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Original article

Evolution of the epicormic potential on 17-year-old *Quercus petraea* trees: first results

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Abstract – The epicormic potential was represented by the number of visible epicormic buds (primary and secondary) present at a given time and on a given length of stem. Data were collected from sixty-six 4-year-old annual shoots on 17-year-old *Quercus petraea* with 3 stand densities. We estimated the epicormic potential in 1997 and then followed its evolution over the next 2 years. Preliminary results showed that the epicormic potential decreased from 1997 to 1999, independently to the stand density. The loss of epicormic buds (death or development into shoots) was not compensated by the production of new epicormic buds. Furthermore, we report that the composition of the epicormic potential was unchanged for these 2 years: one third were primary epicormic buds and two thirds were secondary epicormic buds. Secondary epicormic buds were mainly found as individual and located at the base of branches. No formations of large clusters of epicormic buds were observed.

***Quercus petraea* / epicormic potential / bud / shoot / estimation / evolution**

Résumé – **Évolution du potentiel épicormique sur des chênes sessiles âgés de 17 ans : premiers résultats**. Le potentiel épicormique est représenté par le nombre de bourgeons épicormiques visibles (primaires et secondaires) présents à un moment donné sur une unité de longueur définie. Les données ont été collectées sur la pousse annuelle âgée de 4 ans de 66 chênes sessiles âgés de 17 ans répartis dans 3 densités de culture. Nous avons évalué le potentiel épicormique en 1997 puis nous avons suivi son évolution les 2 années suivantes. Les premiers résultats ont montré que le potentiel épicormique a diminué de 1997 à 1999, indépendamment des densités de culture. La perte de bourgeons épicormiques (mort ou développement en gourmands) n'a pas été compensée par la formation de nouveaux bourgeons épicormiques. De plus, nous avons constaté que la composition du potentiel épicormique restait inchangée au cours de ces 2 années et comprenait toujours un tiers de bourgeons épicormiques primaires et deux tiers de bourgeons épicormiques secondaires. Ces derniers étaient essentiellement isolés et localisés à la base des branches. Aucune formation de groupes de bourgeons n'a été observée.

***Quercus petraea* / potentiel épicormique / bourgeon / pousse / évaluation / évolution**

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1. INTRODUCTION

Quercus petraea Matt. Liebl. plays an important role in French and European forestry for lumber production [1]. Timber quality of oak, as in many hardwoods [2, 3, 10, 14], however, can be reduced by the emergence and the persistence of epicormic shoots along the trunk, because they may create knots, blemishes and rot in the wood [13, 17, 19]. In order to gain more information on epicormic shoots, 2 subjects can be investigated [17]: the first, based on factors influencing the development of epicormic shoots and the second, oriented on the origin of the epicormic shoots, the epicormic buds. In this paper, we have focused on the epicormic buds.

Our recent investigations on epicormic buds on *Q. petraea* focused on their origin, their organization and their fate [6, 7]. Our results were similar to those described in *Fraxinus americana* [8], *Acer saccharum* [4], *Liquidambar styraciflua* [12], *Betula pubescens* [11] and in *Euptelea polyandra* [15]. In *Q. petraea*, epicormic buds were all of proventitious origin; they were primary or secondary: primary when they consisted of primary axillary buds which did not develop into branches and secondary, when they were produced by a primary axillary bud after its development or its death. These buds initially comprised a terminal meristem surrounded solely by scales and then, secondary buds developed as growth occurred, thus leading to a discreet increase in the number of buds on the trunk. These secondary buds could become visible following a partial abscission of the primary epicormic bud or its development into shoot. In both cases, secondary buds were found as individuals or in clusters on the remnant of the initial bud or on the short remaining portion of the dead shoot. The emergence of secondary buds characterized a visible proliferation of the number of buds. The number of visible epicormic buds (primary and secondary) present at a given time, on a given length of stem, represents the epicormic potential. According to Blum [3], if the epicormic potential is only composed of proventitious epicormic buds, it is quantifiable and its evolution become predictable from the initial number of epicormic buds. In contrast, if additional adventitious buds are present, the evolution of the epicormic potential is unpredictable since the formation of adventitious buds is random each year. In woody species including *Q. petraea*, to our knowledge, there are no data on the estimation and on the evolution of the epicormic potential over time. At present, this work could be initiated in *Q. petraea* since all epicormic buds are of proventitious origin and since the different kinds of epicormic buds are characterized along the trunk [6, 7].

Our long-term goal is to determine the influence of the stand density on the number and fate of epicormic buds. According to their fate (survival, death with or without production of new buds, development into shoot with or without formation of new buds) the epicormic potential will increase, be stable or decrease over the years. The specific objective of this paper is to estimate and follow the epicormic potential of an annual-shoot from 1997 to 1999 on young *Q. petraea*.

2. MATERIALS AND METHOD

2.1. Experimental site description

The experimental field is located in the Montrichard forest (47º98'55" N, 1º55' E), central France, which is managed by ONF (Office National des Forêts). The site is at an altitude of 121 m, has a soil composed of loamy sand, an average annual temperature of 11 ºC and an average annual precipitation of 666 mm.

Q. petraea trees were 17 ± 3 years old in 1997. In the experimental field, we selected 3 stand densities, which were defined according to the Reineke index [5]. The Reineke index (Rdi) establishes a relationship between the number of trees and their average quadratic diameter, i.e. the diameter of the intermediate tree. The value index varied from 0 to 1, thus a dense stand is near to 1 whereas a widely spaced stand is close to 0. In our study, the densities were 599 trees ha^{-1} (Rdi 0), 17, 800 trees ha^{-1} (Rdi 1/2) and 46, 500 trees ha^{-1} (Rdi 1) respectively. In each stand, 22 dominant trees selected by foresters were sampled. A dominant tree was a tree dominating the stand by its dimensions (diameter at 1.3 m, total height, crown length) and its quality.

2.2. Study annual shoot

In 1997, the 4-year-old annual shoot on each tree was selected. It was located between 2 and 3 meters high which corresponds to the mid-point of the butt-log that will represent the main part of the timber wood of the crop tree [18].

On each 4-year-old annual shoot, we distinguished the 2 faces, North and South, for practical reasons. On each face, all structures present were listed and we

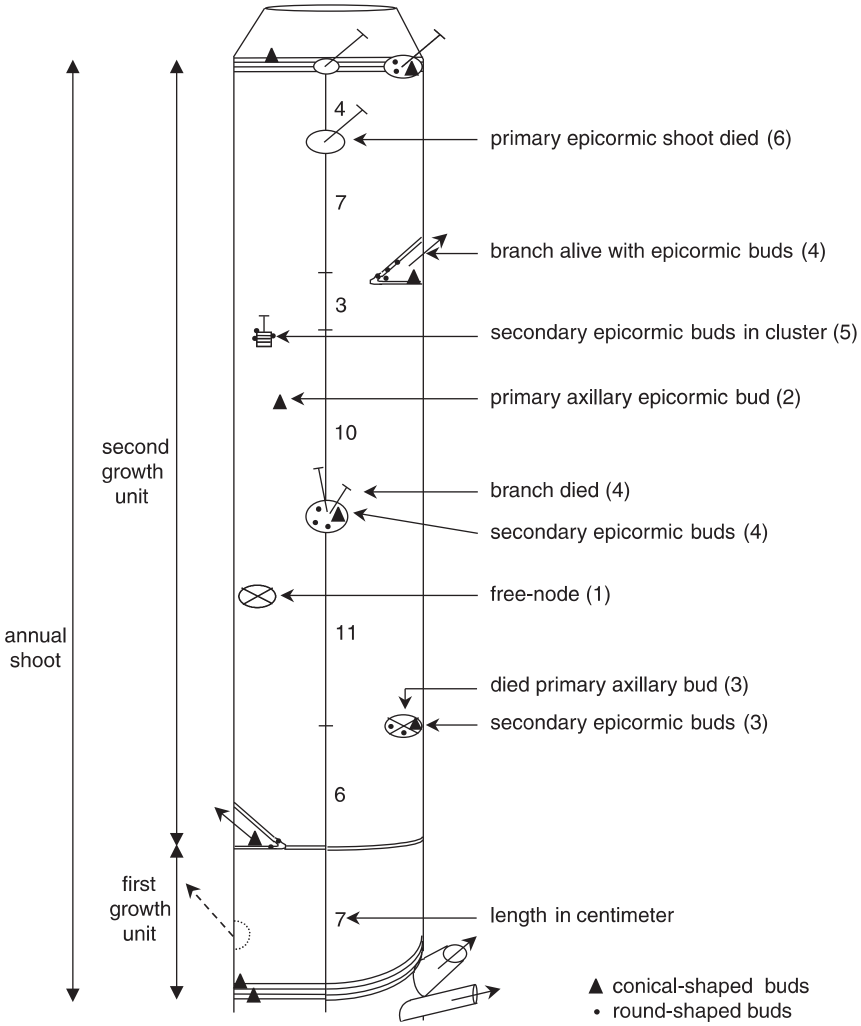

Figure 1. Example of a 4-year-old annual shoot mapping: North face.

characterized (*figure 1*): 1) free-nodes following the death of a primary axillary bud; 2) individual primary axillary epicormic buds; 3) individual secondary epicormic buds originating from a primary bud; 4) branches: dead or alive and with or without secondary epicormic buds at their base; 5) secondary epicormic buds in cluster; 6) epicormic shoots: primary or secondary and dead or alive.

Data were collected on the 4-year-old annual shoots (N-4) in October 1997. The experiments were repeated in October 1998 and in October 1999 on these annual shoots which were then 5 years old (N-5) and 6 years old (N-6) respectively.

2.3. Data analysis

A simple comparison of the number of buds between stand densities was not possible since the number of buds is correlated to the length of the 4-year-old shoot and each annual shoot studied had a given length. In order to compare data, we used percentages or the ratio of total number of buds per length of the shoot in centimeters.

2.3.1. Fate of primary axillary buds from 1993 to 1997

To determine whether the 3 fates (death, giving rise to an epicormic bud, development into a branch) of the primary axillary buds from 1993 to 1997 were significantly different in each stand density (Rdi 1, Rdi 1/2, Rdi 0), data were analyzed with a chi-square test [16]. In parallel, a comparison between the 3 stands was also performed by a chi-square test of homogeneity.

2.3.2. Estimation of the epicormic potential in 1997

First, we examined the proportion of primary and secondary (individual or in clusters) epicormic buds. For clusters of secondary buds, we counted the number of clusters and not the number of buds in each cluster. Then, we described in detail the origin of the individual secondary buds, either following the death of a primary bud or after its development into shoot.

2.3.3. Evolution of the epicormic potential from 1997 to 1999

To analyze the annual evolution of the epicormic potential in each stand density, a Sign-test (S) of the median was applied at 0.05 level, according to Sprent [20]. The Sign-test, a nonparametric test, is supported by a distribution which is not symmetrical and is adapted to compare paired observations.

The comparison between each stand density was performed by an ANOVA test followed by a Student's *t* test on the ratio of number of buds per centimeter of shoot.

3. RESULTS

Our study on the estimation of the epicormic potential confirms the conclusions obtained in previous works on the biological basis of the epicormic buds in *Q. petraea* [6, 7]. In this species, all epicormic buds were of proventitious origin since they were located in the axils of a foliar organ (leaf, scale), at the base of a dead bud or at the base of a branch. No adventitious buds were detected on the wounds caused by insects.

3.1. Fate of primary axillary buds formed in 1993

The average length of the sample annual shoots varied from 38.7 ± 9.4 (stand Rdi 0) to 44.9 ± 15.1 cm (stand Rdi 1) (*table I*). In 1993, the mean number of primary axillary buds on the shoots did not exceed 1 bud per centimeter in the 3 stands and it varied from 0.7 ± 0.2 (stand Rdi 1) to 0.8 ± 0.2 (stands Rdi 1/2 and Rdi 0).

At each stand density, the development of primary axillary buds into primary epicormic buds was significantly higher than their death or their development into a shoot (*table I*, *figure 2*). Similar results have been reported by Harmer [9] on a 2-year-old annual shoot of *Q. petraea*.

Between stand densities, no significant differences for the formation of epicormic buds and the development into shoots were observed, whereas for the death of primary axillary buds, we can distinguish the stand density

Table I. Primary axillary buds present on the 1-year-old annual shoot in 1993: quantity and fates in 1997 and in the 3 stand densities.

	Stand density		
	Rdi 1	Rdi 1/2	Rdi 0
Number of primary axillary buds per shoot in 1993	34.0 ± 11.5	31.9 ± 7.2	32.5 ± 10.5
Length of the shoots (cm)	44.9 ± 15.1	41.1 ± 11.1	38.7 ± 9.4
Number of buds per cm	0.7 ± 0.2	0.8 ± 0.2	0.8 ± 0.2
Fate of these primary axillary buds			
Dead (%)	8.9 ± 4.5b (26 *B*)	9.9 ± 3.6b (31 *A*)	10.7 ± 6.6b (33 *A*)
Epicormic buds (%)	14.0 ± 6.0a (41 *A*)	12.5 ± 4.8a (39 *A*)	11.8 ± 5.7a (36 *A*)
Developed into branches (%)	11.1 ± 5.1b (33 *A*)	9.5 ± 3.7c (30 *A*)	10.0 ± 3.6c (31 *A*)

Results are given as means ± SD and percentages in brackets. For the fate of the primary axillary buds, in each column, there is no significant difference between means followed by the same small letter, according to a chi-square test at the 5% level; between each column, there is no significant difference between values followed by the same capital letter, according to a chi-square test at the 5% level.

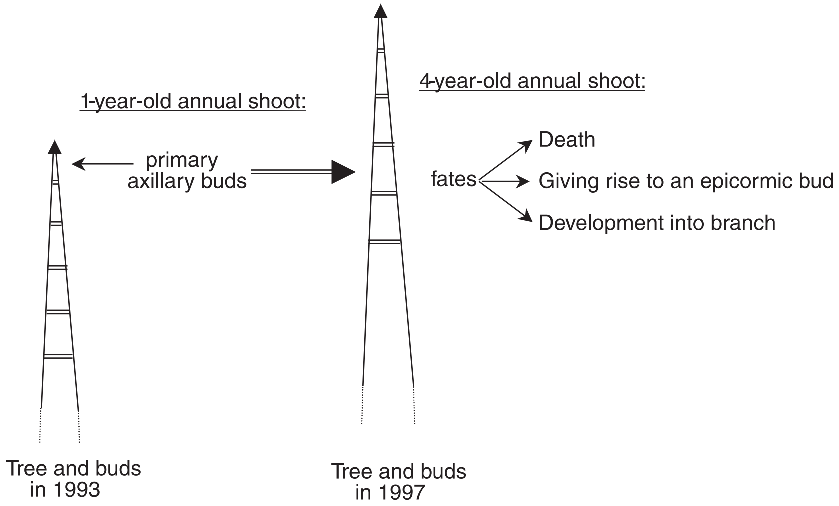

Figure 2. Fates of the primary axillary buds from 1993 to 1997.

Rdi 1 from the others. The death of the primary axillary buds was significantly lower in the stand Rdi 1 than in both stands Rdi 1/2 and Rdi 0.

We cannot clearly distinguish any of the 3 stands on these characters, probably because of the recent installation of the 3 densities in the experimental site. The different densities were applied only in 1995. Thus, from 1993 to 1995, primary buds developed under the same silvicultural conditions.

3.2. Epicormic potential in 1997

3.2.1. Estimation of the epicormic potential

From 1993 to 1997, in both stands Rdi 1/2 and Rdi 0, the number of buds was stable (*table II*). Although there was an increase in the stand Rdi 1, this was significant according to a Sign-test. The number of buds per centimeter rose from 0.7 ± 0.2 to 0.9 ± 0.4.

From 1993 to 1997, in all stands, the increase in the number of buds was probably related to the formation of secondary buds additional to the primary epicormic buds.

3.2.2. Origin of epicormic buds

In 1997 and in the 3 stand densities, the epicormic potential was composed of approximately one third of primary epicormic buds and of two thirds secondary epicormic buds (*figure 3*). Among the secondary epicormic buds, we distinguished individual buds to those clusters. Our results showed that the number of

Table II. Estimation of the epicormic potential in 1997 and 1999 in the 3 stand densities.

		Stand density		
Year	Buds	Rdi 1	Rdi 1/2	Rdi 0
1993	Primary axillary	34.0 ± 11.5	31.9 ± 7.2	32.5 ± 10.5
	Buds per cm	0.7 ± 0.2	0.8 ± 0.2	0.8 ± 0.2
1997	Epicormic	40.7 ± 19.7	32.0 ± 13.3	32.8 ± 10.5
	Buds per cm	0.9 ± 0.4	0.8 ± 0.3	0.8 ± 0.3
1999	Epicormic	36.3 ± 18.6	27.3 ± 12.2	27.5 ± 13.1
	Buds per cm	0.8 ± 0.3	0.6 ± 0.3	0.6 ± 0.3

Results are given as means ± SD. For the number of buds, in each column, a Sign test at the 5% level was performed and for the number of buds per cm, between each column, an ANOVA test followed by a Student test at the 5% level were applied.

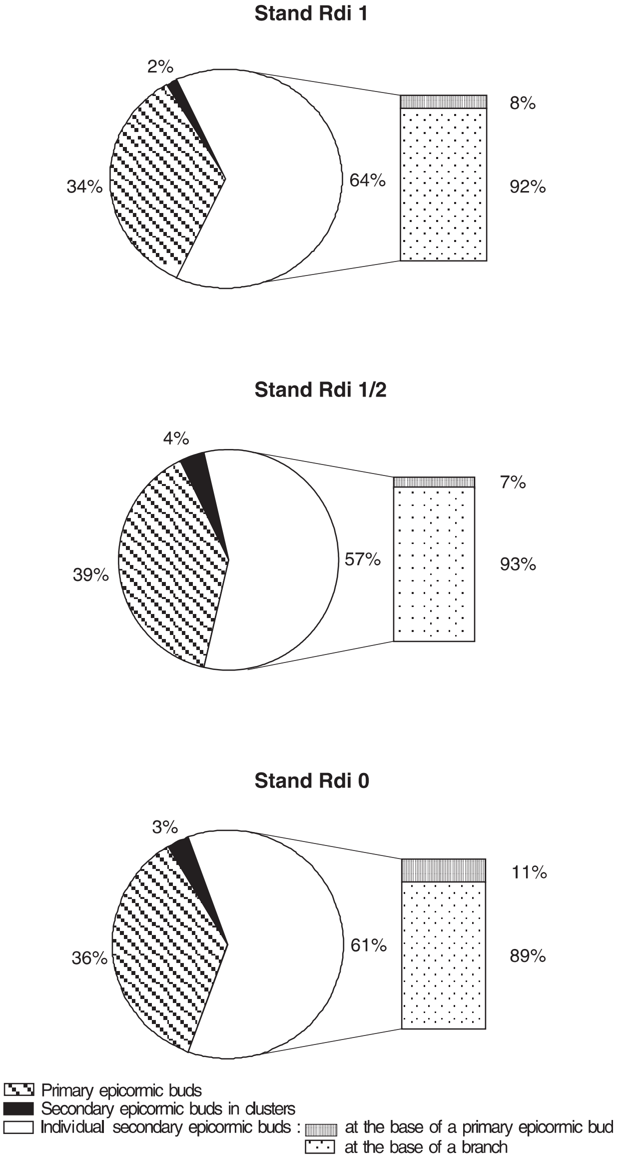

Figure 3. Composition of the epicormic potential in 1997 in the 3 stand densities.

secondary buds in clusters was small and represented less than 5% of the total epicormic potential. Individual secondary buds constituted the epicormic potential from 57% in the stand Rdi 1/2 to 64% in the stand Rdi 1 (*figure 3*). In the 3 stands, more than 89% of these buds were located at the base of branches and less than 11% on nodes formed after the death of primary buds (*figure 3*).

Bases of branches possessed individual secondary epicormic buds in more than 70% of cases whatever the stand density (*figure 4*). When buds were present, we observed that a base of branch had between 1 and 11 buds; however, the formation of more than 4 buds was rare (*figure 4*).

After the death of a primary bud, secondary epicormic buds appeared in less than 20% of cases (*figure 5*). Between 1 and 4 secondary epicormic buds were counted, however, in most cases, one bud was detected (*figure 5*).

3.3. Evolution of the epicormic potential from 1997 to 1999

The evolution of the epicormic potential depends on the balance between the loss of epicormic buds (death, development into shoot) and the formation of new epicormic buds.

3.3.1. Estimation of the epicormic potential

From 1997 to 1999 and in the 3 densities, the total number of epicormic buds decreased slightly, however this difference was not significant according to a Sign-test (*table II*).

The loss of epicormic buds was identical in the 3 stand densities since a Student test showed no significant difference for the number of buds per centimeter between them (*table II*). The number of epicormic buds per centimeter of shoot went from 0.9 ± 0.4 to 0.8 ± 0.3 in the stand Rdi 1 and in both stands Rdi 1/2 and Rdi 0, from 0.8 ± 0.3 to 0.6 ± 0.3.

Next, we studied in detail the fates of the epicormic buds (primary or secondary) in the 3 stand densities from 1997 to 1999 in order to determine: firstly, which of the fates of the buds was responsible for the decrease in epicormic potential, and secondly, whether the fate implied in the 3 densities was identical.

3.3.2. Fates of the epicormic buds

In the 3 stand densities, the number of primary epicormic buds decreased slightly due to their death or to their development into epicormic shoots. The rate of mortality was few and varied from 11 to 18% (*table III*). Furthermore, following the death of these buds, secondary buds could be formed, however, the production remained very small (*table III*). Less than 10% of the primary epicormic buds gave rise to epicormic shoots in the stands. The evolution into clusters was low in both stands Rdi 1/2 and Rdi 0 and was zero in the stand Rdi 1 (*table III*).

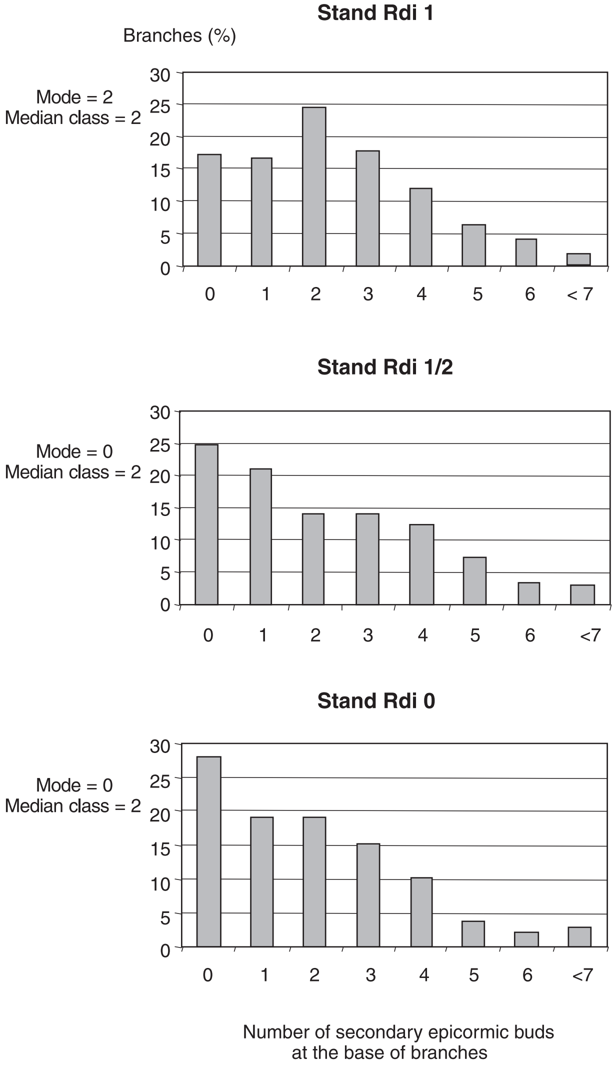

Figure 4. Distribution of branches according to the number of secondary epicormic buds formed at its base in 1997 and in the 3 stand densities.

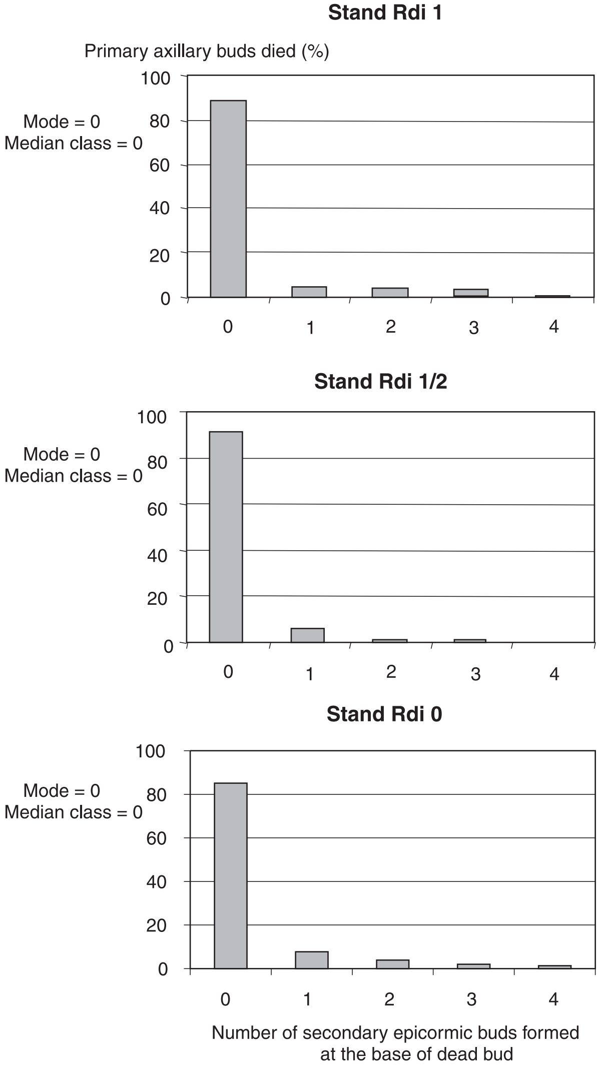

Figure 5. Distribution of primary buds died according to the number of secondary epicormic buds formed at its base in 1997 and in the 3 stand densities.

The number of individual secondary buds also decreased slightly in the 3 stands from 1997 to 1999 (*table IV*). The loss of buds was the result of their death or their development into shoots. The rate of bud death varied between 8.5 (stand Rdi 1) and 14% (stand Rdi 1/2). After their death, the emergence of secondary buds was only detected in the stand Rdi 0 and was low. *Table IV* shows also that the number of secondary buds developing into a shoot was 1%, independent of the stand. The formation of clusters from individual secondary buds was 1% in the stand Rdi 0 and was non-existent in both stands Rdi 1 and Rdi 1/2.

The number of clusters of secondary buds was equal from 1997 to 1999 in the stands Rdi 1/2 and Rdi 0, whereas it decreased slowly in the stand Rdi 1 as a consequence of their death (*table V*). In one case in the stand Rdi 0, a secondary bud of a cluster gave rise to an epicormic shoot. We never observed the formation of a cluster from a secondary bud belonging to a cluster, thus leading to a large cluster of epicormic buds as described by Kauppi et al. [11].

Within the 3 stand densities, in spite of the mortality or of the development into shoot of the different kinds of buds, the composition of the epicormic potential was similar to that described in 1997: one third of primary epicormic buds and two thirds of secondary epicormic buds (data not shown). For the secondary epicormic buds, they were mainly found as individuals rather than in clusters and individual buds were essentially located at the base of branches.

3.3.3. Results of the evolution of the epicormic potential

Results were synthesized in the *figure 6* for the stand density Rdi 0. Our study began in 1997 and all buds observed on the 4-year-old annual shoot, for example

Table III. Fate of the primary epicormic buds from 1997 to 1999 in the 3 stand densities.

	Stand density		
	Rdi 1	Rdi 1/2	Rdi 0
Number of surviving buds (%)	86	82.5	74.5
Number of buds dead (%)	11	11	18
Number of buds died with formation of secondary buds (%)	3	3	8.5
Number of buds developed into shoots (%)	3	6	5.5
Number of buds which gave rise to clusters (%)	0	0.5	2

Table IV. Fate of the individual secondary epicormic buds from 1997 to 1999 in the 3 stand densities.

	Stand density		
	Rdi 1	Rdi 1/2	Rdi 0
Number of surviving buds (%)	90.5	85	85.5
Number of buds dead (%)	8.5	14	12.5
Number of buds died with formation of tertiary buds (%)	0	0	2
Number of buds developed into shoots (%)	1	1	1
Number of buds which gave rise to clusters (%)	0	0	1

Table V. Fate of the clusters of secondary epicormic buds from 1997 to 1999 in the 3 stand densities.

	Stand density		
	Rdi 1	Rdi 1/2	Rdi 0
Number of surviving clusters (%)	86	100	100
Number of clusters dead (%)	14	0	0
Number of clusters died with formation of tertiary buds (%)	0	0	0
Number of buds developed into shoots (%)	0	0	4
Number of buds which gave rise to clusters (%)	0	0	0

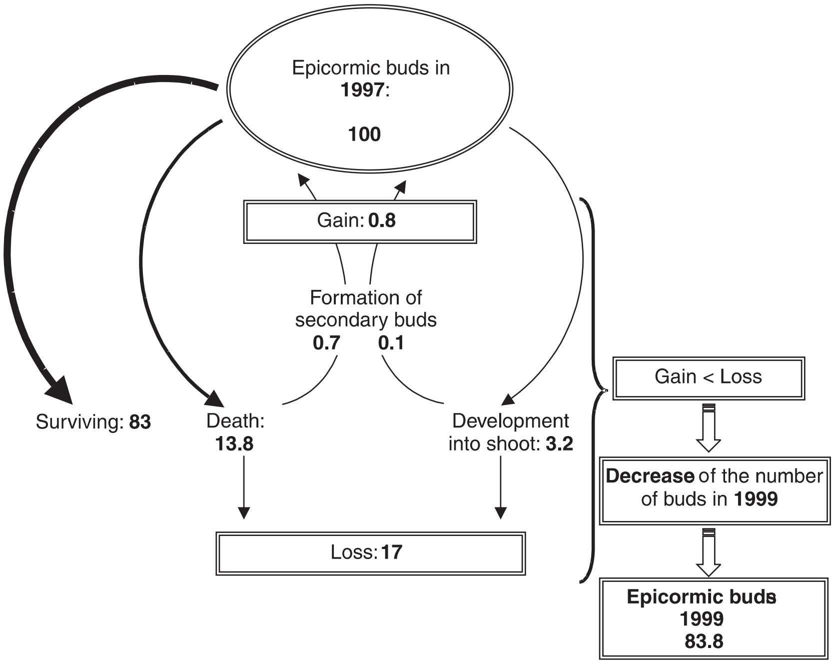

Figure 6: Synthetic representation of the evolution of the epicormic potential from 1997 to 1999 in the stand density Rdi 0 (599 trees ha^{-1}).

100 buds, were epicormic. In 1999, 83 of these epicormic buds survived, 13.8 died and 3.2 developed into epicormic shoots. The death and the development into shoots induced a loss of epicormic buds. Nevertheless, after the death and the development into shoots, 0.7 and 0.1 of new epicormic buds appeared, respectively. This formation of new epicormic buds was a gain for the epicormic potential but this was very small and could not compensate the loss of epicormic buds. Finally, from 1997 to 1999, the number of epicormic buds decreased and in 1999, only 83.8 epicormic buds were counted on the 6-year-old annual shoot.

4. DISCUSSION

Our preliminary results described in *Q. petraea* cannot be compared with those in other species, since no information is available for other species on the estimation and on the evolution of the epicormic potential.

4.1. Origin of the epicormic potential: the fate of the primary axillary buds

Our results showed that, from 1993 to 1997, the loss of primary axillary buds by their death or by their development into branches was compensated by the formation of secondary epicormic buds. More than 89% of these secondary buds were formed by branches and less than 11% after the death of a primary axillary bud, however the number of dead primary axillary buds was similar or slightly greater than branches. The explanation of this difference (89–11%) was that a branch could develop more buds at its base than a bud after its death. Thus, we could suggest that a prevention of the development of primary buds into branches will induce a lower epicormic potential.

The number of buds at the base of branches is not uniform. This would be related to the branch size of oak trees. In many trees [21] including *Q. petraea* [9], the branches produced on the upper surface of the shoots were significantly shorter than those on the lower surface. It will be interesting to study the relationship between the branch size and the number of buds developed at its base.

4.2. Evolution of the epicormic potential

From 1997 to 1999, our results showed that the epicormic potential decreased slightly in the 3 stand densities since the loss of epicormic buds, primary and secondary, was not compensated by the formation of new buds. The loss of epicormic buds was found to be related mainly to their death rather than their development into epicormic shoots. Thus, this evolution of the epicormic potential has a favourable effect on the preparation of the timber quality since it implied a smaller formation of epicormic shoots. Moreover, we could suppose that less secondary epicormic buds were formed after the death of a primary epicormic bud than at the base of an epicormic shoot. An epicormic shoot like a branch could produce several buds at its base (data not shown).

This study related a great difference between the proportion of epicormic buds that remained dormant and the proportion of epicormic buds that were stimulated to grow out. The reasons for this contrast are unknown but may include: the size of the bud, the position of the bud on the shoot, physiological mechanisms that control the bud dormancy and environmental factors.

5. CONCLUSION

In our study, we do not report a great difference on the composition and on the evolution of the epicormic potential between the 3 stand densities selected because these densities were only installed in 1995. Nevertheless, we have detected a small trend in the stand Rdi 1 (dense stand) to produce more epicormic buds than in both stands Rdi 0 and Rdi 1/2.

In order to confirm whether the diminution of the epicormic potential is the general trend, the study will be followed for several years. Moreover, we will hope to gain more knowledge on the formation of large clusters of buds and of epicormic shoots in group.

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