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Original article

The incidence of recurrent flushing and its effect on branch production in *Quercus petraea* (Matt) Liebl growing in southern England

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Summary — The incidence of recurrent flushing on leading shoots and major branches of *Quercus petraea* growing in southern England was examined over an 8-year growth period. Three types of shoot section were defined: SPRING – initial flushes produced in spring that did not form a 2nd flush; FIRST – initial flushes produced in spring that formed a 2nd flush; SECOND – those formed by recurrent flushing. The proportion of shoots forming a SECOND flush varied from 4–100%, the leaders flushing more frequently than branches. There were differences between trees in the tendency to recurrent flushing, in general one SECOND flush was produced for every 1.4 flushes initially produced. The SECOND flush was always longest. The number of branches produced by each type of flush varied but this was related, in part, to differences in shoot length. The effect of recurrent flushing on branching and stem form is discussed.

***Quercus petraea* / recurrent flushing / branching**

Résumé — **Fréquence d'apparition d'une croissance polycyclique et son effet sur la production des branches du *Quercus petraea* (Matt) Liebl dans le Sud de l'Angleterre.** *La fréquence d'apparition d'une croissance polycyclique sur les pousses apicales et les branches principales du* Quercus petraea *dans les conditions du Sud de l'Angleterre, a été examinée sur une période correspondant à 8 années de végétation. Trois types de pousses ont été définies : PRINTEMPS – premières pousses produites au printemps ne donnant pas de 2^e pousse; PREMIÈRES – premières pousses produites au printemps formant ensuite une 2^e pousse; DEUXIÈME – pousses formées par croissance polycyclique. Le pourcentage de pousses donnant une DEUXIÈME pousse variait entre 4 et 100%, le polycyclisme apparaissant plus fréquemment sur les pousses apicales que sur les branches. On a observé des différences entre arbres en ce qui concerne la tendance au polycyclisme. En général, on a compté une DEUXIÈME pousse pour 1,4 pousses initialement produite, cette DEUXIÈME pousse étant toujours plus longue que les pousses à l'extrêmité desquelles elle apparaissait. Chaque type de pousses a donné un nombre de rameaux variable, en partie fonction de la longueur de la pousse. L'effet de la croissance polycylique sur la ramification et la forme des tiges fait l'objet d'une discussion.*

Quercus petraea *| croissance polycyclique / ramification*

INTRODUCTION

Shoot elongation in *Quercus petraea* is episodic with phases of rapid shoot extension alternating with periods of apparent inactivity when the terminal bud is developing. This recurrent or polycylic pattern of growth is well known, and most studies of the phenomenon in oak have investigated the endogenous and environmental factors that control terminal bud activity (Lavarenne, 1969; Borchert, 1975; El Nour and Riedacker, 1984; Barnola *et al,* 1986; Alatou *et al,* 1989). Most studies have been short-term, carried out in controlled conditions and have largely ignored the wider effects of recurrent flushing on growth and form.

Oaks show weak apical control but strong apical dominance (Brown *et al,* 1967). When growth of overwintered shoots occurs in spring many buds can form branches but in the subsequent flushes during summer the development of lateral buds is suppressed by the terminal bud and fewer form branches. In addition, growth in oak is acrotonic and branches form near the shoot tip. Thus, the pattern of lateral branch formation on shoots that have produced a summer flush may be different from those that have not. If this is true, then the pattern of branch distribution and crown form of trees with shoots that show regular recurrent flushing may be different to those that normally produce only one flush of growth.

This study of *Quercus petraea* in southern England, which was undertaken as part of a tree improvement programme, was carried out to investigate not only the incidence of recurrent flushing over an 8-year time period but also how the pattern of branch production varied between shoots formed during the different flushes of growth.

MATERIALS AND METHODS

In January 1988, ten 8-year-old *Quercus petraea* trees grown 2 m apart in the Alice Holt Forest, southern England (Harmer, 1991) were felled and returned to the laboratory for further study. The 4 major crown branches and the leading shoot were then cut from each tree. The leading shoot was defined as that part of the main stem between the tip and the junction with the main stem of the first large crown branch that extended to the periphery of the crown. The branches and leading shoots had been produced over several years and consisted of many readily identifiable sections of shoot produced during separate flushes of growth: the length, viablity of the terminal bud and number of lateral branches on each section of stem were scored prior to assessment of age by counting annual rings. Each section was then assigned to one of the following types of flush (fig 1): a), SPRING: a section of shoot formed during spring that did not produce a second flush in the same season; b), FIRST: a section of shoot formed during spring that developed a second flush of growth in the summer; c), SECOND: the second flush of growth produced during summer by the FIRST section (b) above).

The type of each section that formed the main trunk in the crown of each tree was also assessed; the leading shoot was the top part of this trunk.

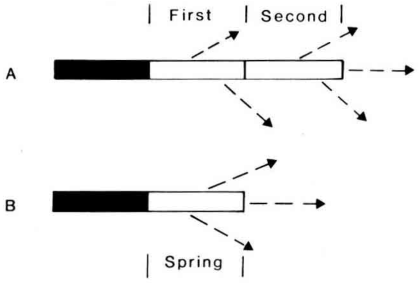

Fig 1. Diagrammatic representation of different types of section of leaders and branches of oak. A = shoot with FIRST and SECOND sections of shoot; B = shoot with SPRING section of shoot only; ■ = sections produced in previous year; ❑ = sections produced in current year; ---- = lateral branches and terminal growth in following year.

Recurrent flushing on trees in the same stand was also assessed for 1988 and 1989/1990 using 10 and 21 trees respectively; shoots formed in 1990 were observed in February 1991. In the analysis of data shoots were only included if their type could be definitely determined: thus, on any branch or leading shoot all sections produced during the oldest year of growth were excluded. Where the terminal bud or shoot of the main axis of the leader or branch died, the lateral that formed the new leader was not scored as a branch.

RESULTS

The main trunks plus the leading shoots consisted of 9–13 sections and the branches 4–13 sections; this variation was not only due to differences in age of material sampled but also the differences between trees in the tendency to recurrent flushing. The oldest sections of main trunk and branches that produced data were 7 and 6 years old respectively. However, most branches were younger and the amount of data available declined with age; only 6 branches provided data for 1982 (table I). Approximately 5% of SECOND flush shoots produced a third flush of growth and these occurred primarily on trees 4 and 5 which were prone to recurrent flushing.

The percentage of shoots showing SECOND flushes of growth between 1981 and 1990 are given in table I. The proportion of leading shoots forming a second flush varied between 100% in 1981/1987 and 40% in 1983/1984. The proportion of branches that produced a SECOND flush varied between 4 and 95% for 1989 and 1987 respectively (table I). In general a smaller proportion of branch shoots produced a SECOND flush than the leading shoots. Within most years there were too few data to analyse each individually, but a χ^2 of the larger study made in 1990 showed that significantly more leading shoots prduce SECOND flushes than branches ($P \leq 0.01$). However, as there

Table I. Percentage of shoots showing a SECOND flush and the percentage of SECOND and SPRING flush shoots with live overwintering terminal buds for shoots produced in different years.

Year	*Occurrence of SECOND flush*		*Presence of live terminal buds*	
	Leader	*Branches*	*SECOND*	*SPRING*
1981	100 (1)	+	+	+
1982	60 (10)	50 (6)	0 (9)	50 (7)
1983	40 (10)	48 (21)	50 (14)	91 (17)
1984	40 (10)	50 (30)	71 (19)	41 (21)
1985	90 (10)	74 (39)	45 (38)	56 (9)
1986	70 (10)	63 (40)	58 (32)	87 (18)
1987	100 (10)	95 (40)	62 (47)	100 (2)
1988	+	14 (50)	+	+
1989	+	4 (105)	+	+
1990	76 (21)	33 (78)	40 (42)	88 (57)
	$\bar{x} = 68$	$\bar{x} = 59$	$\bar{x} = 55$	$\bar{x} = 74$

Figures in brackets are number of leaders or branches producing useful data. Leader : leading shoots; branches = major crown branches. x = mean value for years in which data present for all values; + = data not available.

was large variation between years there was no statistically significant difference in the overall mean values for branches (59%) and leaders (68%) shown in table I.

The viability of overwintering terminal buds for SECOND and SPRING flushes in the different years is also shown in table I. Data for leading shoots and branches have been combined. For both types of flush there were considerable differences between years in the proportion of buds remaining live overwinter, the percentage varying between 0–71% for SECOND flush terminal buds and 41–100% for those on the SPRING flush. Despite a large difference between overall means, which were 55 and 74% for SECOND and SPRING flushes respectively (table I), these were not significantly different. Thus, there was no apparent difference in the overall viability of SECOND and SPRING flush terminal buds. However, when all shoots in the large sample in 1990 were investigated separately, $\chi 2$ analysis showed that there were significantly fewer live terminal buds on SECOND flush than on SPRING flush shoots ($P \leq 0.001$).

During collection of the data it became evident that there were obvious differences between trees in the tendency to form a SECOND flush of growth. The mean proportion of SECOND flush sections on the branches of each tree, expressed as No of SECOND ÷ (No of FIRST + SPRING) is shown in table II. When the ratio is equal to 1.00, then half of the sections on the branch were produced by a recurrent flush. The values varied between 0.38 for AH306/6 to 1.00 for AH306/5; on the latter, every shoot formed during the 1st flush of growth in spring produced another section of shoot by a recurrent flush. Over all shoots on all trees 1 SECOND flush was produced for every 1.4 flushes of growth during spring (*ie* FIRST + SPRING). Casual observation suggested that differences between trees may be related to the length of the shoots produced but although there was a significant difference between trees in the overall mean length of all sections on the branches (table II) there was no obvious relationship with the proportion of sections formed by a SECOND flush.

Table II. Mean proportion of sections on a branch produced by a SECOND flush and mean length (mm) of sections on branches of different trees.

Tree	*Proportion*	*Length*
AH306/5	1.00^{b}	12^{a}
AH306/4	0.85^{ab}	14^{ab}
AH306/7	0.78^{ab}	14^{ab}
AH306/10	0.78^{ab}	24^{c}
AH306/3	0.69^{ab}	21^{bc}
AH306/8	0.66^{ab}	18^{abc}
AH306/9	0.66^{ab}	17^{abc}
AH306/2	0.56^{ab}	17^{abc}
AH306/1	0.54^{ab}	14^{a}
AH306/6	0.38^{a}	19^{abc}
	$\bar{x} = 0.69 \pm 3$	$\bar{x} = 17 \pm 1$
	$P \leq 0.05$	$P \leq 0.01$

Proportion = SECOND ÷ (FIRST ÷ SPRING); x = mean over all trees; within each column figures with different subscripts are significantly different.

Only 1985 and 1986 data provided sufficient information for a detailed analysis of lateral branch production on sections produced by each type of flush. In both years significantly more lateral branches were produced on SECOND than FIRST flush sections (table III). In 1986 the SECOND flush of leading shoots formed 8 times as many lateral branches as the FIRST flush. For major branches the differences were less, 1.8 and 2.2 times greater for 1985 and 1986 respectively (table III). Results for SPRING flush were inconsistent: in 1985 they produced fewer, and in 1986 more, lateral branches than SECOND flush sections (table III).

Table III. Mean number of lateral branches (±SE) and mean length (±SE) of SECOND, FIRST and SPRING flushes produced during different years on major crown branches and leading shoots.

Major crown branches	*No of lateral branches*			*Length (mm)*		
Year	*SECOND*	*FIRST*	*SPRING*	*SECOND*	*FIRST*	*SPRING*
1985	4.4 ± 0.4 *n* = 28	2.5 ± 0.4 *n* = 28	2.4 ± 0.5 *n* = 9	19 ± 2 *n* = 28	16 ± 2 *n* = 28	15 ± 2 *n* = 9
1986	5.6 ± 0.5 *n* = 25	2.6 ± 0.4 *n* = 25	6.5 ± 1.0 *n* = 15	22 ± 2 *n* = 25	11 ± 1 *n* = 25	19 ± 2 *n* = 25
1987	+	+	+	27 ± 2 *n* = 38	15 ± 1 *n* = 38	+
Leading shoots						
1986	8.0 ± 1.5 *n* = 4	1.0 ± 0.7 *n* = 4	+	41 ± 2 *n* = 4	14 ± 3 *n* = 4	+
1987	+	+	+	48 ± 5 *n* = 10	19 ± 5 *n* = 10	+

n = No of replicates; + = data unavailable; SE = standard error.

The number of branches produced by each type of flush is related to the length of the section and in this study SECOND flush sections were always longer than those of the other types of flush (table III). The difference varied from ≈ 0.2–2-fold for major branches to ≈ 2–3-fold for leading shoots (table III). Multiple regression analysis showed that the length of the flush of growth produced during spring was positively related to the number of lateral branches produced at the same time on the preceding year's shoot: shoots that formed the longest flushes also produced most lateral branches. The length of the FIRST flush of growth in 1987 was related to the number of branches growing on the 1986 SECOND flush shoot ($P \leq 0.01$) and the length of the FIRST flush in 1986 on the number of branches on the FIRST flush shoot in 1985 ($P \leq 0.05$).

The linear regression relationships between lengths of major branch sections and the number of lateral branches that they produced for 1985 and 1986 are shown in figures 2 and 3. In both years there were some significant differences between the lines but the differences were not consistent. In 1985, the lines for the FIRST and SECOND were significantly different ($P \leq 0.01$) but neither of these differed from the SPRING flush (fig 2). However, in 1986 the SPRING flush produced more branches per unit length than the SECOND flush (fig 3): data for the FIRST flush 1986 has been plotted for comparison but the best fit line was not significant. Viability of the terminal bud appeared to have no effect on the number of branches produced. These analyses were carried out combining data from all trees and as they showed different tendencies to pro-

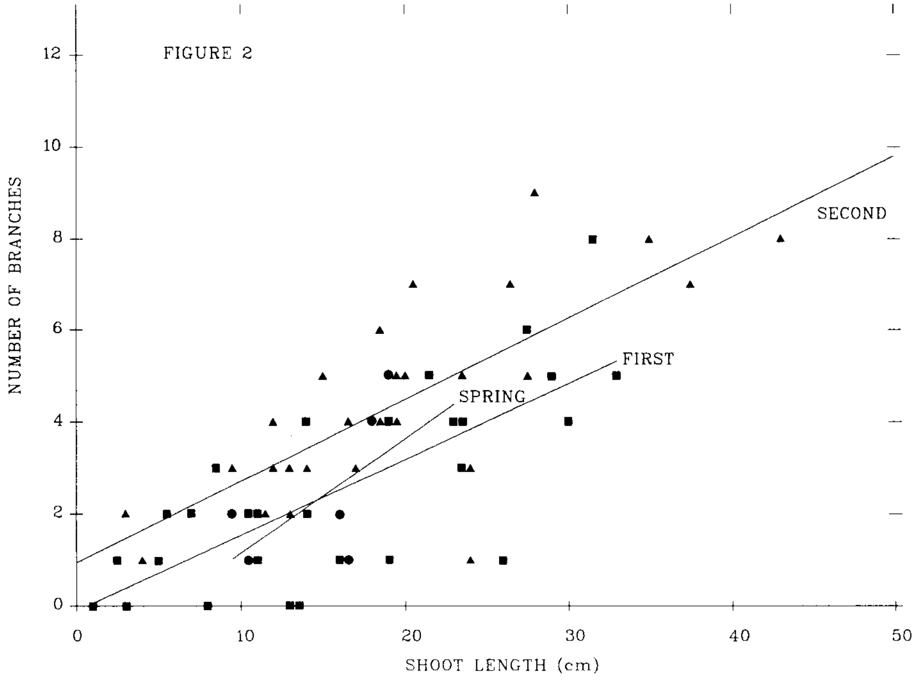

Fig 2. Linear regression lines for number of branches against 1985 shoot length for: FIRST flush (■) $y = 0.165\ x - 0.11$, $R^2 = 55.8$ ***; SECOND flush (▲) $y = 0.177\ x + 0.94$, $R^2 = 57.8$ ***; SPRING flush (●) $y = 0.248\ x - 1.34$, $R^2 = 55.3$ *.

duce a SECOND flush the trees are not equally represented within each type of flush, *eg* trees which always produce a SECOND flush cannot provide data for SPRING flush sections. Thus, differences between flushes reflect, in part, variation between trees.

DISCUSSION

The proportion of shoots that produced a SECOND flush of growth varied considerably between years, trees and whether the shoot was the leader or a branch. In some years almost all shoots on all trees had 2 flushes of growth whereas in other years many shoots formed only a single SPRING flush. The reasons for this are unknown. The rhythmic pattern of bud activity may be controlled by both long and short distance correlative inhibitions (Champagnat, 1989) and a number of environmental and endogenous factors including day length (Wareing, 1954), plant growth regulators (Hardwick *et al,* 1982), and internal competition for water (Borchert, 1975), have been implicated in the processes involved. Other work has shown that the supply of nutrients is important (Bond, 1945; Gilliam and Wright, 1978) and recently Barnola *et al* (1990) have proposed a nutritional hypothesis for rhythmic growth which is based on the relationships between the apical meri-

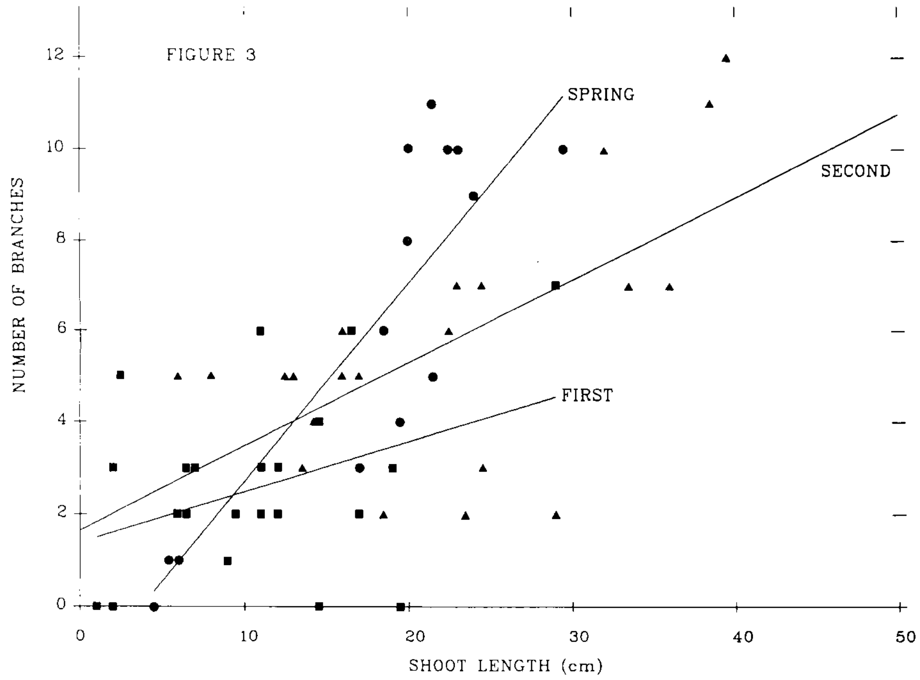

Fig 3. Linear regression lines for number of branches against 1986 shoot length for: FIRST flush (■) $y = 0.109x + 1.39$, $R^2 = 13.5\%$ NS; SECOND flush (▲) $y = 0.182x + 1.65$, $R^2 = 36.7\%$ **; SPRING flush (●) $y = 0.434x - 1.65$, $R^2 = 75.3\%$ ***.

stem, associated axial tissues and very young leaves. There is probably also a genetic element to this phenomenon. In this study some trees regularly produced a SECOND flush of growth and study of a field trial in Germany showed that some progeny produced more SECOND flushes than others (Harmer, unpublished observations). Although the variation in frequency of recurrent flushing found between years probably reflects environmental and genetic factors, other features such as tree age or insect defoliation may also be important (Longman and Coutts, 1974).

In southern England most of the shoots produced by the SECOND flush in summer become infested with mildew and many do not appear to reach full maturity. In general, fewer SECOND flush shoots produced a viable shoot from a terminal bud than SPRING flush shoots, but this varied considerably between years and the difference was not always statistically significant. As recurrent flushes of growth are usually restricted to the areas of most vigorous growth, such as the leader and tips of the major branches (Longman and Coutts, 1974) any death or dieback is likely to occur in the most important parts of the crown. This is important in young trees as they produce SECOND flushes most frequency and regular loss of the leading shoot will adversely affect the form of the main stem.

The difference in lengths between FIRST and SECOND flush shoots has also been observed in clonal material derived from the trees studied and is frequently observed in seedlings after their first winter (Harmer, unpublished observations) suggesting that this is a typical pattern of growth. Reasons for these differences may be due to changes in source–sink relationships. As oak leaves do not export photosynthate until they have reached 75% or more of their final size (Tselniker and Malkina, 1986; Dickson, 1989), shoot extension of the FIRST flush will depend on stored carbohydrates. In contrast, current photosynthate is available during growth of SECOND flush shoots.

Individual shoots produced different numbers of branches. Apical dominance restricts the number of lateral buds that develop into branches during the SECOND flush which may increase length of SECOND flush shoots by reducing competition for available nutrients. If competition for nutrients restricts growth, then shoots producing more lateral branches may form shorter FIRST flush sections. However, in this study, relationships between length of FIRST flush and lateral branch formation were positive, suggesting that competition between apical shoot and developing lateral branches has little effect on the length of the FIRST flush. But this study was simple and did not record the length of lateral branches, which is probably important in determining the size of the sink, and the analyses did not account for between tree variation. Differences between FIRST and SECOND flush lengths may be related to the overall activity of the plant: the FIRST flush is produced during a period of reactivation after winter dormancy whereas SECOND flushes grow when the plant is already actively growing. Alternatively, the length of the FIRST flush, which is produced from an overwintered bud, may be determined during the previous growing season; the lengths of FIRST and SECOND flushes reflecting, in part, different patterns of growth, physiology and apical dominance in plants with post-dormant overwintered buds and resting summer buds (Champagnat, 1989). In order to obtain a greater understanding of shoot growth, further studies should include the timing of reactivation, growth and development of the vascular and root systems and their ability to supply water and nutrients for shoot extension and leaf expansion (Bond, 1945).

Interpretation of the data for lateral branch production by sections of shoot formed during FIRST, SECOND and SPRING flushes of growth is difficult. There were significant differences in the relationships between numbers of branches and shoot length but they were not consistent between years. In addition, there were significant differences between trees in the tendency to form a SECOND flush and in each year not all trees produced shoots in each type of flush. In both 1985 and 1986 the slopes of the lines of SPRING flushes were greater than those for either FIRST or SECOND (figs 1, 2) suggesting that they produced more branches per unit length of shoot. Further data are needed to substantiate these observations.

Growth of oak is acrotonic, the size and number of branches present on the shoot declining basipetally (Harmer, 1991). On an annual basis the distribution of lateral branches will differ between shoots showing only a SPRING flush and those showing 2 flushes. On those showing a single SPRING flush, branches will be concentrated at the tip of the annual increment in length whereas there will be 2 centres of branching on 2 flush shoots: branches will be produced at the tip of the shoot and just below the junction of the 2 flushes.

Although production of a SECOND flush may influence tree structure by changing the relationship between shoot length and number of branches, and the distribution of branches on the stem, the effects of these on form are not yet known. In contrast, the effects of terminal bud death are easier to predict. When the terminal bud dies a new leader must develop from a lateral bud; this will frequently be one in the dense cluster near the shoot tip. Lateral buds often grow out to form branches at large angles to the vertical; new vertically growing leading shoots are not quickly re-established and the stem becomes crooked. Loss of the terminal bud is particularly important for young trees that are forming their main stem. As recurrent flushing is more likely to occur on the leading shoot of young trees, and the terminal bud or shoot tip on SECOND flush shoots often dies, then young trees that show a strong tendency to produce a SECOND flush may grow into trees with worse form than those that usually flush once. This suggests that tree improvement programmes which aim to select trees with good form should probably try to develop methods of identifying trees that show a reduced incidence of recurrent flushing.

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