Tree numbers are provided below the virtual logs

suppressed bud of primary origin, a sequential branch or an epicormic shoot; transversal-horizontal knots laid down by epicormic shoots (*blue*); clusters of suppressed buds (less than 6) are identified on the stem surface by green circles, while picots are identified on the stem surface by yellow discs. Tree numbers are provided below the virtual logs

mic that annual shoots bear initially, the more epicormics they bear decades later. From this observation, which merits further validation, it can be assumed that the current total frequency can be considered to be a good reflection of the total frequency of epicormics present when sprouting occurred. This relationship illustrates two aspects of the between-tree variability of epicormic composition. The general trend reflects a mainly positive influence of the initial frequency of epicormics. The residuals reflect the variable aptitude of trees to let epicormic shoots emerge; from their initial epicormics, some trees tend to develop or maintain many epicormics (for instance, tree 09) while others do not develop or maintain any epicormics (for instance, trees 18 and 19).

Hypothesis 2 One result, which has been demonstrated statistically, is that the frequencies of all epicormic types or classes (except bud type) are significantly and positively related to past emergence of epicormic shoots. The more epicormic shoots a tree produced in the past, the more epicormics it bears decades afterwards. More specifically, the more epicormic shoots a tree produced in the past, the more bud clusters and burls it bears decades afterwards. Therefore, hypothesis 2 has been fully confirmed. However, this statistical relationship is far from being a direct causal relationship. Based on the structural relationships observed from the CT data, the production of bud clusters from epicormic shoots may occur but only to a limited extent, lacking a strong

Fig. 9 Radial spread of different rameal sequences as interpreted from CT procedures. Notice that all seven epicormic shoot-originating clusters of the 13 bud clusters found in the scanned logs are displayed in this figure). 9L4 log4 of tree 09, L2 log 2, L4 log 4. Colours are the same as in Fig. 8

| Rameal sequence | issuing from | | |
|------------------------|--------------|----|--|
| Primary suppressed bud | pith | a. | |
| Secondary primary bud | bud I | b. | |
| | Seq | c. | |
| | Epic. shoot | d. | |
| Bud cluster | Bud I | e. | |
| | Seq | f. | |
| | Epic. shoot | g. | |
| | | | |
| | | | |
| | | | |
| Sprout | Bud I | h. | |
| | Bud II | i. | |
| Picot | | j. | |

statistical support for the evolution of epicormic shoots→bud clusters. The other reason for a quite strong relationship is that, the higher the total number of epicormic buds and bud clusters in the past, the greater the number of epicormic shoots which could have emerged (Fig. 7). According to the updated epicormic ontogeny, buds that do not transform into epicormic shoots are “available” to form bud clusters, which in turn may extend by adding new buds or transform into burls. Consequently, the more numerous the epicormics in the past the more numerous the

epicormic shoots which could have been produced, and the more numerous the bud clusters and burls produced in parallel.

Lastly, we found considerable differences between experimental sites, especially between the LO experiment and the other experiments. Specific behaviour of the LO experiment consisting in more “developed” epicormics in general may be due to specific stand conditions including specific under-storey, soil (drier than in the other experiments), genetics. This interpretation is only hypothetical and suggests further in-deep investigation. More likely

Table 6 Main quantitative variables obtained from scan images

| Tree | Frequency of rameal sequences | Frequency of rameal sequences with epicormic shoot | Frequency of epicormic shoots | Frequency of bud clusters | Frequency of buds from epicormic shoot | Frequency of bud clusters from epicormic shoot | Frequency of epicormic shoots from epicormic shoots | % epicormic shoot giving no bud | % epicormic shoot giving 1 bud | % epicormic shoot giving >1 bud |
|------|-------------------------------|--|-------------------------------|---------------------------|--|--|---|---------------------------------|--------------------------------|---------------------------------|
| 09 | 114 | 37 | 51 | 7 | 21 | 4 | 0 | 63 | 21 | 16 |
| 15 | 70 | 14 | 20 | 1 | 2 | 1 | 0 | 90 | 5 | 5 |
| 16 | 62 | 2 | 2 | 2 | 0 | 0 | 0 | 100 | 0 | 0 |
| 18 | 89 | 2 | 3 | 0 | 0 | 0 | 0 | 100 | 0 | 0 |
| 19 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| 28 | 47 | 7 | 7 | 0 | 1 | 0 | 0 | 86 | 14 | 0 |
| 42 | 59 | 6 | 6 | 1 | 0 | 0 | 0 | 100 | 0 | 0 |
| 43 | 60 | 21 | 26 | 1 | 10 | 1 | 0 | 61 | 27 | 12 |
| 55 | 61 | 16 | 20 | 1 | 6 | 1 | 1 | 70 | 15 | 15 |

Data of logs L2 and L4 were pooled

this behaviour can be due to the greater age of some trees (acorn mass in 1949, see Table 1) that bear older epicormic composition with more bud clusters, picots and burls. About the LA experiment we saw that the fact that *Quercus robur* was the dominant species did not induce a difference with the GO experiment in the relationship between past epicormic shoots emergence and current epicormic composition.

Silvicultural outcomes From the results of this study, we cannot reject the empirical observation that emergence of

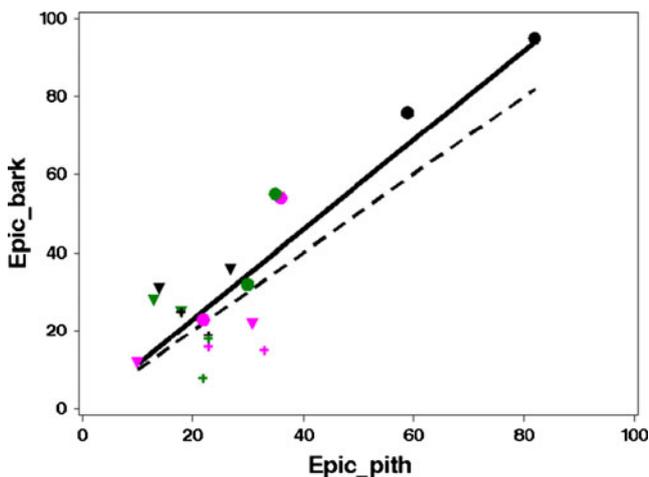


Fig. 10 Relationships between epicormics present in the first 2 cm around the pith (*epic_pith*) and epicormics present near the bark (*epic_bark*), for logs L2 and L4 of all of the nine scanned trees. *Solid line*, fit of the data; *dashed line*, 1:1. Observed values are symbolized as follows: treatment LO98—tree 09 (*black dots*), tree 15 (*magenta dots*) and tree 16 (*green dots*); treatment LO70—tree 18 (*black triangles*), tree 28 (*magenta triangles*) and tree 42 (*green triangles*); and treatment LO42—tree 19 (*black plus*), tree 43 (*magenta plus*) and tree 55 (*green plus*)

epicormic shoots exhausts epicormic composition. Indeed, for medium or low “sprouter” trees (i.e. with a low aptitude to let epicormic shoots emerge), when emergence occurs it exhausts the epicormic potential to some extent because a bud has been used and the epicormic shoot will then die very quickly, especially if the under-storey is relatively dense. For strong “sprouter” trees on the other hand, sprouting is an accompanying phenomenon which, amongst others, participates to some extent in the maintenance of a large epicormic composition. The emergence of epicormic shoots does not greatly increase the epicormic composition since it is still very high in this case. Apart from the idea that epicormic shoot emergence must exhaust epicormic potential, some foresters assume that it could be useful to induce epicormic shoot emergence by heavy thinning of 12- to 15-m-tall trees to distinguish trees with future low or high quality; we cannot reject this assumption either. Indeed, past epicormic shoot emergence was obviously related to large current epicormic composition and especially to large proportions of bud clusters and burls pooled together. Consequently, past epicormic shoot emergence has “helped” in identifying strong “sprouters”. In conclusion, all this information makes it possible to orient silvicultural practises towards better and earlier selection of “low sprouter” crop trees such as trees 43, 55 and 28 and the removal of “strong sprouters” such as trees 09, 15 and 16. This is possibly true for both sessile and pedunculate oaks.

This must be made probably more carefully on pedunculate oak, which is empirically known to bear more epicormics (Courraud 1987), probably because it reacts more strongly to stand manipulation. Indeed, from ONF tallies we observed that the heavier the thinning, the lower the emergence of epicormic shoots. This corroborates observations by Courraud (1987) that long-crowned

pedunculate oaks have less epicormic shoots than short-crowned ones and the observations by Lemaire (1992) that external quality (unfortunately combining the presence of epicormics and straightness) was improved with heavy thinning. This supports the recommendation of heavier thinning in pedunculate oak stands than in sessile oak stands as already prescribed in silvicultural guides (Jarret 2004; Sardin 2008). However, our result concerns a limited sample. In addition, surprisingly very few epicormics were observed in the control treatment. Consequently, further investigation on the comparative aptitude for epicormic shoot emergence of sessile and pedunculate oak is required.

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