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## Sprouting of seedlings of three *Quercus* species in relation to repeated pruning and the cotyledonary node

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**Abstract.** We studied sprouting of three oak species (*Quercus humilis* Miller, *Q. ilex* L. and *Q. suber* L.) at the seedling stage to examine the role of the cotyledonary node in the production of new shoots after disturbance. The aerial biomass was removed three successive times above and below the point of attachment of the cotyledons. All three *Quercus* species produced new shoots when the aerial biomass was removed above the cotyledonary node. However, the number of sprouts per seedling, the length and leaf number of the sprouts, and root diameter decreased with repeated pruning. Because of their underground dormant buds only *Q. suber* seedlings could sprout and survive when the aerial biomass was removed below the cotyledons. These results show that in *Q. suber* seedlings the cotyledonary node forms a true functional lignotuber and suggest that the presence of clusters of hidden underground cotyledonary dormant buds is limited to *Q. suber*.

### Introduction

Traits that permit a plant to survive natural or anthropogenic disturbance are significant in explanations of the distribution pattern of the plant and its relative abundance in ecosystems. Most tree species growing in Mediterranean areas, in which fire, herbivore activity and clear-cutting are common disturbances, possess adaptative traits that make subsequent survival, regeneration and/or reproduction possible. For example, burnt areas are rapidly reoccupied by species able to sprout (Trabaud 1987). Sprouting capacity is an ancient adaptive modification of the reproductive strategies which accounts for the extent and speciation of woody genera of the chaparral (Wells 1969).

In the last decade, society has become more aware of the need to protect, preserve and understand its natural habitat. One of the major consequences has been increased interest in maintaining biodiversity and restoring native forests. In the Western Mediterranean basin, the use of *Quercus* spp. in reforestation has increased considerably (Ocaña *et al.* 1996). However, available data about oak seedling behaviour and morphological and physiological features in its early life stages are scarce. More knowledge along these lines would help define criteria for evaluating and improving the quality of nursery seedlings.

Three *Quercus* species—pubescens oak (*Q. humilis* Miller, subgenerum *Quercus*), holm oak (*Q. ilex* L., subgenerum *Sclerophylloids* O. Schwarz) and cork oak (*Q. suber* L., subgenerum *Cerris* (Spach) Örsted)—are commonly used in reforestation. These species form the native forest and provide very valuable cork (*Q. suber*) and fuel. Cork and holm oaks are evergreen with broadly sclerophyllous leaves; pubescens oak is a winter-deciduous species. A common characteristic of these *Quercus* species is their great sprouting capacity from the root-crown region after disturbance (e.g. Di Pasquale and Garfi 1998 for *Q. humilis*; Ducrey and Turrel 1992, López-Soria and Castell 1992, Retana *et al.* 1992 and Fuente *et al.* 1997 for *Q. ilex*; Pausas 1997 for *Q. suber*; and Trabaud 1987 for *Q. ilex* and *Q. suber*). However, there is no information available on sprouting capacity at the seedling stage, although seedling establishment is one of the most critical stages of the plant life cycle and one of the major constraints in forest regeneration in disturbance-prone ecosystems (Kozłowski 1971; Harper 1977).

The cotyledonary node is known to play an important role in the origin of anatomical structures related to sprouting such as the lignotuber in eucalyptus (Chattaway 1958; Carr *et al.* 1982; Carter and Paton 1985; Graham *et al.* 1998), basal

chichi in *Ginkgo biloba* (Tredici 1992) and burls in birch (Stone and Cornwell 1968; Kauppi and Rinne 1987). In previous papers we described the anatomy of the cotyledonary node of *Q. suber* during embryo maturation and germination (Molinas and Verdaguer 1993a, 1993b). In this species, the cotyledonary node, which is buried about 12 cm underground during germination, can be divided into two portions: an upper portion in which the embryonic axis is free between the cotyledonary petioles and bears two or three pairs of dormant buds, and an enlarged lower portion in which the cotyledonary tissues are fused with the embryonic axis and contains three or four pairs of buds. Moreover, starch granules accumulate in the cork oak cotyledonary node giving rise to a lignotuberous structure. The maintenance of a bud stock and starch reserves in underground organs is an advantage in Mediterranean ecosystems (James 1984; Koop 1987), providing new shoots for quick recovery of leaf area after a disturbance. Plant survival after fire was related to below-ground unburnt dormant buds (Auld 1990; Moreno and Oechel 1991). While herbivores commonly feed on tender shoot tissues, seriously endangering dormant buds located above ground (Herrera 1995).

The aim of the present paper is (i) to investigate the sprouting capacity of *Q. humilis*, *Q. ilex* and *Q. suber* at the seedling stage after removal of the aerial biomass above or below the point of attachment of the cotyledons (hereafter, cotyledonary node) and (ii) to estimate sprouting capacity when the above-ground biomass was repeatedly removed.

## Materials and methods

### Plant material

Acorns of *Q. humilis*, *Q. ilex* and *Q. suber* were obtained from trees growing in the province of Girona (north-eastern Spain) in autumn 1996. Acorns were stored in darkness at 4°C until seeding. In January 1997, 130–150 acorns of each species were sown 1 cm deep in 25-cm-deep flowerpots in a mixture of 25% vermiculite and 75% peat. Germinated acorns were allowed to grow for about 2 months before the beginning of the pruning treatments. All experiments were conducted in a greenhouse heated to a minimum temperature of 18°C and cooled to a maximum temperature of 30°C. The irrigation procedure consisted of two waterings per week.

### Experimental treatments

In March 1997, three sets of 30–50 seedlings for each species were selected from seedlings with stems measuring *c.* 10 cm in length. At this stage, the cotyledons had dried and had partially fallen, so we cut them. Each set received one of the following treatments: (i) removal of the aerial biomass above the cotyledonary node (hereafter, AC-treated); (ii) removal of the aerial biomass below the cotyledonary node (hereafter, BC-treated); and (iii) unpruned control.

To study the influence of repeated pruning, the aerial biomass was removed three successive times. The first pruning involved cutting off the stem 2–3 mm above (AC-treated) or below (BC-treated) the cotyledonary node. One month after the first pruning, the number of seedlings sprouted were recorded and the sprouts were removed (second pruning). All the sprouts were cut off at the base to avoid sprouting from leaf axillary buds. After the second pruning, the seedlings were left to grow another month, then measurements were taken of the sprouted seedlings

and the sprouts were removed again (third pruning). The third pruning was conducted in the same way as the second. One month after the third pruning, sprouted seedlings were measured again.

### Measurements

For each set of treated seedlings, a subset of five specimens was harvested for measuring one month after each pruning intervention. A subset of five control seedlings was also measured on about the 30th of each month from February to July 1997, except in April.

On harvested AC- and BC-treated seedlings, the number of sprouts per seedling, the length of the longest sprout, the diameter of the longest sprout at 2 cm from the origin, the number of leaves on the longest sprout and the diameter of the primary root at 2 cm below the cotyledonary node were measured. In control seedlings, the main stem length, the stem diameter at 2 cm above the cotyledonary node, the main stem leaf number and the root diameter at 2 cm below the cotyledonary node were measured. The only variable that could be measured (and thus compared) in both control and treated plants was root diameter obviously because only treated plants sprouted. The control was run mainly to compare survival (in addition to root diameter) of control *v.* treated plants.

### Statistical analysis

Categorical variables (sprouting/not sprouting) were analysed with log-linear models. Log-linear models are the multidimensional generalisation of the chi-square test of independence for two-dimensional contingency tables (Sokal and Rohlf 1995). Measurement variables (length, diameter, number) were analysed with two-way analysis of variance (ANOVA). All factors (treatment, pruning intervention, species) of ANOVA were considered to be fixed effects. Multiple comparison of means was not used because significant interaction was generally present and prevented the meaningful analysis of main effects (Sokal and Rohlf 1995) and because only two groups were generally present in the treatment factor. Size variables (length and diameter) were log-transformed and the numbers were square-root transformed (Sokal and Rohlf 1995) because homoscedasticity and normality assumptions were improved. All sums of squares of ANOVA are type-III. All statistical analyses were computed with the SPSS 7.5 package.

## Results

### The effect of pruning on survival and sprouting

A hierarchical log-linear model showed that the capacity of sprouting was mostly dependent on treatment (partial  $G^2 = 210.5$ , d.f. = 1,  $P < 0.00005$ ) and species (partial  $G^2 = 113.9$ , d.f. = 2,  $P < 0.00005$ ). The three oak species showed a high sprouting capacity (>89 %) in the AC-treatment (Table 1). In contrast, only *Q. suber* seedlings were able to survive in the BC-treatment, while all *Q. ilex* and *Q. humilis* died in a few days.

**Table 1.** Percentage of *Quercus ilex*, *Q. humilis* and *Q. suber* seedlings that sprouted after cutting the shoot above (AC) or below (BC) the attachment point of the cotyledons in the first, second and third pruning intervention

Repeated pruning	<i>Quercus ilex</i>		<i>Q. humilis</i>		<i>Q. suber</i>	
	AC	BC	AC	BC	AC	BC
First pruning	92.5	0	88.9	0	100	75.8
Second pruning	96.9	—	93.0	—	90	95
Third pruning	96.2	—	97.3	—	100	100

The proportion of *Q. suber* seedlings sprouting significantly increased with repeated pruning (partial  $G^2 = 34.0$ , d.f. = 2,  $P < 0.00005$ ).

For *Q. suber*, sprouting capacity was significantly higher for the AC- than for the BC-treatment (Table 1; partial  $G^2 = 4.5$ , d.f. = 1,  $P = 0.034$ ). For the BC-treated seedlings, the proportion sprouting increased with repeated pruning, while it was always high for AC-treated seedlings (sprouting  $\times$  treatment  $\times$  pruning: partial  $G^2 = 4.5$ , d.f. = 1,  $P = 0.034$ ).

#### *The role of the cotyledonary node: treatment effects in the root diameter and Q. suber*

The most important source of variation in root diameter was treatment  $\times$  pruning interaction (Table 2), because root diameter decreased with repeated pruning while it increased in control seedlings for all three species (Fig. 1). The overall effect of AC-treatment was greater in *Q. humilis*. (Table 2, Fig. 1B).

For *Q. suber*, the rest of variables also showed significant interaction (Table 3). The number of sprouts per seedling was 1 or 2 (Fig. 2A), with no significant variation with pruning intervention or treatment (Table 3). However, while in the AC-treatment most seedlings emitted two sprouts at the first intervention, in BC-treatment this was at the second intervention (hence, the significant interaction). Both sprout length and leaf number of the longest sprout were significantly higher in AC- than in BC-treated seedlings (Table 3) but

decreased with the pruning intervention in the former whereas increased in the BC-treatment (Fig. 2B, C). In both AC- and BC-treated seedlings, new shoots measured 1 mm in diameter at 2 cm from the base.

#### *AC-treatment: effects of repeated pruning and differences among Quercus species*

In AC-treated seedlings, there was no significant species  $\times$  pruning interaction for any variable (Table 4), showing that the effects of pruning intervention were similar in the three species. The number of sprouts per seedling significantly decreased with repeated pruning (Table 4, Fig. 3A). After the first pruning most seedlings showed one or two sprouts, but in all three species the number of seedlings with only one sprout increased when pruning was repeated. The sprout length and leaf number of the sprouts also decreased with repeated pruning (Table 4, Fig. 3B) and showed significant differences among species, being much higher in *Q. suber*. In all three oak species, the diameter of the new shoots at 2 cm from the base was c. 1 mm (Table 4, Fig. 3C).

#### Discussion

The results provide evidence that *Q. suber* has a sprouting capacity in relation to its cotyledonary node different from *Q. humilis* and *Q. ilex*. Only *Q. suber* seedlings sprouted when pruned below cotyledons. When the aerial biomass was removed in this species, the lignotuberous structure formed

**Table 2.** ANOVA of the treatment (control, AC and BC) and pruning effects on the root diameter (log-transformed) of the three *Quercus* species

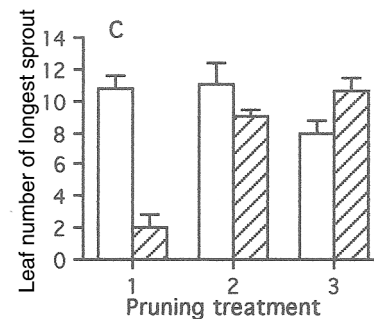
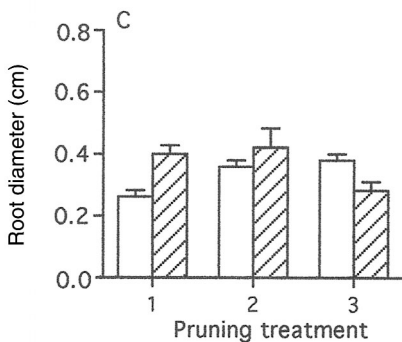
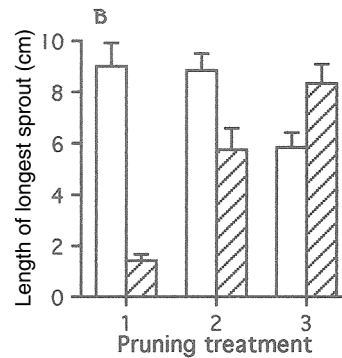
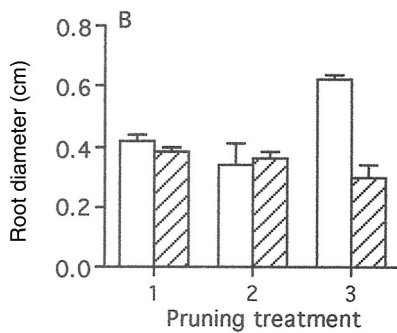
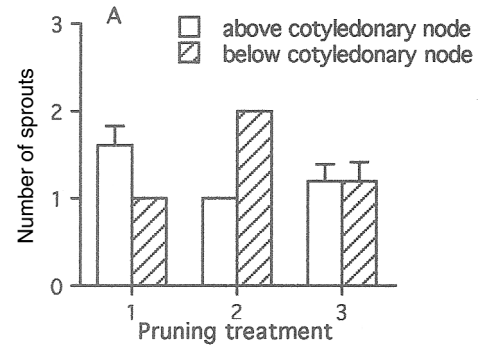
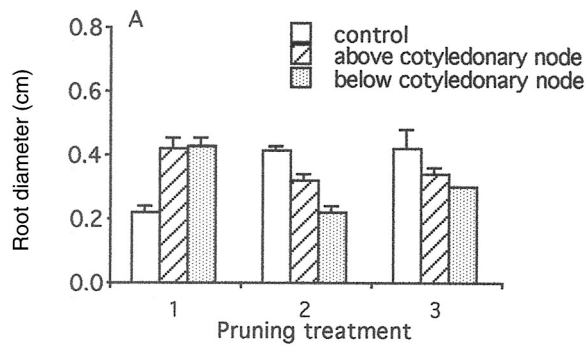
BC treatment was only included for *Q. suber* because all seedlings died in the other species; see Materials and methods for treatment details

Source of variation	<i>Quercus ilex</i>			<i>Q. humilis</i>			<i>Q. suber</i>		
	SS	d.f.	<i>P</i>	SS	d.f.	<i>P</i>	SS	d.f.	<i>P</i>
Treatment	0.007	1	0.47	0.158	1	<0.0005	0.034	2	0.07
Pruning	0.034	2	0.27	0.005	2	0.65	0.025	2	0.14
Treatment $\times$ pruning	0.141	2	0.009	0.099	2	0.001	0.447	4	<0.0005
Error	0.291	24		0.119	22		0.205	35	

**Table 3.** ANOVA of the treatment (AC v. BC) and pruning effects on the number of sprouts and the length and leaf number of the longest sprout in *Quercus suber* seedlings

Length was log-transformed and numbers were square-root transformed; see Materials and methods for treatment details

Source of variation	Sprout number			Sprout length		Leaf number	
	d.f.	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>
Treatment	1	0.020	0.35	0.58	<0.0005	2.16	0.001
Pruning	2	0.052	0.33	0.55	<0.0005	3.81	<0.0005
Treatment $\times$ pruning	2	0.522	<0.0005	1.09	<0.0005	7.29	<0.0005
Error	21	0.463		0.32		3.01	



**Fig. 1.** (A) Effect of removal of the aerial biomass above and below the cotyledonary node on mean root diameter in *Quercus suber*. (B, C) Effect of removal of the aerial biomass above the cotyledonary node on mean root diameter in (B) *Q. humilis* and (C) *Q. ilex*. Values shown are means + s.e.;  $n = 5$ , except for the first pruning in BC-treated *Q. suber* ( $n = 4$ ) and the third pruning in AC-treated *Q. humilis* ( $n = 3$ ).

**Fig. 2.** Effect of removal of the aerial biomass above and below the cotyledonary node on mean number of sprouts per seedling, longest sprout length and longest sprout leaf number in *Quercus suber*. Values shown are means + s.e.;  $n = 5$  except for the first and second pruning in BC-treated *Q. suber* ( $n = 4$ ).

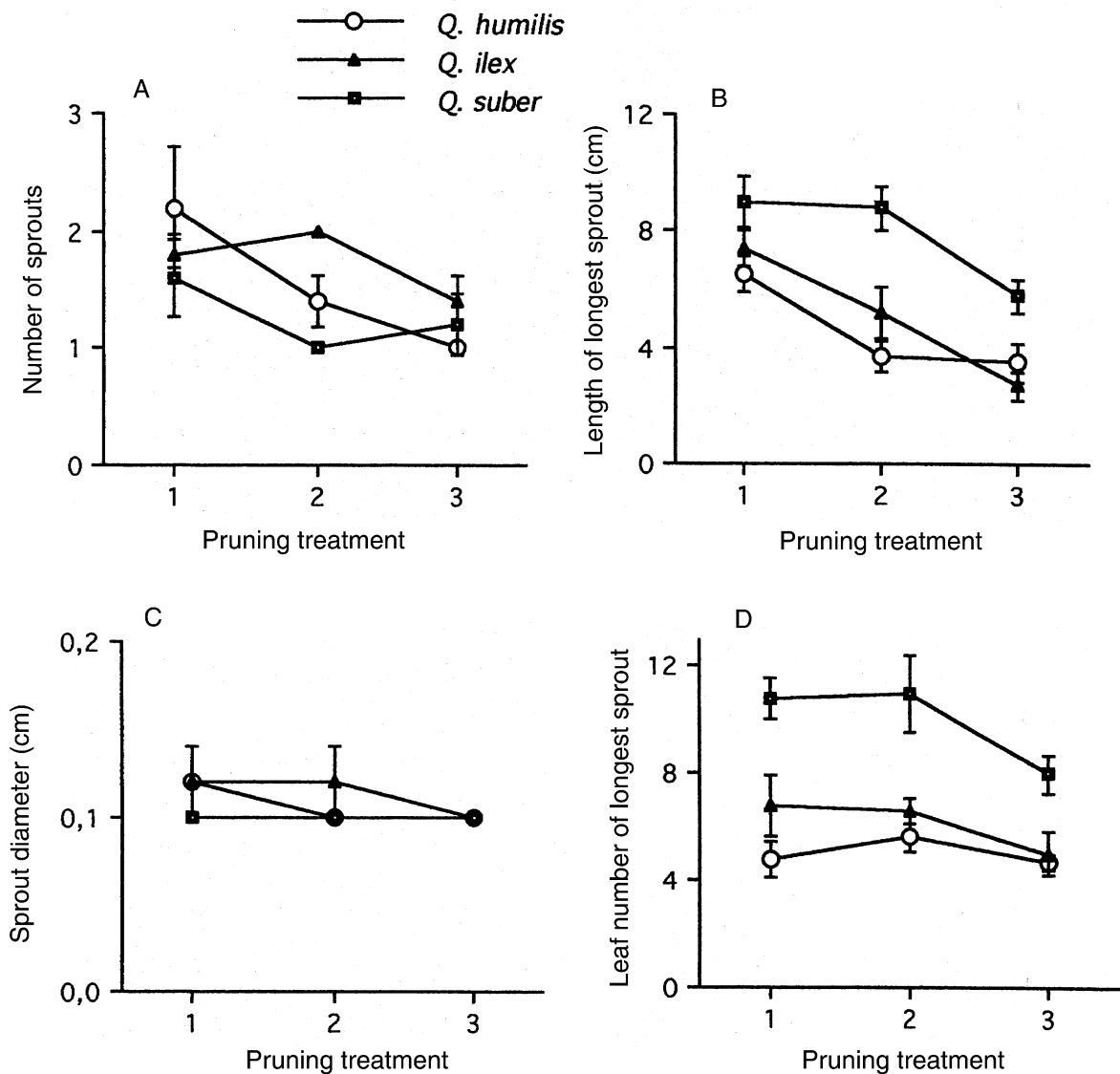
during germination and early seedling growth (Molinas and Verdaguer 1993b), remained undisturbed and the stock of dormant underground buds supported the development of new shoots. This shows that the lignotuber is a functional

structure at the seedling stage. The presence of clusters of underground hidden accessory buds is probably limited to *Q. suber*. Observations of acorns and seedlings of *Q. humilis* and *Q. ilex* did not show the presence of underground dormant

**Table 4.** ANOVA of the species and pruning effects on the number of sprouts and the length, diameter and leaf number of the longest sprout in AC-treated seedlings

Length and diameter were log-transformed and numbers were square-root transformed; see Methods for treatment details

Source of variation	Sprout number			Sprout length		Sprout diameter		Leaf number	
	d.f.	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>
Species	2	0.25	0.098	0.55	<0.0005	0.070	0.025	5.44	<0.0005
Pruning	2	0.41	0.027	0.65	<0.0005	0.044	0.09	0.96	0.006
Pruning × species	4	0.30	0.23	0.16	0.12	0.008	0.91	0.33	0.41
Error	33	1.67		0.66		0.280		2.68	

**Fig. 3.** Effect of repeated pruning of aerial biomass above the cotyledonary node on mean number of sprouts per seedling and sprout diameter, length and number of leaves on longest sprout in *Quercus humilis*, *Q. ilex* and *Q. suber*. Values shown are means  $\pm$  s.e.; sample sizes as in Fig. 2.

buds or any structure equivalent to the lignotuber of *Q. suber*, while some buds were seen in the upper axillary position. A detailed histological study of the cotyledonary region would be required to determine the presence of dormant buds in the hypogeous tissues of *Q. humilis* and *Q. ilex*.

*Quercus suber* is a species that has evolved certain morphological and physiological strategies that favour its growth in the Mediterranean basin (Verdaguer and Molinas 1999). For example, Zeller (1957) described that in the forest of Catalonia (Iberian peninsula), *Q. suber* was the dominant species (43 000 ha), even though in natural conditions it competed closely with *Q. ilex*. He attributed the dominance of *Q. suber* to cultural procedures aimed at improving cork production, as well as morphological characteristics of the species such as the presence of a thick and insulating bark protecting the stem buds and permitting the trees to recover after fire. The high capacity of young *Q. suber* seedlings to sprout even when the cotyledonary node is removed could also be an important factor to explain its distribution. It would be interesting to analyse the possible ecological advantages of this characteristic for seedling establishment in field conditions in which intense grazing and fire are common. In some Australian genera, such as *Banksia*, that include fire-killed and resprouting species, a more widespread presence of the resprouters than the seeders has been described, and this has been related with a greater environmental tolerance of resprouter species (Lamont and Markey 1995). Moreover, in *Eucalyptus gummifera* (Mullette 1978) the presence of lignotuber is considered an advantage for the species, the aerial part of which is commonly exposed to damage from different environmental factors, such as fire.

In *Q. suber* seedlings, the shorter shoot length after first pruning in BC-treated seedlings than in AC-treated seedlings seems to be related to the deeper position of the buds. The deeper in the soil the bud to be activated is, the greater the post-emergence hazards and the later its appearance at the surface (Noble 1985). Likely, the sprouts of *Q. suber* seedlings pruned below cotyledons required more time to reach the same length as the sprouts of AC-treated seedlings. However, the degree of maturation of the buds should also be considered. In the formation of the lignotuber in the *Q. suber*, buds follow a basipetal ontogenetic sequence. Buds located in the upper portion, above the point of attachment of the cotyledons, form a short stalk and laminar scales. Buds in the lower portion, hidden by fused cotyledonary tissue, multiply to form bud clusters and remain less developed (Molinas and Verdaguer 1993b). The increase in the shoot length in the second and third pruning in the BC-treated seedlings could be related to a positive influence of the first pruning over the resting buds that would qualify them to sprout quickly after disturbance.

The seedlings of all three *Quercus* species sprouted from cotyledonary axillary buds when repeatedly pruned above the point of attachment of cotyledons. The repeated pruning

done in our experiment, which could simulate herbivory, positively influenced the capacity of plants to sprout. It is likely that the more the tree sprouts at the first pruning the better it responds to subsequent prunings. The high resilience of the sprouting *Quercus* species to successive disturbances is significant in maintaining the species composition of the plant communities and determining the type of plant succession after perturbations (Noble and Slatyer 1977). However, the results obtained for *Quercus* species contrast with findings for other Mediterranean ecosystem species, such as the *Erica multiflora* L. shrub (Vilà and Terradas 1995) for which repeated pruning has a severe effect, with two prunings causing 80% plant mortality. The resilience of Mediterranean species to successive disturbances and their significance in the succession of plants deserve further study.

In the *Quercus* species studied, the percentage of plants sprouting increased with repeated pruning. However, a negative effect of repeated pruning was observed in the number of sprouts per seedling, the length of the sprouts and the thickness of the root. The sprouting potential of a species has been related to bud presence and starch reserves in what remains of the plant (Bell and Pate 1996). Since at the time the experiment finished, the dormant buds in all three *Quercus* species were still in an axillary position at the attachment point of the cotyledons, the negative effects of repeated pruning seemed more closely related to the depletion of starch in the root stock than to the exhaustion of bud. The *Q. suber* seedlings presented the most vigorous sprouts and the highest number of sprouts, probably because of the presence, at the seedling stage, of the lignotuber with reserve substances accumulated to support the emission of new shoots. A comparative study of the starch quantity at the cotyledonary region and root stock of the seedlings could help in understanding the behavioural differences between species.

Very few sprouts occurred after pruning, one or two in the seedling of all three *Quercus* species. Developing new shoots prevents the activation of more buds. This behaviour is associated with a rather general pattern of growth of woody species; shrubs show basitony and tree species in which terminal buds are dominant show acrotony (Mesléard and Lepart 1989).

The establishment of nursery-grown seedling is one of the most important factors in successful reforestation. Growth and survival of out-planted seedlings are affected by nursery practices, including the planting procedures (Kozłowski and Pallardy 1997). Normal planting practices with oak seedlings consist of sowing the acorns superficially or burying them *c.* 6 cm deep in the soil, depending on the season (Catalán 1977). The results obtained from the *Quercus* species in this study show that maintaining the cotyledonary node undamaged is crucial for plant survival. Therefore, we recommend that acorns should always be buried in the soil and that the effect on germination of sowing acorns deeper than 6 cm in

order to increase the protection and insulating effect of the soil should be tested. Acorn predation would decrease, whereas germination would increase. Germination would probably be improved because the fluctuations in soil temperature are less pronounced deeper in the soil and also as the soil temperature rises water availability increases (Larcher 1995). Flinn and Wein (1977) found evidence to relate the depth of underground organs implied in the sprouting capacity of some species growing in fire-prone ecosystems and their survival rate. They report that plants surviving severe fires have organs capable of vegetative reproduction at c. 25 cm below the surface. Therefore, we recommend that the cotyledonary node of nursery seedlings planted in the forest should be buried because the deeper this part of the plants is located in the soil, the better it will be protected.

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