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Height growth, shoot elongation and branch development of young *Quercus petraea* grown under different levels of resource availability

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Summary – Two-year-old sessile oaks were grown under various levels of resource availability in a semi-controlled conditions experiment. After 2 years, the growth and the branching of the seedlings were assessed. A large number of seedlings showed an important development of lateral branches and sprout shoots growing from the root collar. Mortality of the apical bud, changes in the allocation of shoot elongation between several shoots and changes in dominance occurred frequently. Higher resource availability increased annual shoot elongation by increasing the number of growth flushes produced in the growing season as well as the number and the length of the internodes produced in each flush. Resource availability also had a negative effect on the form of the seedling, those grown under high resource availability showing more changes in dominance.

apical control / recurrent flushing / internode / bud / sprout shoot

Résumé – Effet de la disponibilité en ressources sur la croissance en hauteur, l'élongation des rameaux et le développement des branches de jeunes *Quercus petraea*. Des chênes sessiles âgés de 2 ans ont été installés dans des conditions d'alimentation hydrique et minérale contrastées, dans une expérimentation en milieu semi-controlé. La crois-sance et la branchaison des plants après deux ans ont été évaluées. Un grand nombre d'arbres ont présenté un développement important des branches latérales et des rejets se développant depuis le collet du plant. L'allon-gement des rameaux était fréquemment réparti entre plusieurs tiges, et les plants ont souvent montré des changements de dominance entre les différentes tiges. Le taux de mortalité des bourgeons apicaux était de 20 % par an. L'amélioration de la disponibilité des ressources a induit un plus fort allongement annuel des rameaux, en augmentant le nombre de vagues de croissance effectuées dans l'année, ainsi que le nombre et la longueur des entre-nœuds produits lors de chaque vague de croissance. En revanche, la disponibilité des ressources a eu un effet négatif sur la forme des plants, et les plants placés dans les meilleures conditions ont montré des changements de dominance plus fréquents.

contrôle apical / croissance polycyclique / entre-nœud / bourgeon / pousse rejet

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INTRODUCTION

Oak (*Quercus petraea* (Matt) Liebl together with *Quercus robur* L) is one of the most important commercial timber species in Europe. In France, sessile and pedunculate oak cover 41% of the total commercial forest area (Ningre and Doussot, 1993). Traditionally, oak stands were renewed using natural regeneration, but the frequency of artificial regeneration by planting is increasing (Fernandez, 1990). The objective of artificial regeneration is to produce fast growing seedlings which exhibit few branching defects, but a prerequisite to developing silvicultural practices geared toward this objective is to understand the effects of environmental conditions on the growth and branching of young oaks.

Oak grows rhythmically: during the growing season, shoot elongation occurs by rapid flushes lasting about 2 weeks, which alternate with longer resting periods (Borchert, 1975; Reich et al, 1980; Cobb et al, 1985; Champagnat et al, 1986). In controlled conditions, young *Q petraea* can produce up to 16 successive growth flushes (Lavarenne-Allary, 1965). In natural conditions, they may produce up to four or five flushes in a growing season if conditions are favorable. However, limiting growing conditions often confine production to only one or two flushes, thus restricting the full growth potential (Lavarenne-Allary, 1965; Longman and Coutts, 1974). The number of growth flushes produced by the seedlings increases with resource availability (light, water, nutrients) for *Q rubra* L (Phares, 1971; Cabanettes et al, 1995), *Q petraea* (Harmer, 1989b) and *Q prinus* L (Tworkoski et al, 1990).

Resource availability may influence annual shoot elongation, through an effect on the number of flushes produced annually, but also through an effect on shoot elongation during each growth flush: Harmer (1989a, b) noted a positive effect of fertilization on shoot length of *Q petraea*. Shoots can be divided into nodes which are the points of the stem where a lateral appendage (foliar or scale leaf) is attached, and internodes which are the portions of stem between two nodes (Critchfield, 1985). Shoots elongate as the result of the production of new nodes by the apical meristem and the elongation of the internodes in the subapical part of the shoot. Apical and subapical activities constitute two distinct processes and are both under the control of environmental and internal factors (Kozlowski, 1971). For *Q prinus* seedlings, Tworkoski et al (1990) observed that resource availability did not influence the number or the length of internodes, whereas on *Q petraea* seedlings, Harmer (1989a) showed that a better resource availability increased the number of internodes but had no effect on internode length. On other species, both internode number and length have been shown to increase in response to higher resource availability (Kozlowski, 1971).

Oak is described as having strong apical dominance and weak apical control. The development of the lateral buds produced during the current flush is inhibited by the apex of the shoot, but these buds may develop into shoots during the next growth flush (Brown et al, 1967). The lack of strong apical control in young oaks induces branching defects which may persist and reduce the future value of the stem. Many authors have reported the frequent occurrence of seedlings developing a multi-stemmed morphology, which results from the death of the top or of the entire stem, followed by respouting of shoots from dormant buds at the root collar (Bey, 1964 on *Q alba* L, *Q velutina* Lam and *Q coccinea* Muenchh; Hibbs and Yoder, 1993 on *Q garryana* Dougl; Collin et al, 1986; Crow, 1988, 1992; Cabanettes et al, 1995 on *Q rubra*). According to Hibbs and Yoder (1993), stem dieback and subsequent sprouting of new stems may be related to low moisture availability. On the other hand, high resource availability may increase branching defects by inducing multiple flushing. Indeed, multiple flushing has been shown to be associated with increased lateral branch production (Harmer, 1989a, b on *Q petraea*). Furthermore, an important part of the growth may be allocated to the lateral branches and the sprouting shoots, and multiple flushing may be associated with a strong development of the lateral shoots (Cabanettes et al, 1995 on *Q rubra*).

The mechanisms of inhibition of lateral shoots in trees have been widely studied, and most investigators stress the importance of the control on the axillary buds by the apical part of the shoot (Kramer and Kozlowski, 1979). Observations of the effects of the natural death of the apical bud during the winter, and of experimental decapitation of the shoot apex on *Q petraea*, have clearly shown that loss of the apical bud increases lateral branch production (Harmer, 1992b, 1995). In addition to the stimulation of lateral branch development, the death of the apical bud may also cause a crooked stem form (Harmer, 1992b). In natural conditions, the death of the apical bud during the winter is not uncommon (Drénou, 1994 on *Q robur*). Moreover, it is well known that high resource availability, which allows the growth of abnormal late-season shoots, may induce the formation of a terminal bud which is more susceptible to winter injury because it has not adequately hardened (Kozlowski, 1971). Thus, one might expect that resource availability may increase the occurrence of death of the apical bud and, therefore, may increase the occurrence of branching defects.

These studies clearly show that resource availability strongly influences both the growth and the branching of oak seedlings, and that there may be a trade-off between the two parameters. These results, however, are based on a variety of oak species and more information for individual species is needed. The objective of our study was to describe the effects of resource availability on the growth and branching of *Q petraea* seedlings, and to examine if there is a trade-off between growth and branching when grown under various levels of resource availability. The material we used came from a larger experiment investigating the combined effects of herbaceous competition and irrigation on oak seedlings (Collet et al, 1996).

MATERIALS AND METHODS

One-year-old sessile oak seedlings (*Q petraea*) were collected in March 1991 from a selected seed stand within a naturally regenerating forest, in the Moselle region (northeastern France), and stored. In June 1991, 200 seedlings were transplanted into 40 large boxes (2 m width x 2 m width x 0.6 m depth) built under a transparent plastic roof and containing a fertile sandy loam soil. Twenty randomly chosen boxes were sown with *Deschampsia cespitosa* (L) Beauv seeds, and the remaining boxes were kept without grass. The grass and the bare soil were maintained by regular manual weeding for 3 years. In the first year (1991), all the boxes were well-watered so the plants could establish. In 1992 and 1993, half of the boxes sown with *Deschampsia* were subjected to summer drought, while the other half were regularly irrigated throughout the growing season. Measurements of foliar nutrient (N, P, K, Ca, Mg) concentration made at the end of 1992 indicated that nutrient supply was slightly lower in the two grass treatments. Measurements of soil water potential during summer 1992 and 1993 showed that in both years soil water potential stayed close to the maximum in the bare soil and grass irrigated treatments, and decreased to –2 MPa in the grass nonirrigated treatment, indicating a strong water deficit. The three treatments corresponded to three levels of growing conditions for the oak seedlings: high resource availability (H, bare soil), medium resource availability (M, grass and irrigation) and low resource availability (L, grass and no irrigation). Eighteen, 30 and 30 seedlings were sampled in treatments H, M and L, respectively.

At the end of each year, total height of each seedling was measured. In November 1993, the leading axis, or axes, of the seedlings were determined, and selected for growth measurements. We defined a leading axis as a shoot developed before 1992, which grew vertically and which could build the future stem. Only the dominant axis was selected on single-stemmed seedlings, whereas two or three codominant axes were selected on multi-stemmed seedlings. On these axes, all the growth units produced during 1992 and 1993 were delimited. A growth unit (GU) is the portion of a shoot produced during a single growth flush (Barthélémy and Caraglio, 1991). The GUs are delimited by scars left by the scales which protected the apical bud during the resting period (fig 1). Each GU consists of a series of internodes of variable length. Internodes located at the base of the GU are very short, those in the middle are longer

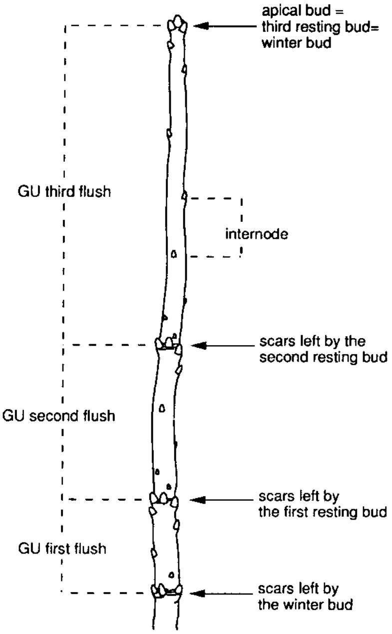


Fig 1. Morphology of an annual shoot of *Q petraea*, represented without any leaves or lateral branches. The shoot consists of three growth units (GUs), produced during three successive growth flushes.

and those at the top are short (Champagnat et al, 1986). The total number of axes and GUs we sampled in each treatment for the growth description are given in table I. The number of trees or axes sampled may be higher than the number of GUs for some flushes because the trees did not necessarily produce GUs in each flush. On the other hand, the number of trees or axes sampled may be lower than the number of GUs, because some axes forked and the two shoots were then sampled. When possible we determined for each GU, the year and the flush number during which the GU grew by: i) counting the scars delimiting the GUs, ii) looking at the aspects of the bark and iii) for the GUs produced in 1993, looking at leaf characteristics (size, aspects). The length of each GU produced in 1993 was measured, and on each GU all the internodes of significant (ie, visible) length were counted. The fate (alive, dead or developed into shoot) of the terminal and axillary buds on each GU was assessed.

The following variables were assessed and analyzed for each axis or for each seedling: i) annual height increment, ii) number of growth flushes produced each year, iii) length of the GUs elongated during each flush, iv) number and v) length of the internodes produced during each flush, vi) appearance of sprout shoots, vii) development of axillary buds into lateral shoots, viii) location on the seedling of the longest GU of each flush and ix) fate of the apical bud.

RESULTS

Seedling height

Seedling height growth was related to the level of resource availability (table II). By the end of the first growing season, seedlings were significantly taller in treatment H than in treatments L and M. Significant differences between treatments L and M appeared during the third growing season. By the end of 1993, seedlings growing in treatment H averaged three times the height of seedlings growing in treatment L.

Table I. Number of oak seedlings, axes and growth units (GUs) produced for each flush in 1992 and 1993, sampled for each treatment.

			GUs 1992				*GUs 1993*			
Treatment	*Trees*	*Axes*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*
L	30	30	30	18	3	0	31	31	2	0
M	30	32	29	21	10	1	33	35	14	0
H	18	22	17	21	21	17	24	24	20	5

L, M, H: low, medium and high resource availability, respectively.

Number of growth flushes, length of the growth units and number of internodes

Most of the seedlings in treatments L and M produced one or two growth flushes in 1992, and two flushes the next year (table III). In treatment H, most of the seedlings produced four flushes in 1992 and three flushes in 1993. The lower number of growth flushes produced in 1993 by the seedlings from treatment H was clearly related to cold temperatures which occurred at the end of September 1993 and which completely stopped shoot elongation. The GUs were always longest in treatment H and shortest in treatment L, but differences were significant only for the second flush of 1992, and for the first and second flush of 1993. In both years, average values of GU length increased with the flush number, from 36.8 to 344.0 mm between the first and the fourth flush in 1992, and from 113.1 to 404.6 mm between the first and the third flush in 1993. The GUs from the fourth

Table II. Seedling height measured in 1991, 1992 and 1993, for each treatment.

	Height		
Treatment	*1991*	*1992*	*1993*
L	16.3^{a}	25.2^{a}	54.8^{a}
M	17.2^{a}	30.7^{a}	86.8^{b}
H	20.4^{b}	80.7^{b}	182.3^{c}
P	0.0002	0.0001	0.0001

Results of the analysis of variance testing the effect of the treatments are indicated. a, b, cMeans within the same column not followed by the same letter differ significantly ($P \leq 0.05$); n = 18 to 30; L, M, H: low, medium and high resource availability, respectively.

Table III. Number of seedlings having produced one, two, three or four growth flushes in 1992 and 1993, and length of the growth units (GUs) (mm) measured for each growth flush, in the three treatments.

		Treatment			
Year	*Flush*	*L*	*M*	*H*	P
Growth flush frequency					
1992	1	12	10	0	
	2	15	10	0	
	3	3	10	2	
	4	0	0	16	0.0001
1993	1	0	0	0	
	2	28	17	2	
	3	2	13	13	
	4	0	0	3	0.0001
GU length					
1992	1	33.8	34.0	40.9	ns
	2	71.4^{a}	99.5^{ab}	127.1^{b}	0.02
	3	175.7	189.6	223.3	ns*
	4	–	–	344.0	–
1993	1	82.3^{a}	110^{a}	156.4^{b}	0.0001
	2	232.2^{a}	267.3^{a}	486.4^{b}	0.0001
	3	109.5	376.7	453.7	ns*
	4	–	–	319.3	–

Results of a $\chi 2$ testing the effects of the treatments on the number of flushes produced and of the analysis of variance testing the effect on GU length are indicated. a bMeans within the same line not followed by the same letter differ significantly ($P \leq 0.05$). *ANOVA performed only between treatments M and H; n = 1 to 35; L, M, H: low, medium and high resource availability, respectively; ns: not significant.

flush of 1993 were shorter because their elongation was stopped by cold temperatures.

The number of internodes per GU, calculated for all the treatments pooled, is shown in figure 2 for each growth flush in 1992 and in 1993. The distributions were all unimodal, with values ranging between extremes of 2 and 35. In both years, the modal class value increased when the flush number increased. The average number of internodes per GU was generally

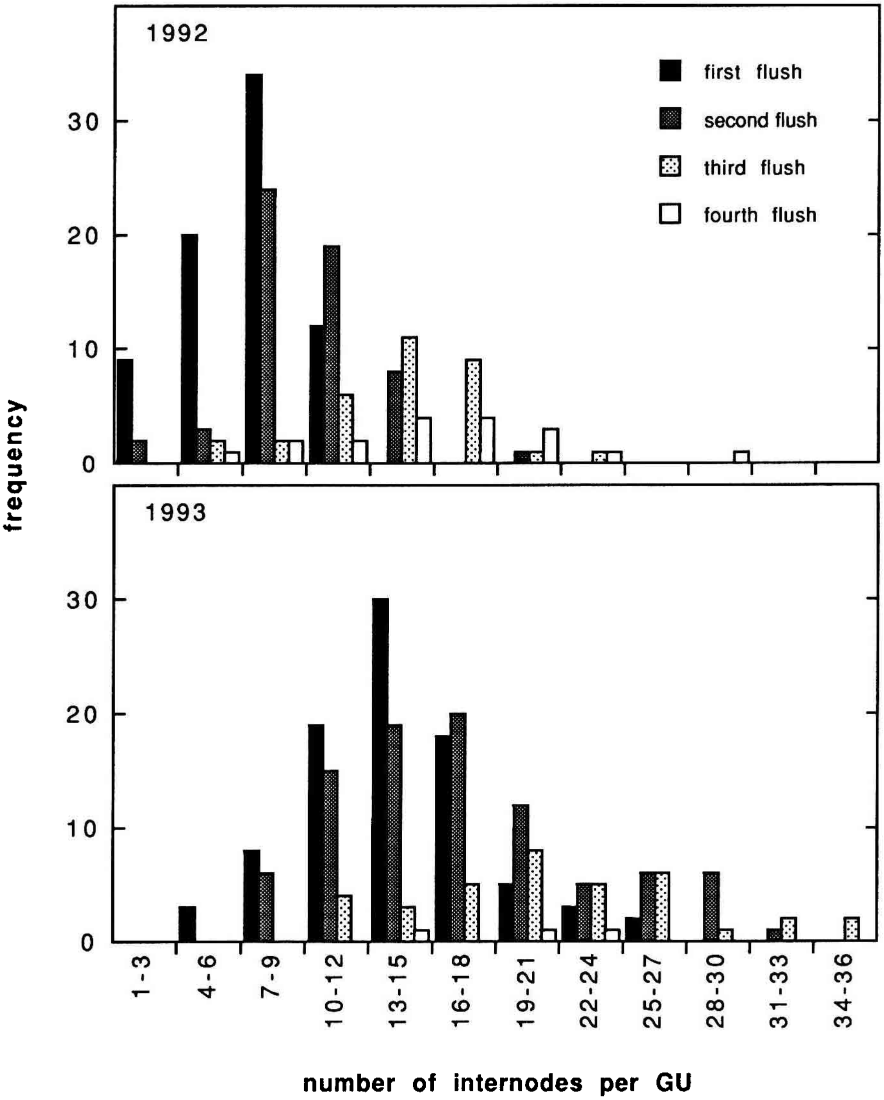


Fig 2. Distribution of the number of internodes per growth unit (GU) counted on the GUs of the first, second, third and fourth flushes of 1992 and 1993. Data from the three treatments were pooled.

higher in treatment H than in treatments L and M during each growth flush, but differences were significant only for the first and second flushes of 1993 (table IV).

For each GU, average internode length was calculated as GU length divided by the number of internodes (table IV). In 1992, average internode length did not differ significantly between the three treatments, and increased from 4.4 mm in the first growth flush to 12.8 mm in the third flush. In 1993, significant differences were found among the treatments. The internodes were on average longer in treatment H than in treatments L and M. Differences in average internode length among treatments and flushes were related to a greater elongation of the internodes, and not to variations in the proportion of short internodes (located at the base and at the top of the GU) since this number was similar among treatment and flushes (data not shown).

Longer GUs were associated with both a higher number of internodes and longer internodes. The relationship between the number of internodes and GU length measured in 1993 is shown in figure 3. A graphic analysis showed that the relationship between GU length and the number of internodes was similar in the three treatments; thus, data from the different treatments were pooled. No differences appeared among the second, third and fourth flushes; only the first flush differed. Therefore, data from the second, third and fourth flushes were pooled. These data and the data from the first flush were then fitted separately with a logistic nonlinear model:

$$L = K \times \frac{1}{1 + e^{a(n_0 - n)}} \qquad [1]$$

where L is the length of the GU expressed in mm, n is the number of internodes, and K, a and n_0 are the parameters of the model (table V). Differences between the regressions performed on the two sets of data were significant [F (3, 393) = 98.44**].

Table IV. Average number of internodes per growth unit (GU), and average internode length (in cm) calculated in each flush produced in 1992 and 1993, for the three treatments.

		Mean			
Year	*Flush*	*L*	*M*	*H*	P
No of internodes					
1992	1	7.81^{a}	7.83^{a}	8.44^{a}	ns
	2	10.27^{a}	10.47^{a}	10.90^{a}	ns
	3	16.00	13.89^{a}	15.05^{a}	ns*
	4	–	10	19.00	–
1993	1	13.55^{a}	14.24^{a}	17.92^{b}	0.001
	2	16.00^{a}	16.60^{a}	22.87^{b}	0.0001
	3	15.50	20.23^{a}	23.70^{a}	ns*
	4	–	–	15.90	–
Internode length					
1992	1	4.12^{a}	4.71^{a}	4.47^{a}	ns
	2	7.34^{a}	8.84^{a}	9.60^{a}	ns
	3	10.71	12.48^{a}	13.31^{a}	ns*
	4	–	3.5	16.88	–
1993	1	5.75^{a}	6.94^{ab}	8.44^{b}	0.002
	2	14.11^{a}	15.32^{a}	20.76^{b}	0.0001
	3	6.99	17.23^{a}	15.52^{a}	ns*
	4	–	–	14.98	–

Results of the analysis of variance testing the effect of the treatments are indicated. $^{a\,b}$Means within the same line not followed by the same letter differ significantly ($P \leq 0.05$). *ANOVA performed only between treatments M and H; n = 1 to 35; L, M, H: low, medium and high resource availability, respectively; ns: not significant.

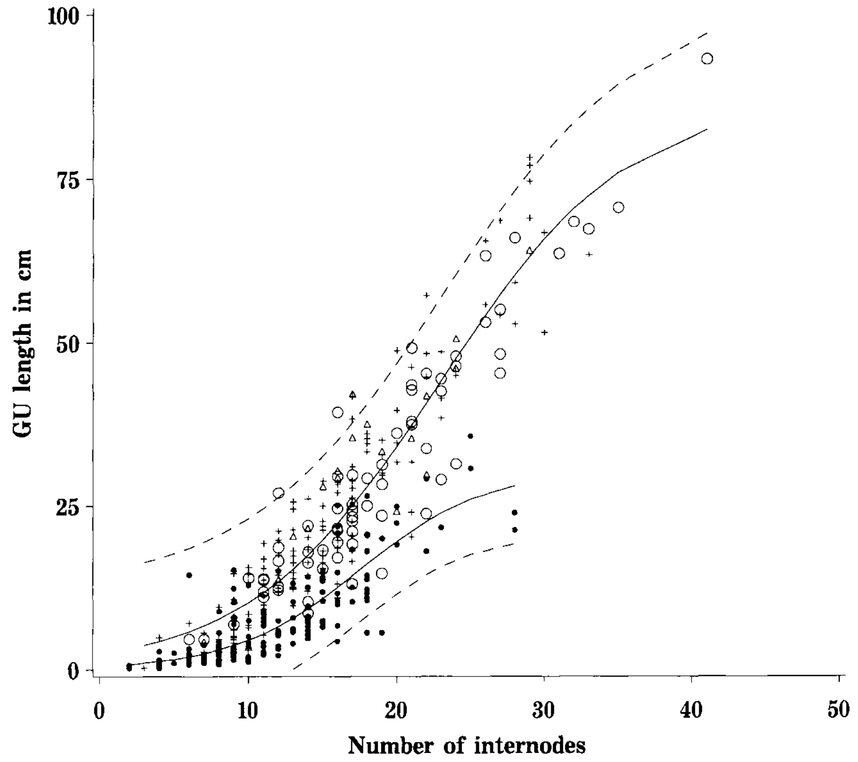


Fig 3. Growth unit (GU) length in relation to the number of internodes per GU. Data from the three treatments were pooled, and data from the second, third and fourth flushes were also pooled. Solid lines indicated the regression i) for the first flush (black dots), and ii) for the second, third and fourth flushes pooled (crosses, open circles and triangles). Dashed lines indicate the lower limit of the confidence interval at 95% for regression i) and the upper limit of the confidence interval at 95% for regression ii).

The differences we observed in average internode length between the treatments and between the growth flushes were, except for the first flush, only associated with differences in GU length. In contrast, differences in average internode length in the first flush were also associated with a different relationship between the number of internodes and GU length.

Death of the apical bud

The frequency of the death of the resting apical buds was higher in winter than during the growing season (table VI). Eighteen percent of the apical buds produced during the 1992 growing season died during the next winter, and 7% of the apical buds produced in the 1993 growing season died during the resting periods between two growth flushes. There was no statistically significant difference among the three treatments.

Development of axillary buds into shoots

At the end of each year, lateral branches on the current year shoot were not uniformly distributed. More branches appeared on the GUs from the first flush than on the GUs from the second or third flush, and branches were formed on the GUs of the last flush. In contrast, after 2 years, branch formation was more important on the GUs from the late flushes. The increased branch formation on the late flushes was a consequence

Table V. Regression coefficients (est), asymptotic standard errors (ASE) of the coefficients, residual mean square (MS) and residual degrees of freedom (df), for estimating growth unit (GU) length from the number of internodes per GU.

	Regression flush 1	*Regression flush 2+3+4*
est(K)	30.48	87.10
est(a)	0.2325	0.1561
est(n_o)	17.46	22.81
ASE(K)	3.241	5.095
ASE(a)	0.0257	0.0092
ASE(n_o)	1.086	0.8832
Residual MS	15.76	41.44
Residual df	160	233

Table VI. Number of apical buds produced during 1992 growing season which died during the following winter, and number of apical buds produced during 1993 growing season which died before the end of the growing period (during the resting periods separating two consecutive growth flushes).

	Buds which died/buds produced	
Treatment	*Winter 1992*	*Growing season 1993*
L	4/30	2/64
M	7/32	7/82
H	4/22	3/71
Total	15/84	12/155
χ^2	0.77 ns	2.36 ns

These numbers are based on the total number of apical buds produced for the three treatments. The results of a $\chi 2$ test analyzing the differences in the number of buds which died, between the treatments are indicated; ns: not significant; L, M, H: low, medium and high resource availability, respectively.

of both a higher number of axillary buds produced on the GU, and a higher proportion of buds growing into shoots.

The number of 1992 buds which developed into shoots the same year was much higher in treatment H than in treatments L and M (table VII). In contrast, the number of 1992 buds forming shoots the next year was lower in treatment H. Over the 2 years, differences between the treatments in the number of buds which formed shoots varied according to the flush number: more branches grew from the buds produced during the first flush of 1992 in treatment H than in treatments L and M, whereas no differences occurred between the treatments for the buds formed during the second and third flush of 1992. The 1993 buds behaved similarly to the 1992 buds during their first year.

Development of sprouts

We defined a sprout as a shoot produced from a bud located at the root collar of the seedling. Thirty percent of the seedlings produced at least

Table VII. Number of buds formed during the different growth flushes of 1992 and 1993 which developed into shoots in 1992 and in 1993, for the three treatments.

		No of lateral shoots appeared in 1992				*No of lateral shoots appeared in 1993*			
Year	*Flush*	*L*	*M*	*H*	P	*L*	*M*	*H*	P
1992	1	0.17^{a}	0.03^{a}	2.44^{b}	0.0001	1.33^{b}	0.66^{a}	0.12^{a}	0.008
	2	0.00^{a}	0.05^{a}	1.50^{b}	0.001	3.17^{b}	2.37^{ab}	1.35^{a}	0.02
	3	0.00	0.00	1.15	–	6.00	4.88	4.60	–
	4	–	–	–	–	–	–	9.76	–
1993	1	–	–	–	–	0.81^{a}	1.24^{a}	4.33^{b}	0.000
	2	–	–	–	–	0.00^{a}	0.63^{a}	3.42^{b}	0.000
	3	–	–	–	–	0.00	0.00	0.25	–
	4	–	–	–	–	–	–	–	–

Results of the analysis of variance testing the effect of the treatments are indicated. [a b]Means within the same line not followed by the same letter differ significantly ($P \leq 0.05$). n = 1 to 35; L, M, H: low, medium and high resource availability, respectively.

Table VIII. Number of seedlings which produced at least one sprout during 1992 or 1993, based on the total number of trees described, in the three treaments.

	No of trees	
Treatment	*With sprout*	*Total*
L	15	30
M	10	30
H	5	18
Total	30	78
χ^2	2.89 ns	

The results of a χ^2 test analyzing the differences in the number of seedlings which produced a sprout between the treatments are indicated; ns: not significant; L, M, H: low, medium and high resource availability, respectively.

one sprout during 1992 and 1993 (table VIII), and about one-fifth of those sprouts developed into leading axes (data not shown). There was no statistically significant difference for sprout formation among the treatments.

Changes in the leading axes

Changes in the leading axes between the beginning and the end of the growing season occurred frequently. Thirty-eight percent of the seedlings in treatments L and M, and 84% of the seedlings in treatment H, showed at least one change in 1992 or 1993 (table IX). The differences between the treatments were significant ($\chi 2 = 12.86$, df = 2, $P < 0.01$). In the three treatments, changes occurred more frequently in 1992 than in 1993, and some seedlings exhibited a change both years. On 70% of the seedlings which experienced a change, the dominant axis became codominant with other axes, and on 30% of the seedlings, the dominant axis became dominated by other axes. Fifty percent of the changes occurring in 1993 occurred on seedlings for which the apical bud of the dominant axis died during the previous winter (data not shown).

Changes in the leading axes are related to the allocation pattern of shoot elongation between the different axes. In 60% of the seedlings, the longest GUs produced during the different growth flushes were found on different shoots (table X). In the remaining 40%, one shoot produced the longest GUs for all growth flushes. The proportion of seedlings which showed changes in the location of the longest GU did not seem to be related to the number of growth flushes produced nor to the treatment. Within a growing season the longest GUs could change between two or three axes, as illustrated by the example in figure 4. These changes may occur between codominant axes which were present at the beginning of the growing season (44% of the seedlings) between the dominant axis and a sprout (23% of the seedlings), or between the leader shoot of the dominant axis and its lateral shoots (33% of the seedlings) (table XI).

DISCUSSION

The *Q petraea* seedlings showed a growth (height increment and flushing recurrence) similar to young oaks under natural conditions

Table IX. Changes in the leading axes from the beginning to the end of the growing season, in 1992 and 1993.

	Changes in 1992		*Changes in 1993*		*No*	*Total no of*
Treatment	*D→d*	*D→coD*	*D→d*	*D→coD*	*change*	*seedlings*
L	4	4	0	1	21	30
M	3	6	1	5	16	30
H	4	8	0	6	3	18
Total	11	18	1	12	40	78

The number of seedlings on which the dominant axis at the beginning of the growing season became nondominant (D - > d) and the number of seedlings on which the dominant axis became codominant with other axes (D - > coD) are indicated for each year. The seedlings which showed no change in the leading axes in 1992 and 1993 kept the same leading axes throughout the 2 years; L, M, H: low, medium and high resource availability, respectively.

Table X. Number of seedlings in which changes in the longest growth units (GUs) occurred in 1993 (ie, the longest GUs in the different flushes are not located on the the same shoot), based on the total number of seedlings which produced two, three or four growth flushes during the growing season.

	No of seedlings with changes/total no of seedlings			
Treatment	*2 flushes*	*3 flushes*	*4 flushes*	*Total*
L	16/28	1/2	–	17/30
M	8/17	5/18	–	13/30
H	1/2	10/13	2/3	13/18
Total	25/47	16/28	2/3	47/78
χ^2	–	–	–	3.84 ns

Results of a χ^2 test analyzing the differences between the treatments are indicated; ns: not significant; L, M, H: low, medium and high resource availability, respectively.

planted on a good quality site with or without grass competition (Collet and Frochot, 1996). Seedlings in treatment H and those in treatments L and M grew similarly to seedlings planted in good or medium conditions, respectively. No treatment reflected the poor conditions which often prevail in oak plantations, and where the growth and the survival rates of the seedlings are low. In such conditions, the response of the seedlings, in terms of growth and branching, may be more pronounced than what we described. The environmental conditions in our experiment were close to conditions prevailing in oak plantations where the vegetation is completely suppressed (treatment H) or were the hardwood vegetation is controlled (treatments L and M). These conditions are very different from those found in natural regeneration, or in plantations where the hardwood vegetation is still present (Temen, 1994). In such conditions, the seedlings probably grow and develop very differently from the seedlings in our experiment. In France, however, oak regeneration by planting is increasing (Fernandez, 1990), vegetation control is strongly recommended in order to enhance initial seedling growth (Frochot et al, 1986) and the conditions created in such regeneration are close to those in our experiment.

Shoot elongation

Resource availability influenced annual shoot elongation by modifying both apical and subapical activity. The total number of growth flushes produced in the growing season, the number of internodes produced in each flush and the average internode length increased with higher resource availability. However, the number of flushes differed among the three treatments in both years whereas the number and the length of the internodes, responded to treatments only in 1993 and rarely differentiated between treatments L and M. The higher responsiveness of the number of flushes to variations in resource availability, compared to the number and the length of the internodes has been also observed by Harmer (1989a) on *Q petraea* and Tworkoski et al (1990) on *Q prinus*. This is probably related to the fact that the three variables integrate different periods of time: the number of flushes reflects the growth over the entire growing season, whereas the number and the length of the internodes in each flush reflect the growth over shorter periods of time.

A consequence is that variations in annual shoot elongation were more related to variations in the number of flushes than to variations in the number or the length of the internodes in each flush. Furthermore, since the GUs of the late flushes appeared to be longer than the GUs of the early flushes, their production constitutes an important part of annual growth, and annual shoot elongation is strongly related to the total number of flushes produced in the growing season (fig 5). Longer late-season GUs, compared to early-season GUs, has also been reported by Harmer (1992a) on *Q petraea*, and by Tworkoski et al (1990) on *Q prinus*. In the

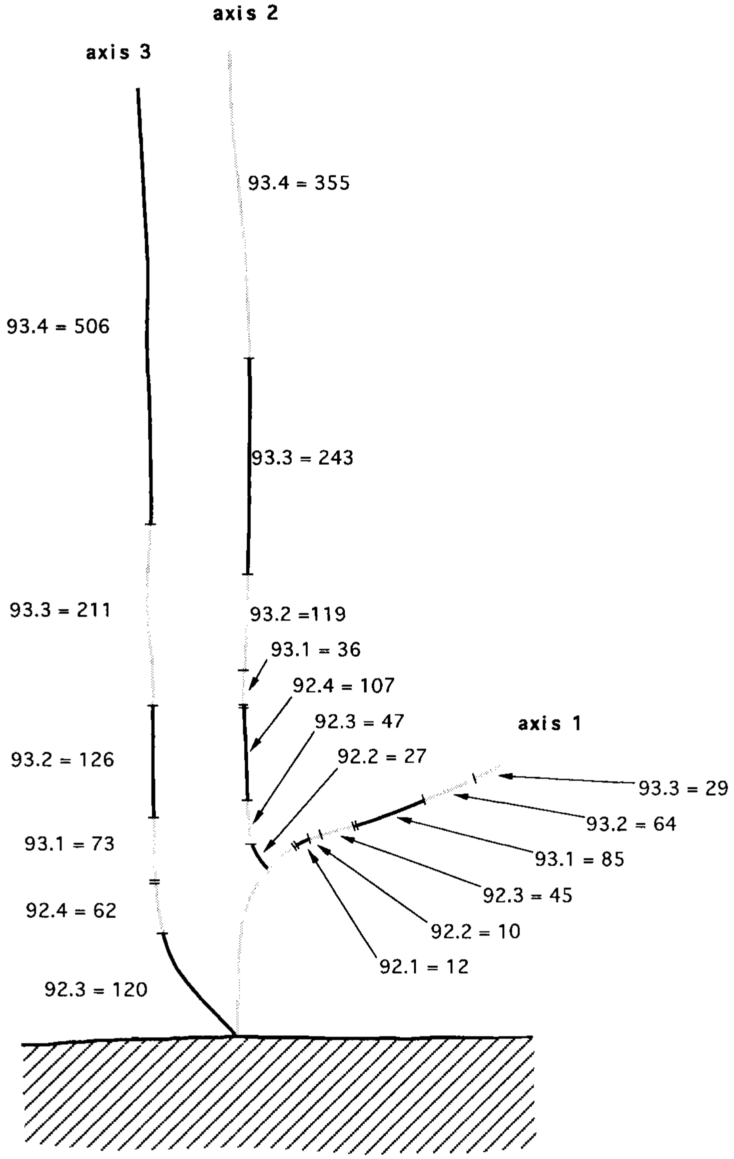
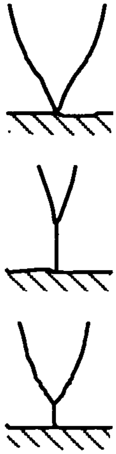
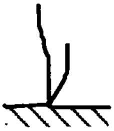
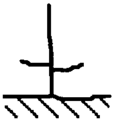


Fig 4. Example of changes in the location of the longest growth units (GUs) between three axes, on a 4-year-old seedling (h = 1.09 m) under high resource availability (treatment H). Axis 1 is the initial axis produced from the seed epicotyl, axis 2 is a branch that appeared on axis 1 in the second growth flush of 1992 and axis 3 is a sprout shout that appeared on axis 1 in the third flush of 1992. Lateral branches on these three axes are not represented. All the GUs produced in 1992 and 1993 are represented. The longest GU found on the seedling at each flush is drawn in black and the other GUs are drawn in gray. For each GU, the period when it was produced and its length in millimeters are indicated (year-flush = length).

Table XI. Changes between several axes in the location of the longest growth unit (GU) during 1993.

Treatment	*No of seedlings*			
	Total	*Type I*	*Type II*	*Type III*
L	17	4	7	6
M	13	4	3	6
H	13	11	0	2
Examples				

The seedlings are classified into three types: type I, changes in maximum growth between axes which were present at the end of 1992; type II, changes in maximum growth between an axis which was present at the end of 1992 and a sprout axis which appeared in 1993; and type III, changes in maximum growth between the leading axis and its lateral shoots. These numbers are based on the total number of seedlings which showed changes between the leading axes. Examples of seedlings in the three types are given. The dotted lines indicate shoots developed in 1990–91–92 and the solid lines represent shoots developed in 1993; L, M, H: low, medium and high resource availability, respectively.

same experiment, Tworkoski et al (1990) noted no difference in the length of GUs from successive flush on *Q coccinea* seedlings, and Cobb et al (1979) even noted shorter late-season GUs on seedlings of the same species. In species which produce late-season GUs shorter than the early-season GUs, annual shoot elongation is determined more by the length of the GUs in each flush (thus by the number and the length of the internodes) than by the number of flushes (Kozlowski, 1971). In contrast, in *Q petraea*, which tends to produce longer late-season GUs, annual shoot elongation is mainly determined by the number of flushes.

Apical control

The seedlings from the three treatments exhibited weak apical control, which was revealed by the development of dormant buds into lateral branches and sprout shoots, and by the changes in the allocation of the longest GUs.

All the axillary buds located on the currently elongating GUs were inhibited by the apical meristem and did not develop into shoots, whereas a high proportion of the buds located on the previously formed GUs grew into shoots. These observations agree with those of Brown et al (1967) who described oak as having strong apical dominance and weak apical control. The ter-

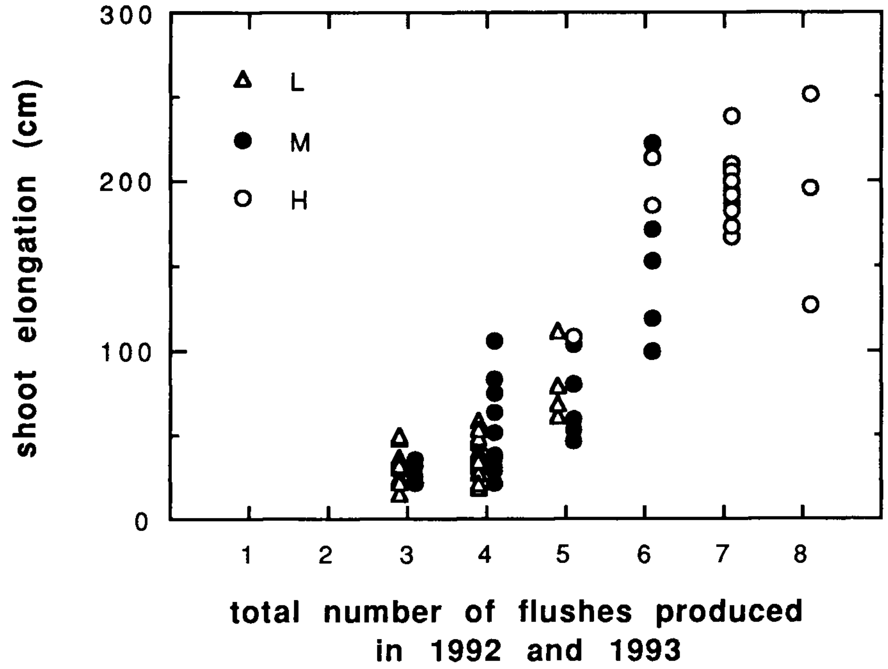


Fig 5. Total shoot elongation in 1992 and 1993 in relation to the total number of flushes produced by the seedlings over the 2 years, for oak seedlings grown under low (L), medium (M) or high (H) resource availability. Each point represents a seedling.

minology of apical dominance versus apical control has proved to be useful to describe general patterns of tree growth (Brown et al, 1967). In species having a periodic growth such as oak, it is possible to refine the notion of apical control, and to distinguish an inter-annual apical control which designates the pattern of bud inhibition on previous year GUs, and an intra-annual interflush apical control which designates the pattern of inhibition of the buds located on the GUs formed during the previous flushes of the current year. On the seedlings from the three treatments, both inter- and intra-annual apical control were weak.

Lateral branch production appeared to be strongly dependent on the total number of flushes produced by the seedling. A bud formed during a given growth flush may turn into a shoot during each subsequent flush and therefore the opportunity for each bud to form a shoot increases with the number of flushes produced. Moreover, for a bud formed during a given flush, each subsequent flush may reduce the inhibition exerted by the apical meristem and, therefore, may increase the capacity of the bud to develop.

We found a significant positive effect of resource availability on branch formation during the first year. In a 1 year experiment, Harmer (1989b) also noted a positive effect of mineral nutrition on lateral branch production. However, this effect disappeared in the second year and no clear among-treatment differences occurred in the number of lateral branches present on a GU after 2 years. Nevertheless, in treatment H most of the lateral branches located on the GUs from the first and second flushes were formed in the same year as the GUs on which they grew. In contrast, in treatments L and M most of the lateral branches grew during the next year. As a consequence, at the end of 1993, the lateral branches which developed on the 1992 shoot were older and were probably more developed in treatment H than in treatments L and M.

Sprout shoots developing from dormant buds located at the collar of the seedling appeared on 40% of the seedlings. This frequently occurs following shoot dieback on young oaks growing in natural conditions, as previously reported by Liming and Johnston (1944, on various oak species), Merz and Boyce (1956), Sander (1971), Johnson (1979, on *Q velutina* and *Q alba*), Tryon and Powell (1984, on various oak species), Crow (1988, 1992, on *Q rubra*), Hibbs and Yoder (1993, on *Q garryana*) and Cabanettes et al (1995, on *Q rubra*). The development of sprout shoots which replace the leading shoot has been described as resulting from poor growing conditions. Tryon and Powell (1984) suggested that it could result from stem suppression due to light limitation, whereas Crow (1988) argued that this could be a response to soil water deficit because it reduces the shoot-to-root ratio. However, Crow (1992) showed that seedlings grown under light-limiting conditions developed less sprout shoots, and observations made by Hibbs and Yoder (1993) did not support the hypothesis that development of sprout shoots were the consequence of low water availability. In our experiment, the light conditions were not limiting, and we observed no statistically significant effect of resource availability on the occurrence of sprout shoots. Therefore, the appearance of sprout shoots was not clearly related to limitation of resource availability.

The apical control of a tree is characterized by the differences in bud development and in shoot elongation among variously located shoots (Zimmermann and Brown, 1971; Kramer and Kozlowski, 1979). In addition to lateral branch and sprout shoot production, another expression of the weak apical control was the frequent within-season changes of axes having maximum elongation. The longest GU of each flush was not produced by the same shoot, but by several shoots for more than half of the seedlings. Cabanettes et al (1995) also reported changes in maximum elongation on *Q rubra* seedlings, although they did not quantify the frequency of occurrence.

A consequence of the lack of strong apical control was the frequent changes in the dominant axis occurring within a growing season. This was recorded on 50% of the seedlings. Changes in dominance resulted from the appearance of sprout shoots and lateral branches, and from the changes in the allocation of the longest GUs between different shoots. Although no statistically significant among-treatment differences arose for any of these three mechanisms, the occurrence of changes in dominance significantly differed among the three treatments.

Changes in the allocation of the longest GUs occurred most frequently in treatment H, sprout shoots appeared least frequently in treatment H (although differences were never statistically significant) and branch production did not clearly vary with treatment. Changes in dominance occurred much more frequently in treatment H than in the two other treatments. Together, these observations suggest that dominance changes may be most closely related to changes in the allocation of the longest GUs among several axes rather than to the development of new axes. In fact, the proportion of changes occurring between two codominant axes or between a dominant and a sprout or a lateral branch varied among the treatments. In treatment H, where the longest GUs were frequently located on several axes, the percentage of changes in dominance occurring between two codominant axes was higher. In treatments M and L, however, where sprout shoot development was frequent, the percentage of changes in dominance occurring between a dominant and a sprout or lateral branch was higher. As a result, changes in dominance were the consequence of both the appearance of sprout shoots and lateral branches and the allocation of maximum elongation to different shoots. The relative importance of these processes varied with the growing conditions. While these results show that dominance changes can occur very frequently in young oaks, it is unclear how long these changes might continue, and at what point a single axis will start to dominate and outgrow the other axes to build the future stem of the tree.

Half of the changes in dominance were associated with the death of the apical bud of the dominant axis. The high frequency of apical bud death (20% of all apical buds, each year) contradicts the usual assertion that shoot elongation in oak is monopodial, based on observations made in controlled environments (Kramer and Kozlowski, 1979; Champagnat, 1989). Our observations agree with those made by Drénou (1994, on *Q robur)* who reported that young sessile oaks often showed monopodial growth during the growing season and sympodial growth at the beginning of each growing season. Apical bud growth in oak is potentially indeterminate, and when growing under good conditions, seedlings show monopodial shoot elongation. However, the apical bud is sensitive to environmental factors such as cold temperatures, mildew and aphid attacks. Under natural conditions, death of the apical bud occurs frequently, leading to sympodial growth. The proportion of shoots showing monopodial or sympodial growth depends on the environmental conditions.

We did not observe any effect of resource availability on the death of the apical buds. However, it must be noted that 1991 and 1992 had mild winters with no early or late frost. Early frost occurred at the end of summer 1993 and stopped the elongation of the shoots which were still growing. Important among-treatment differences in the frequency of apical bud death may have arisen this year, since the seedlings in treatment H were still growing when the frost occurred, whereas the seedlings in treatments L and M had already stopped growth and developed frost-hardened buds.

Height growth

Seedling height increment is a function of i) the vigor of the plant, which determines the potential elongation of the dominant shoot, and ii) the apical control of the plant, which determines how potential shoot elongation is allocated between the dominant shoot and the other shoots. In oaks, because they show weak apical control, potential shoot elongation may not be allocated exclusively to the dominant axis, and important losses in height growth may then occur. Therefore, to predict the height increment of a seedling, it is necessary to evaluate its apical control in addition to its vigor. In our study, seedling vigor could be estimated from the number of growth flushes produced, and apical control from the frequency of changes in dominance. Actually, the number of flushes is determinant for annual shoot elongation, and changes in dominance, being the consequence of both lateral shoot formation and elongation, constitute a synthetic expression of apical control.

Resource availability can influence both the vigor of a seedling and its apical control. As expected, we found that better resource availability induced higher vigor for the seedlings. But a trade-off between the vigor and the apical control occurred as seedlings growing under high resource level also showed weaker apical control and exhibited more changes in dominance.

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