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Regeneration by sprouting of holm-oak (*Quercus ilex*) stands exploited by selection thinning

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Abstract

Holm-oak forests of the Montseny Massif have traditionally been exploited by selection thinning, which consists of a partial removal of standing trees and biomass. Cutting percentages within each size class indicate that this management technique represents a compromise between forest improvement and harvesting.

Sprouting is the mean regeneration process of these holm-oak stands. The mean number of living sprouts per stool is considerably higher than in other coppiced hardwood species, and decreases along the cutting-cycle according to a negative exponential function. Mean number of surviving sprouts per stool is significantly correlated with regenerative age and stool size. Death of sprouts throughout the cutting cycle is compensated by growth of surviving sprouts. Thus, the weight of living sprouts per stool increases linearly with time, and also with the basal area coppiced.

Sprouts developing within the first fifteen years of regeneration belong to a single cohort that appears during the first year after cutting. After that period of time, new sprouts appear from dormant buds, so that after 30 years of regeneration a wide range of cohorts of different ages are present.

Introduction

One of the most important mechanisms of plant regeneration under natural and anthropogenic perturbations is resprouting, i.e. the production of sprouts from buds on preexisting plant organs. Many shrub and tree species of the Mediterranean region are able to produce new shoots from dormant buds located on stumps, roots and specialised underground organs (James 1984; Koop 1987). Much interest has focused on studying regeneration of natural populations under natural perturbations, particularly fire. Nevertheless, many tree species, such as holm-oak (*Quercus ilex*) have been managed for centuries as a source of wood for different purposes and the way in which they have been exploited should be regarded as one of the most important sources of man-made perturbations.

Holm-oak is a slow growing species with little seasonality and low production rates (Ferrés 1985), as can be expected for a species adapted to nutrient-poor soils and irregular precipitation (Escarré *et al.* 1984). In holm-oak trees, sprouting after cutting occurs by activation of dormant buds on the stump or the underground organs (Cucó 1987).

Holm-oak forests covering 15,000 ha of the Montseny massif in northeast Spain had been continuously exploited for charcoal before 1950 (Llobet 1947; in Ferrés 1984). Nowadays, the demand for big holm-oak trees for fire wood has increased considerably and so, forest management by selection thinning over relatively long periods of time between harvests (about 25–30 years) is now the most common practice. This is a special feature with respect to other holm-oak forests of the Mediterranean region, where exploitation is predominantly carried out by clear felling practices (Romane *et al.* 1988). In selection thinning management, individual trees are selected for harvesting. The period of time between harvests is usually known as the 'cutting cycle' (Buongiorno & Lu 1990).

Restocking of the stand during the cutting cycle is left to occur by natural regeneration by sprouting (coppicing). In general, coppicing is an essential condition for short rotation in forestry and also an ancient form of woodland management in many types of forests (Ford & Newbould 1970), though sometimes regarded as an undesirable form of regeneration because of poor stem form and risk of decay (Lowell *et al.* 1987).

Even though bud activation in sprouting species at the hormonal level is partially known (James 1984), there is little information referring to the development of sprouts at the individual level and, hence, at the population level. More complete studies of sprouting would help to understand regeneration mechanisms and to design management procedures for the future (Keeley & Zedler 1978).

The objective of this paper is to define the main features of the selection thinning management procedures presently used in holm-oak forests in the Montseny Massif, and to characterize natural restocking by coppicing through analyses of changes in sprout number and growth during the cutting cycle.

Material and methods

The study area is situated in the southern part of the Montseny Massif, 40 km from Barcelona. In an uneven-aged montane holm-oak forest, six stands belonging to a chronosequence of 1,2, 4,7,12 and 30 years from the last thinning have been selected. Aspect of the stands varies from SW to NW, altitude from 450 to 600 m, and slope from 20 to 25°. Soils are xerochrept having developed on a bed-rock of metamorphic schists.

In each stand, a circular plot of 10 m radius was established in order to analyze general features and type of exploitation. Dbh of all trees greater than 5 cm and mean diameter of all stumps from the last thinning were measured. From these data, coppiced, non coppiced, and total basal area before last thinning (the sum of coppiced and non coppiced basal area) were calculated. In the 30 year old stand, basal area coppiced was not calculated because stumps from last thinning were not distinguishable. To compute coppiced basal area, dbh of cut stems was estimated from stump diameter using the regression equations described by Pita & Espelta (1990) for holm-oak in Montseny forests. Biomass was estimated from the general regression equations of dry weight on dbh given by Canadell *et al.* (1988) for holm-oak in Montseny forests.

Regeneration by sprouting has been determined using the following parameters: number of living and dead sprouts, sprout diameter distribution, sprout height growth rate and weight of living sprouts per stool. Parameter calculations were obtained through data from ten stools randomly chosen in the plots of 1,2,4,7 and 12 years of regenerative age. In the 30 year old plot, twenty-three stools were chosen to provide a larger sample available for further analyses.

For each sprout the following measures were taken: basal diameter, total height and height growth in the current year. Sprout relative growth rate in height (RGR) was calculated according to:

$$\mathrm{RGR} = \ln (A_t/A_{t-1})$$

where A_t is the height in the current year, and A_{t-1} is the height in the year before.

Sprout weight was calculated using the following allometric regression equation:

$$\log \mathrm{DW} = a \cdot \log(\mathrm{D}^2 \cdot \mathrm{H}) + b$$

where DW is dry weight (g), D is basal diameter (mm), and H is height (cm) of the sprout. This kind of equation has been widely used in other similar studies (Ford & Newbould 1970; Williams & McClenahen 1984).

Different regression coefficients and fitting parameters were developed for each stand (Table 1). In the 30 year old plot cutting of sprouts larger than 5 cm dbh was not possible, and their weight was estimated using the general regression equation of dry weight on dbh calculated by Canadell *et al.* (1988).

Finally, stools were checked for continuous production of sprouts. Age determination of new cohorts was based on the location of terminal bud scars and by assuming that newly appeared sprouts grow under suppressed conditions and produce only one flush per year (Riba 1991).

Results

Forest structure and type of management

Structure and selection-thinning management of the holm-oak forests of the study area are summarized in Table 2. In the study plots, holm-oak forests have a mean density of 1,261 stools · ha^{-1} and 3,043 stems · ha^{-1}, a basal area of 24,7 m^2 · ha^{-1} and an aboveground biomass of 127 t · ha^{-1}. Tree diameter distribution in the studied stands just before thinning is shown in Figure 1. The most abundant diameter classes are those of 6–12 cm dbh (about 50% of the stems), while the percentages of bigger and smaller classes are similar (25% in each case).

Table 1. Regression coefficients and parameters for each regenerative age according to the equation $\log \mathrm{DW} = a \cdot \log(\mathrm{D}^2 \cdot \mathrm{H}) + b$, where DW is dry weight (g), D is basal diameter (mm) and H is height (cm). For each plot, n = 20

Plot	a	b	r^2	S.E.	F-test	p
1	1.015	− 4.986	0.962	0.408	475.4	0.0001
2	1.013	− 5.087	0.980	0.404	869.7	0.0001
4	0.858	− 3.648	0.976	0.251	604.4	0.0001
7	0.847	− 3.306	0.973	0.330	651.1	0.0001
12	0.879	− 3.983	0.978	0.333	851.1	0.0001

According to Table 2, exploitation by selection thinning implies harvesting about 60–70% of standing trees, basal area and aboveground biomass of the stands. Percentage of thinning in all plots is similar: standard errors of the different parameter estimates are smaller than 10% of the mean. Almost all stems with dbh smaller than 5 cm, 35–40% of those of 5–10 cm of dbh, 40–60% of those of 10–20 cm of dbh, and more than 70% of those bigger than 20 cm of dbh, are harvested (Fig. 1).

Regeneration by sprouting

Figure 2 shows how the mean number of living sprouts per stool decreases from 167.0 during the first year of regeneration (n = 10 stools) to 3.5 after 30 years since last thinning (n = 23 stools). Changes in the mean number of sprouts per stool during regeneration can be fitted to a negative exponential function ($R^2 = 0.983$, $p = 0.0001$).

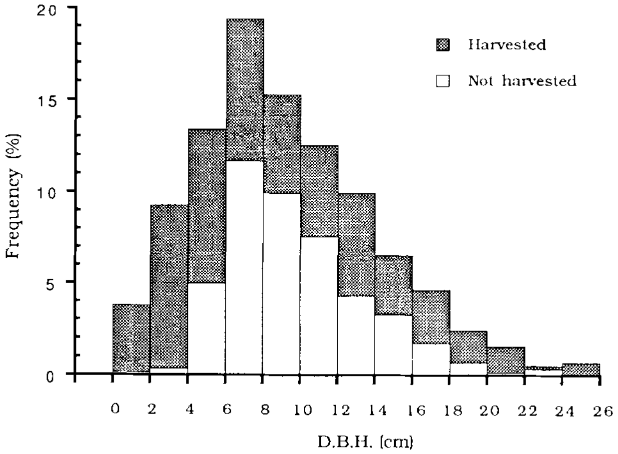

Fig. 1. Total tree diameter distribution prior to selection thinning management in the five studied stands. Shaded sections represent stems harvested after the selection thinning treatment.

Table 2. Mean features of selection thinning management in holm-oak stands in the study area (mean ± standard error, n = 5 plots).

Parameter	Total	Not harvested	Harvested	% Harvested
Density (stems · ha^{-1})	3043.1 ± 485.8	1012.2 ± 86.2	2030.8 ± 469.1	63.5 ± 5.3
Stool density (ha^{-1})	1260.5 ± 225.7	222.8 ± 54.2	1037.7 ± 190.9	83.4 ± 3.8
Basal area ($m^2 \cdot ha^{-1}$)	24.7 ± 1.3	8.0 ± 1.0	16.7 ± 1.8	67.4 ± 4.7
Biomass ($T \cdot ha^{-1}$)	127.1 ± 7.2	40.0 ± 5.5	87.1 ± 8.9	68.2 ± 4.5

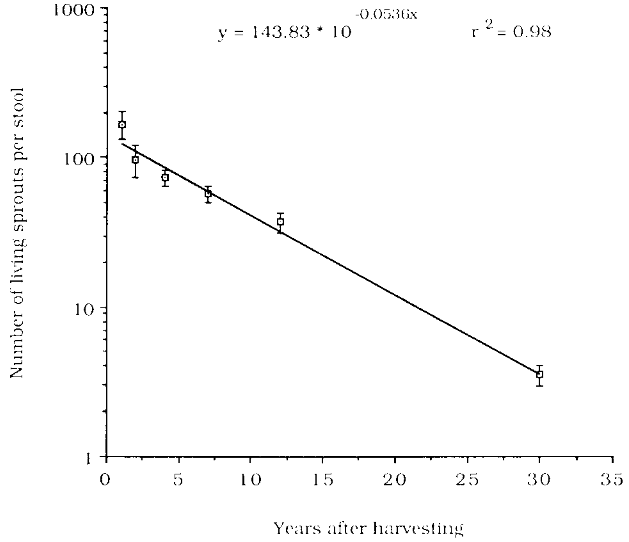

Fig. 2. Change in mean number of living sprouts per stool at different dates after harvesting.

Mean number of living sprouts per stool changes not only according to regenerative age, but also to stool area. A multiple regression analysis was undertaken to evaluate the relative importance of both factors: according to Table 3, there is a significant negative relationship between the total number of living sprouts per stool and the regenerative age of the stand (p = 0.0001), and a positive one between the total number of living sprouts per stool and stool area (p = 0.0001). Both variables have a similar weight in the equation (see partial Fs of Table 3).

The size structure of the sprout population and the changes that occur through time are reflected in the diameter distributions shown in Figure 3. The range of sprout diameter increases with regenerative age: in the 1- and 2-year old plots, most of the sprouts have a diameter smaller than 1 cm: in those from 4 to 12 years old a great part of the sprouts are in the 1 to 3 cm classes, while in the 30 year old plot many sprouts have a diameter between 3 and 14 cm.

During the first year of regeneration there is a minimum mortality of sprouts (about 2 per 1000); later, dead sprouts are mainly found in the smallest size classes (Fig. 3). Size of dead sprouts increases with regenerative age.

The study of height growth has been undertaken analyzing the mean and variance distribution of the relative growth rate (RGR) of terminal shoots of sprouts included in the different diameter classes. Sprout populations for all regenerative ages show a similar pattern (Fig. 4): growth rate is higher in the smallest classes, which also have the greatest variability.

Total living sprout weight per stool increases linearly with time from last thinning (Fig. 5,

Table 3. Multiple regression analysis of the mean number of living sprouts per stool on time from last thinning and stool surface.

D.F. = 55, R-squared = 0.579, F-test = 36.47, p = 0.0001.

Parameter	Beta value	Beta std. value	t-value	Probability	Partial F
Regenerative age (years)	− 15.15	− 0.48	4.49	0.0001	24.42
Stool area (cm^2)	47.51	0.43	4.44	0.0001	19.71

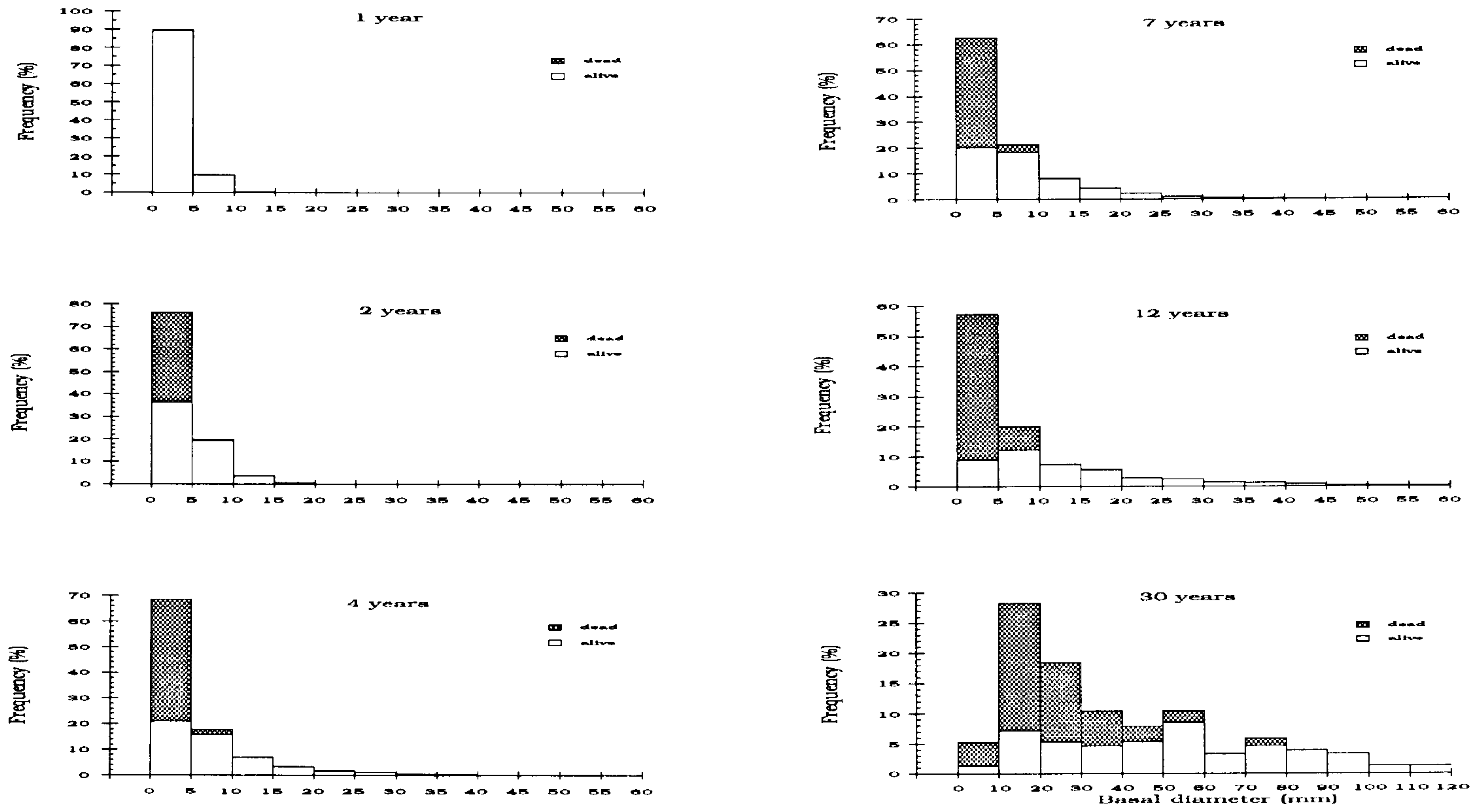

Fig. 3. Diameter size distribution of living (white bars) and dead (shaded bars) sprouts at different times from last thinning.

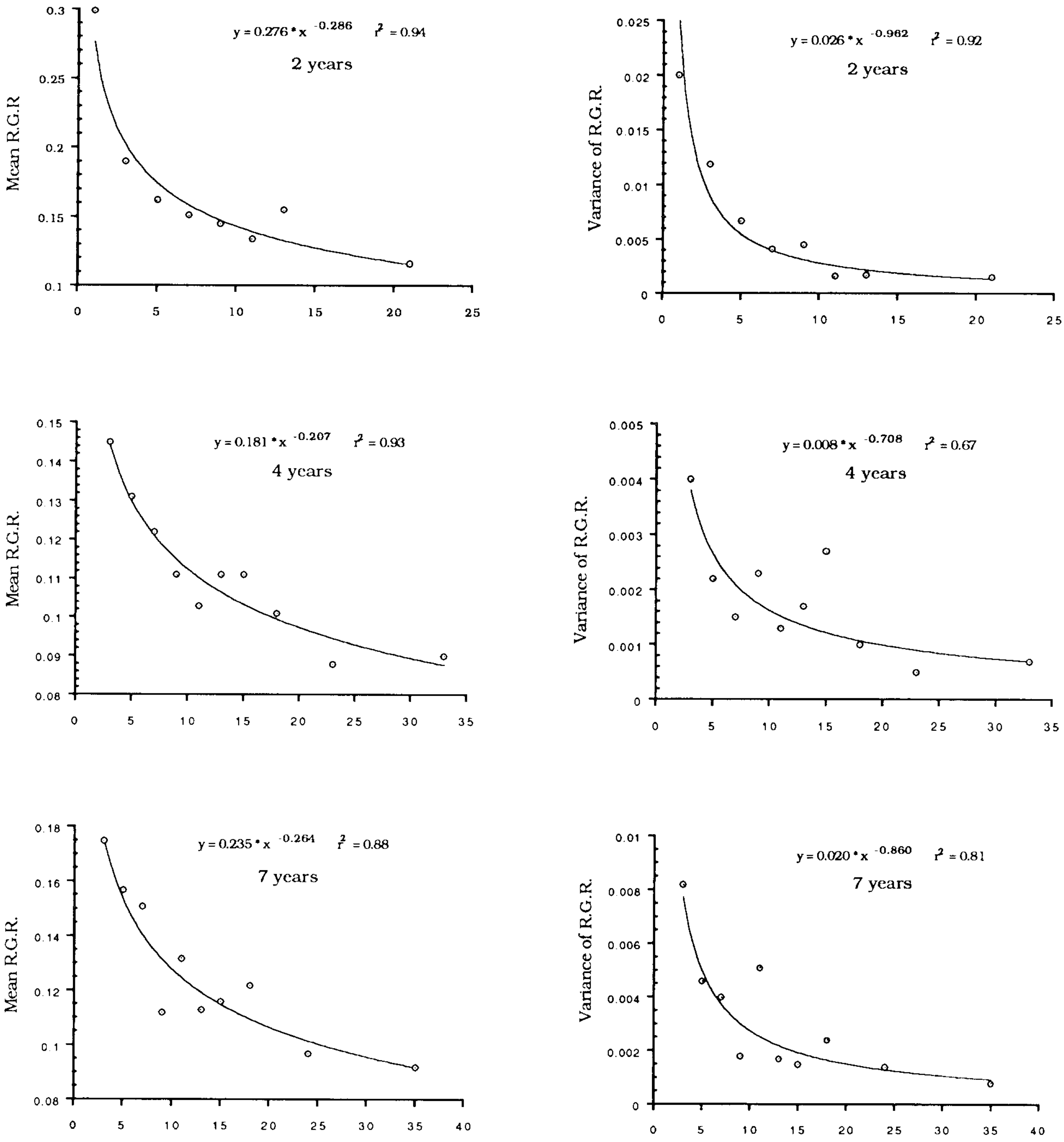

Fig. 4. Mean and variance distributions of the relative growth rate (RGR) of terminal shoots of sprouts included in the different size classes. Patterns found in each regenerative age are shown on different graphs.

$R^2 = 0.986$, $p = 0.0001$). The result of multiple regression analysis of total living sprout weight per stool on coppiced basal area and regenerative age is shown in Table 4. There is a positive correlation in both cases ($p = 0.0001$). The relative contribution of both variables to the equation is similar (see partial Fs, Table 4).

The results presented above correspond to the

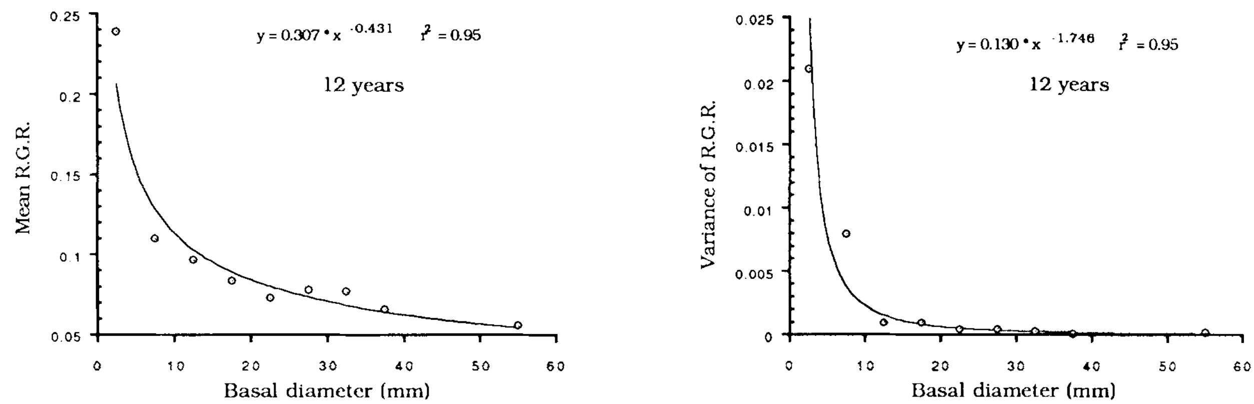

Fig. 4. (continued).

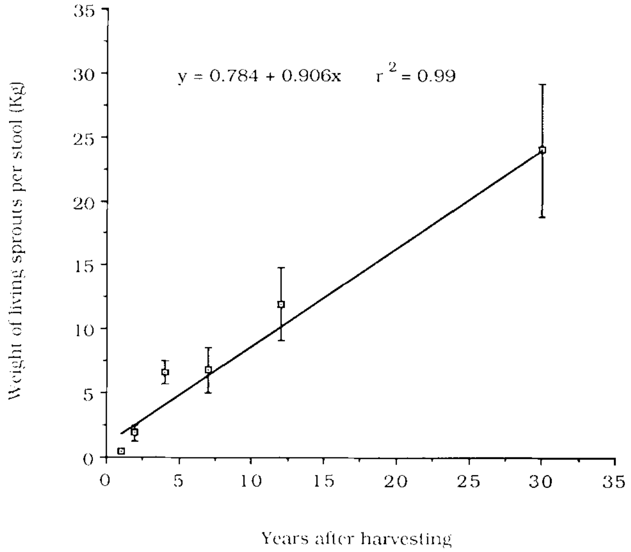

Fig. 5. Variation of total weight of living sprouts per stool at different times after harvesting.

cohort of sprouts which appeared during the first regenerative year. Nevertheless, new cohorts of sprouts are found in the 30 year old plot. The mean number of new sprouts per stool is 5.7. Ages of these new sprouts are in a range of 1 to 18 years (Fig. 6), and sizes range from 0.4 to 11.8 mm dbh.

Discussion

Structural features of the studied holm-oak stands, which refer to stem density, basal area and biomass are within the range of values found for other stands of the Montseny Massif (see review by Mayor 1990). This is due to the similar management techniques followed in the whole massif (see Introduction). These values are quite different from those found in clear-felled stands of southern France (see reviews by Lobreaux 1987, and Romane *et al.* 1988). Clear-felled forests of southern France develop higher tree density, and lower biomass and basal area than selection thinned stands in the Montseny Massif.

Table 4. Multiple regression analysis of total weight of living sprouts per stool (Kg.) on time from last thinning and coppiced basal area.

D.F. = 47, R-squared = 0.52, F-test = 24.35, p = 0.0001.

Parameter	Beta value	Beta std. value	t-value	Probability	Partial F
Regenerative age (years)	1.98	0.44	3.78	0.0005	14.32
Coppiced basal area (cm^2)	104.68	0.41	3.55	0.0009	12.59

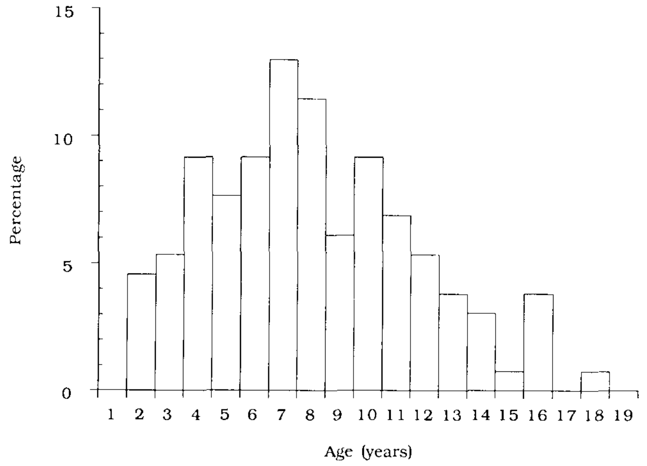

Fig. 6. Percentage of sprouts of different ages of the new cohorts in the 30 year old plot.

Total aboveground biomass harvested by selection thinning represents about 68% of standing biomass. Tree harvesting is not regularly undertaken over the whole stem size distribution. Cutting percentages within each size class indicate that this management technique represents a compromise between forest improvement (cutting of small trees) and harvesting (cutting of big trees) since most of the trees smaller than 6 cm and bigger than 16 cm are cut. The most likely reason for this is that conserves medium-sized trees, which have high growth rates and do not inhibit or reduce sprouting due to shading.

After selection thinning felling, almost all individuals produce sprouts from stumps. The mean number of sprouts per stool present throughout the cutting-cycle is considerably higher than in other coppiced hardwood species. Thus, the average number of 167 sprouts per stool in the first year of regeneration is higher than that of coppiced holm-oak stands in France, with average values ranging from 50 to 90 sprouts per stool (Lobreaux 1987). Mean number of sprouts per stool after two and five years since cutting is also higher than those of other *Quercus* species regenerating by coppicing, such as *Q. prinus*, *Q. coccinea* and *Q. velutina* (Ross *et al.* 1986), and *Q. coccinea*, *Q. falcata*, *Q. velutina*, *Q. alba* and *Q. stellata* (Lowell *et al.* 1987).

The mean number of living sprouts per stool decreases along the cutting-cycle according to a negative exponential function. This implies that the mortality rate is constant throughout the cutting-cycle. Maximum number of stems has been found to decrease exponentially with increasing stand age in many forest stands where differentiation and mortality are occurring (Mc Fadden & Oliver 1988). Percentage of mortality after two and four years, with values ranging from 42 to 56%, is comparable to that stated by Lobreaux (1987) for coppiced holm-oak stands in France.

Mortality of sprouts during regeneration has been regarded as a consequence of competition or interference (see Ford & Newbould 1970; Mac Donald & Powell 1983; Ferm & Kauppi 1990). This would also be the case of holm-oak sprouts developing along the cutting-cycle. The existence of interference among sprouts growing on the same stool or individual during the regenerative period studied can be seen when analysing variability of relative growth rate in height (RGR). Determination of both mean and variance of RGR according to sprout size has shown plastic responses to crowding. Height growth is higher in small sprouts than in big ones, due to dominance and suppression. In addition, not all the small-sized sprouts are subject to the same degree of interference: variance in RGR is higher in small sprouts than in large ones. Such plastic responses are a well known phenomenon (see Harper 1967, 1977), and may be caused by shading (Weiner *et al.* 1990). Small-sized plants of a population have to allocate their scarce production to height growth at the expense of diameter growth (Hara 1984).

Mean number of surviving sprouts per stool was significantly correlated with regenerative age and stool area. As mentioned above, the number of sprouts decreases during the cutting cycle. The existence of positive correlations between mean number of sprouts and stool area can be related to increasing number of buds in the individual bud-bank. The relationship between tree size and the number of sprouts has already been described for this species (Riba 1987), as well as for other

Quercus (Ross *et al.* 1986) and shrub species (e.g. Noble 1984 and Tappeiner *et al.* 1984).

Sprouts developing within the first fifteen years of regeneration belong to a single cohort that appears during the first year after cutting. This is similar to other tree and shrub species regenerating by sprouting, such as *Castanea sativa* (Ford & Newbould 1970), and *Betula pubescens* (Kauppi *et al.* 1988). After 15 years, new sprouts appear from dormant buds, so that after 30 years of regeneration a wide range of cohorts of different ages are present. This new wave of regeneration could be considered as advance regeneration (see Ross *et al.* 1986). It should be regarded as a consequence of a decreasing inhibitory effect on bud activation by those sprouts already present (Riba 1991). This is probably due to the mortality of medium-sized sprouts and the creation of better local light conditions in the lower part of the canopy.

At the individual level, death of sprouts throughout the cutting cycle is clearly compensated by growth of surviving sprouts. Thus, the weight of living sprouts per stool increases linearly with time, with an average of 0.9 kg per year and stool. For one individual, growth potential (accumulation of biomass) depends on coppiced basal area. The relationship between diameter of the stool and growth of sprouts has been shown by Lowell *et al.* (1987) for different species of *Quercus*. The existence of a positive correlation between coppiced basal area and growth of new sprouts may be a consequence of the reduction of the degree of inhibition or interference of the standing biomass, both for aerial and underground resources (see Riba 1991).

In summary, regeneration of holm-oak stands exploited by selection thinning is ensured by sprouting from the stool bud bank. At the individual level, sprout population development, referring to both the number and the total weight of sprouts, is positively related to stool area and basal area coppiced, respectively. The number of sprouts decreases through the cutting cycle, although biomass accumulation rate is constant. This suggests that increasing forest returns can be obtained by lengthening the period between harvests. However, heavy mortality of large sprouts at the end of the usual cutting cycle suggests an eventual mortality of stools (i.e. individuals), which might involve changes in stool density, forest structure, and the regeneration process itself.

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