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Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs

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Summary

1. We investigated whether reserves stored in the lignotubers of two Mediterranean shrubs, *Arbutus unedo* and *Erica arborea*, were significantly mobilized to support the demands of regrowth and respiration after clipping the tops at different frequencies.
2. After a single clipping, *Arbutus* showed a 29% decrease of phosphorus concentration by the end of the first growing season. Two years after recovery from clipping, the starch levels remained lower than those of unclipped plants. Similarly, *Erica* showed depletion of starch, but no nutrient reserves were depleted significantly.
3. Regrowth after multiple clippings mobilized a large fraction of the starch and nutrients stored in the lignotuber. Mean starch concentrations were depleted by 87–93% after multiple clippings and concentrations of nitrogen, phosphorus, potassium and magnesium were depleted by 10–45%, 27–41%, 19–39% and 23–31%, respectively.
4. An average-sized lignotuber produced 288 resprouts for *Arbutus* and 1990 resprouts for *Erica* during a 27 month period of multiple clippings, at the end of which the first plants died.
5. Plant mortality after multiple clipping was 10% for *Arbutus* and 30% for *Erica*, and was primarily attributed to exhaustion of carbon reserves because starch concentrations decreased by 96% in dead plants.

Key-words: Arbutus unedo, burl, disturbance, *Erica arborea*, mineral and carbon resources, mobilization, resprouting

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Introduction

A wide range of woody plants have swelling structures at the stem base, called lignotubers or burls (James 1984; Canadell & Zedler 1995). These can account for up to 80% of the below-ground biomass and 40% of the total plant biomass (Canadell & Rodà 1991; Hilbert & Canadell 1995). Such a major carbon investment in this particular structure is common for, although not restricted to, Mediterranean trees and shrubs with the ability to resprout vigorously after fire or clipping (Kummerow 1981; Canadell, Lloret & López-Soria 1991). Lignotubers are viewed as important storage organs for carbohydrates and nutrients which may play a critical role in the recovery process after disturbances (Mullete & Bamber 1978; DeSouza, Silka & Davis 1986). However, the function of lignotubers as resource storage structures has always been inferred indirectly from studies on plant growth (DeSouza *et al.* 1986; Castell, Terradas & Tenhunen 1994), anatomical structure (Montenegro, Avila & Schatte 1983) or tissue analysis of lignotuber nutrient and carbohydrate contents (Mullete & Bamber 1978; Lopez 1983; Dell, Jones & Wallace 1985). To date, however, direct quantitative observations have not been reported on the use of lignotuber reserves to support regrowth after disturbances.

It is generally believed that stored carbohydrates (mainly starch and soluble sugars) are the most important source of carbon supporting new growth after a disturbance (Ericsson, Larsson & Tenow 1980; Menke & Trlica 1983; Kays & Canham 1991; Miller & Rose 1992). This view has been questioned because studies in grasses and trees have shown no relationship between the initial amount of reserves and the vigour of sprouting (Jones & Laude 1960; Radosevich & Conard 1980; Tromp 1983; Richards & Caldwell 1985; Sparks 1989). In addition, some studies have found that substantial carbohydrate concentrations remain in dead plants killed by sequential experimental clippings (Cremer 1973; George & McKell 1978), suggesting that the depletion of carbon reserves is not the cause of plant death. One interpretation of a plant's failure to use all carbohydrate reserves following disturbances is that depletion of nutrients, such as

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nitrogen and phosphorus, may be more limiting to plant regrowth than are low carbon reserves (Chapin, Schulze & Mooney 1990). The lack of agreement about mobilization of stored reserves may be because species vary in the mobilization efficiency of stored resources from different organs or plant tissues.

Lignotubers have also been described as a source of new meristems, that is, they could serve as a bud bank (Zammit 1988; Mesleard & Lepart 1989; Malanson & Trabaud 1987; Moreno & Oechel 1991) or regenosphere (Mooney & Hobbs 1986).

In the present study, we hypothesize that plant regrowth after disturbances relies on resources stored in the lignotuber. We have tested this hypothesis by answering the following specific questions: (1) do plants mobilize starch and nutrients stored in lignotuber during regrowth events?; (2) if some resources in the lignotuber are depleted after disturbance, how quickly are they replenished?; (3) does depletion of lignotuber reserves explain plant mortality after disturbances? We also measured the size of the lignotuber bud bank.

In our study we considered two disturbance scenarios: 'single disturbances' (one-time disturbance events such as fire) and 'multiple disturbances' (multiple-disturbance events such as fire at high frequency or fire followed by recurrent grazing). These two situations add an ecological dimension which is often overlooked in studies of reserve mobilization in plants.

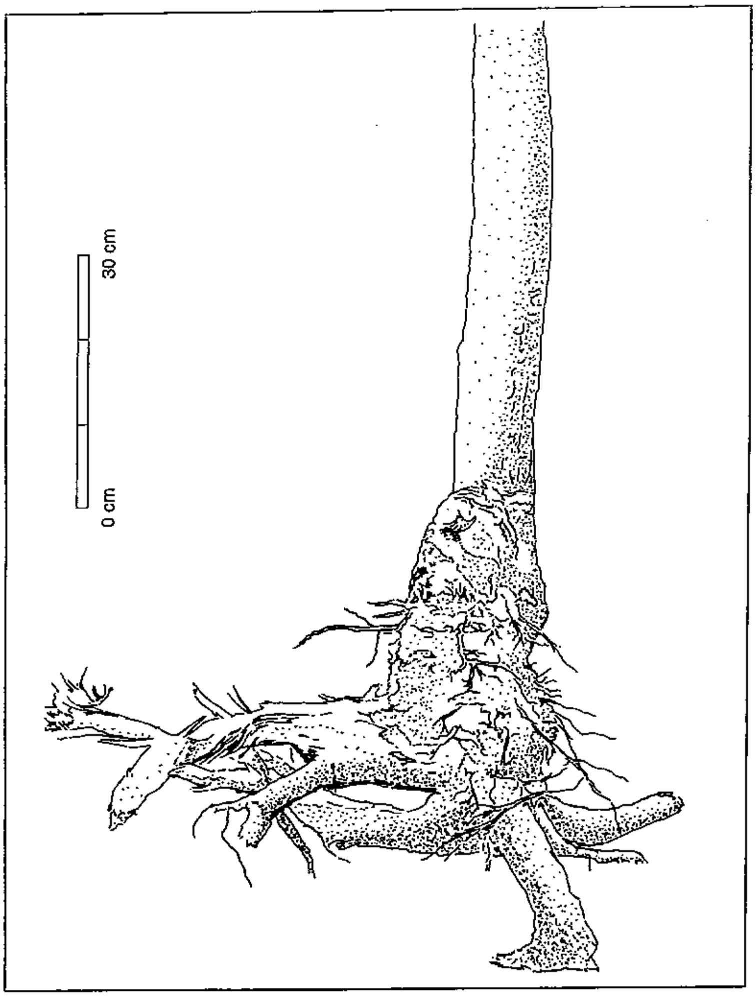

Fig. 1. Stem, lignotuber and roots of an *Arbutus unedo* plant (>35 years) whose above-ground part had not been damaged by disturbances.

Materials and methods

SPECIES CHARACTERISTICS AND STUDY SITE

Erica arborea L. and *Arbutus unedo* L. are long-lived shrub species dominant in the Western Mediterranean Basin. Both species have lignotubers (Figs 1 and 2), and in the area studied they resprout strongly after fires (Canadell *et al.* 1991). The lignotuber becomes differentiated at an early stage of development even in the absence of disturbances. However, plants subjected to several cycles of above-ground destruction and regrowth develop the largest lignotubers. In our plots, lignotubers of *Arbutus* have a mean projected area of 423 cm^2 (range: 41–3068 cm^2) and those of *Erica* have a mean projected area of 284 cm^2 (range: 39–1304 cm^2). On land that is undisturbed for a long time (>50 years), *Erica* and *Arbutus* can form a dense maquis 7–8 m tall. Although both species occur together, *Arbutus* is more common in late successional stages of the *Quercus ilex* dominated forest. On the contrary, *Erica* is more abundant in open and disturbed sites of earlier successional stages.

We conducted two field experiments in El Corredor, Serra de Marina (42° 05'N, 2° 50'E), in north-eastern Spain (1987 and 1989). Two areas were selected, one situated on a 15° south-facing slope, at 630 m a.s.l. (first experiment), and the other area on 4° east-facing slope at 460 m a.s.l. (second experiment). The stands sampled occurred on acid brown soils with sandy texture developed from granite bedrock. Soils were well developed (≥1 m deep) but with low organic matter, nitrogen and phosphorus contents (Canadell & Vilà 1992). Mean annual precipitation in Vallgorguina (199 m a.s.l.), near the experimental areas, is 806 mm. Precipitation was 844 mm for 1988 and 618 mm for 1989.

The vegetation consisted of homogeneous and dense maquis stands about 3·5 m tall dominated by *Arbutus* and *Erica* with a sparse tree layer of *Pinus pinea* and *Quercus suber*. The area had not been disturbed during the previous 30 years. Shoot clipping was used to simulate the effects of agents causing disturbances in natural habitats.

EXPERIMENTAL DESIGN

First experiment

A first experiment was conducted to study changes in lignotuber reserve concentrations during the 2 years following clipping once (single-disturbance treatment) or up to four times (multiple-disturbance treatment).

Shoot growth occurred in both spring and late-summer/autumn (two growing seasons per year).

In the single disturbance treatment, plants were clipped once in April 1988 and allowed to regrow and accumulate reserves during the next four growing seasons (two calendar years). In the multiple disturbance treatment, plants were clipped up to four times to force continual depletion of lignotuber reserves. Each clipping was applied at the end of each growing season (spring or fall) over a period of two calendar years. A third, control treatment consisted of unclipped plants.

The experiment had a randomized complete block design with 24 plots of 6 m in diameter (two blocks × three clipping treatments × four sampling dates). Treatments were randomly assigned to plots within a block, and from each plot five plants of both *Arbutus* and *Erica* were randomly selected. At each clipping date (April 1988, July 1988, October 1988 and July 1989), 10 plants per species/treatment were clipped 5 cm above the lignotuber and samples from the lignotuber were taken for chemical analyses in July 1988, October 1988, July 1989 and December 1989. No plant was sampled for chemical analyses more than once.

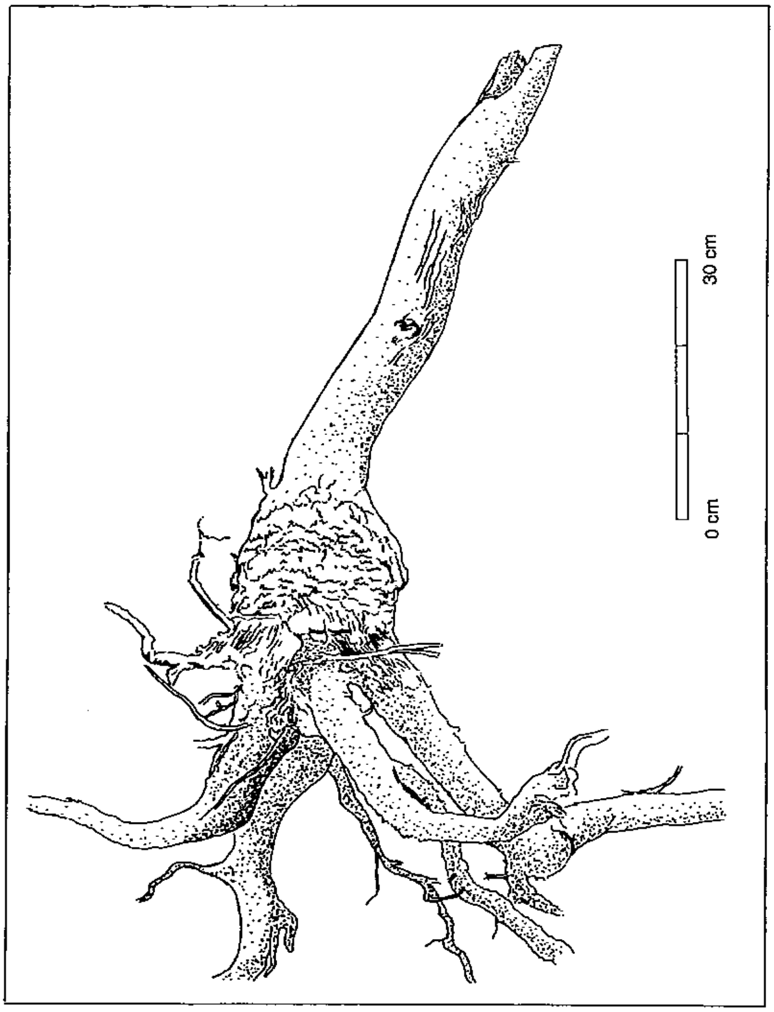

Fig. 2. Stem, lignotuber and roots of an *Erica arborea* plant (>35 years) whose above-ground part had not been damaged by disturbances.

Second experiment

A second experiment was carried out to accelerate reserve depletion to identify whether depletion of lignotuber resources was correlated with plant mortality. This was achieved by clipping the shoots several times until they no longer resprouted.

The experiment had a completely randomized design from which 30 plants of *Arbutus* and *Erica* were selected. Half the plants were randomly selected and clipped every 2 months during growing periods (spring and autumn). The remaining half of the plants were left unclipped and served as controls. Clipping began in autumn 1987 and continued until the first plants no longer resprouted. This occurred 27 months later (December 1989), after the plants had been clipped eight times. The number of resprouts was counted in five of the eight harvests in the second experiment.

SAMPLING AND CHEMICAL ANALYSES

After harvesting the shoots on each sampling date in both experiments, the plants were excavated by digging around their lignotuber to a depth of 30 cm, the area was measured and 1 cm thick external samples of the lignotuber were taken. A composite sample of each plant was obtained by combining six separate samples taken from around the perimeter of the lignotuber. Samples were transported in a cooler and oven-dried at 100 °C for 1 hour and then at 70 °C until constant weight. Decomposing tissue, if present, was cut from the samples, bark and soil particles were removed by vigorous brushing and the tissue was then ground to powder.

The starch was extracted with water followed by perchloric acid and was measured colorimetrically after forming a blue complex with iodine (Allen 1989). Nitrogen was determined by the Kjeldahl method in a Kjeltec Auto 1030 Analyzer. To analyse for phosphorus, potassium, magnesium and calcium, plant samples were subjected to conventional wet digestion in a 2:5 mixture of perchloric and nitric acids. Phosphorus was complexed with vanadomolybdate and read colorimetrically at 420 nm with a spectrophotometer. Potassium, magnesium and calcium were determined by atomic absorption spectrophotometry (Philips-PV9200).

In the first experiment, because of unfortunate damage to some control plants, only data on control treatments for the first and last sampling dates are reported (July 1988 and December 1989). Conclusions are drawn accordingly based on treatment comparisons of those dates.

STATISTICAL ANALYSES

Data were analysed statistically using the general linear model procedure of SuperAnova (Abacus

Concepts 1989); the data were log-transformed when they did not have a normal distribution. Two-way ANOVA followed by a Dunnett's pairwise test were used to study differences between single and multiple clippings, and their corresponding controls in June 1987 and Decemer 1989. Because Block was not significant in any of the ANOVAs performed, Block was removed as a main factor in the analyses following Sokal & Rohlf (1995), and the data were re-analysed with a one-way ANOVA treating the individual plants and independent units.

Results

RESOURCE CHANGES AFTER SINGLE CLIPPING

For both species, starch concentration in lignotubers of clipped plants after one regrowth event tended to be depleted, although not significantly (Figs 3 and 4). Particularly for *Erica*, starch concentration in lignotubers of clipped plants was 19% lower than the unclipped plants. After the first growing season, the starch concentration of clipped treatments dropped and was still significantly lower than that of control plants four growing seasons after clipping (December 1989; see Figs 3 and 4).

Concentrations of all nutrients in the lignotuber, except for phosphorus, were also somewhat depleted, although not statistically different from the controls by the end of the first growing season. Phosphorus concentration in *Arbutus*, however, was significantly lower than that of control plants by 29% ($P<0.001$), showing it to be the most depletion-sensitive resource of all. Lignotuber nutrient concentrations of clipped plants were not different from those of control plants 2 years after a single clipping.

RESOURCE CHANGES AFTER MULTIPLE CLIPPING

Regrowth after multiple clippings mobilized a large fraction of starch accumulated in the lignotuber. In the

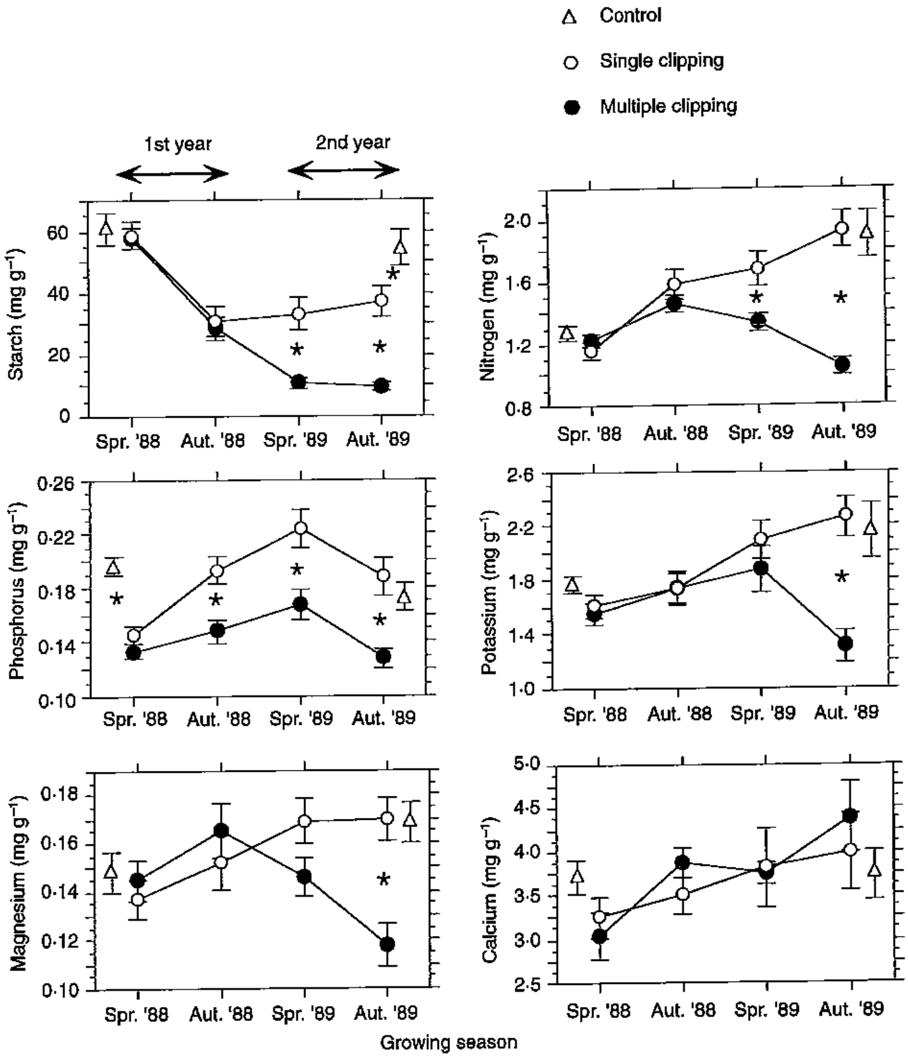

Fig. 3. Lignotuber concentrations (mg g^{-1}) of starch and nutrients (first experiment) of single (open circles) and multiple (solid circles) clippings for *Arbutus unedo* at the end of the first (spring 1988), second (autumn 1988), third (spring 1989), and fourth (autumn 1989) growing seasons after the first clipping (±SE). Control treatments (open triangle) are shown for the first and fourth growing season. *$P<0.05$.

first experiment, where plants were clipped once per growing season, starch concentrations decreased by 83% for both species ($P < 0{\cdot}001$) (Figs 3 and 4). Plants subjected to higher clipping freqency (2 month intervals, second experiment), exhibited lignotuber starch concentrations that were only 7–13% of controls (Table 1).

Arbutus and *Erica* regrowth after multiple clipping also relied on nutrients stored in the lignotuber. In *Arbutus* (first experiment), N, P, K and Mg decreased by 45%, 27%, 39% and 31%, respectively following multiple clipping ($P < 0{\cdot}01$), but Ca increased by 20% ($P = 0{\cdot}18$) compared to control plants in autumn 1989 (Fig. 3). In *Erica*, N, P, K and Mg decreased by 16%, 19%, 19% and 23%, respectively; Ca was unaffected (Fig. 4). In the 2 month clipping-interval experiment, N and P were the nutrients most sensitive to depletion for *Arbutus*, showing a decrease of 35% and 30%, respectively. Calcium tended to increase, although the differences were not statistically significant ($P = 0{\cdot}12$). For *Erica*, unlike *Arbutus*, N concentration was much less sensitive to clipping (9·7% decrease) and, instead, phosphorus was the nutrient most sensitive to depletion by 41% compared to control plants.

BUD-BANK SIZE AND PLANT MORTALITY AFTER MULTIPLE CLIPPINGS

For those plants clipped at 2 month intervals (second experiment), both species showed a high capacity to resprout after each one of the eight clippings. In both species, bud activation and subsequent resprout development decreased in a linear fashion with an increase in number of clippings (Fig. 5). Over time, *Erica* produced 10 times more resprouts than *Arbutus* (data not shown). Based on regression analyses (*Arbutus*: $Y = 73{\cdot}7 - 8{\cdot}4X$, $r^2 = 0{\cdot}44$, $P = 0{\cdot}0001$; *Erica*: $Y = 529{\cdot}3 - 62{\cdot}3X$, $r^2 = 0{\cdot}62$, $P = 0{\cdot}0001$; where Y is number of

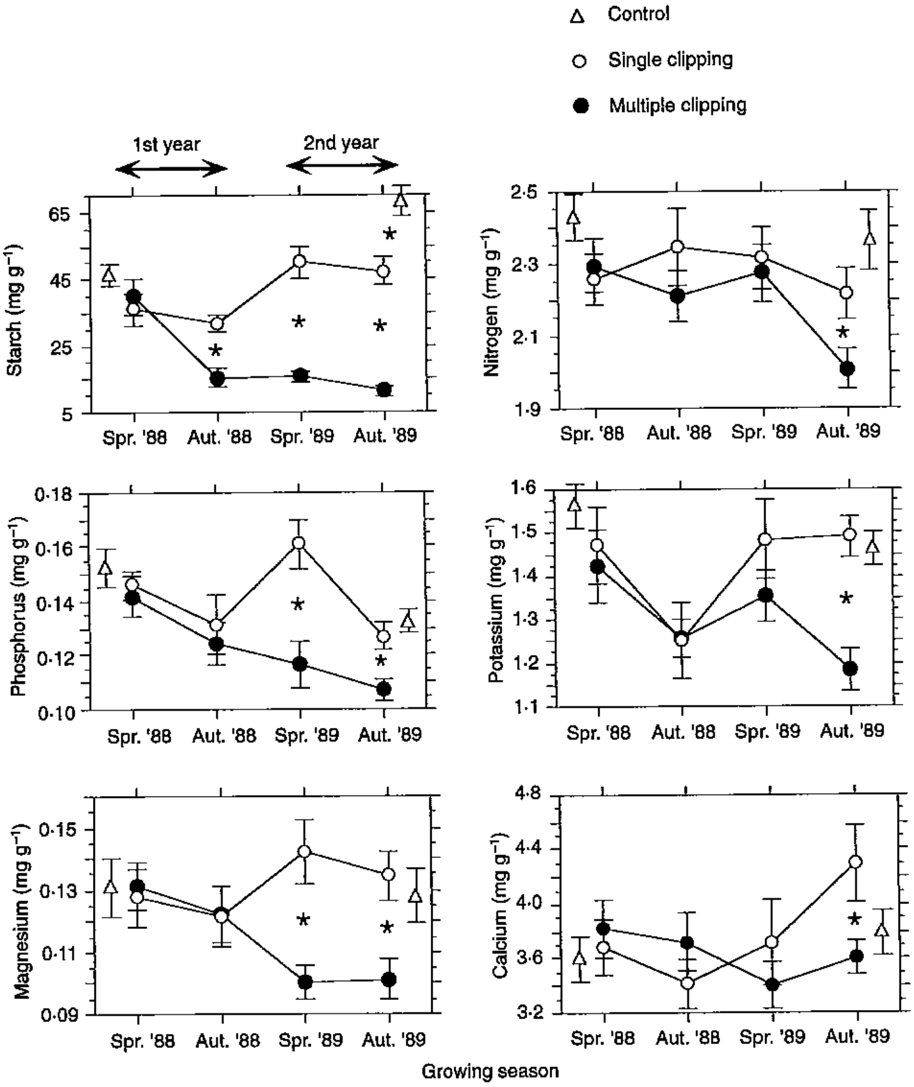

Fig. 4. Lignotuber concentrations (mg g^{-1}) of starch and nutrients (first experiment) of single (open circles) and multiple (solid circles) clippings for *Erica arborea* at the end of the first (spring 1988), second (autumn 1988), third (spring 1989), and fourth (autumn 1989) growing seasons after the first clipping (±SE). Control treatments (open triangle) are shown for the first and fourth growing season. * $P < 0{\cdot}05$.

Table 1. Lignotuber concentrations of starch and nutrients of unclipped plants (control) and plants after eight sequential clippings (second experiment). Mean value (mg g^{-1}) ± SE

	Arbutus unedo			*Erica arborea*		
	Control	Clipped	*P*	Control	Clipped	*P*
Starch	81·7 ± 8·3	10·2 ± 1·6	**	98·1 ± 10·2	7·2 ± 0·9	**
Nitrogen	1·64 ± 0·06	1·07 ± 0·05	**	1·96 ± 0·05	1·77 ± 0·04	*
Phosphorus	0·356 ± 0·020	0·247 ± 0·026	*	0·211 ± 0·007	0·125 ± 0·01	**
Potassium	1·92 ± 0·08	1·41 ± 0·09	**	1·19 ± 0·05	0·89 ± 0·09	*
Magnesium	0·166 ± 0·013	0·156 ± 0·016		0·140 ± 0·010	0·114 ± 0·008	
Calcium	3·41 ± 0·32	4·11 ± 0·30		2·39 ± 0·11	2·71 ± 0·26	

Significant levels: * $P < 0.01$, ** $P < 0.001$.

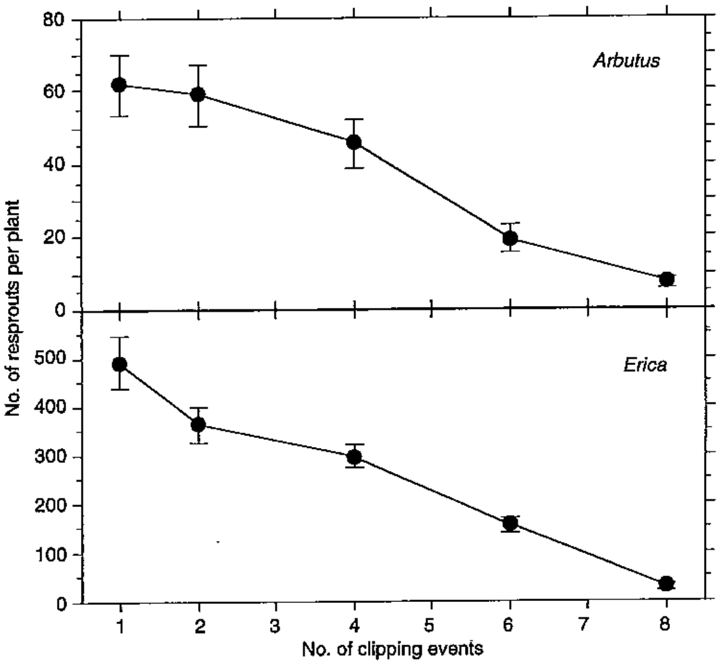

Fig. 5. Number of resprouts for *Arbutus unedo* and *Erica arborea* plants during an eight sequential clipping treatment applied over a 27 month period (second experiment). Mean value ± SE.

resprouts and *X* is number of clippings) we estimated that the number of resprouts produced by an average lignotuber size (A: 423 cm^2; E: 284 cm^2) in eight regrowing events over a 27 month period was 288 for *Arbutus* and 1990 for *Erica*.

Mortality during the eight sequential clippings was 10% in *Arbutus* and 30% in *Erica*; productivity of plants still alive was extremely low by the end of the experiment. For both species, the starch concentration in dead plants was depleted by 96% with a residual concentration of 5 ± 3 mg g^{-1}.

Discussion

Under single disturbances, reserves from the lignotuber were only slightly depleted during the first growing season, but starch concentrations subsequently dropped and were lower than unclipped plants 2 years after clipping. Therefore, recurrent disturbances at frequencies higher than a 2 year interval will diminish a plant's ablity to recover, mainly owing to low availability of carbon reserves. Under multiple disturbances, starch was heavily depleted, which shows that carbon reserves were mobilized and used in the processes of regrowth. However, the contribution of these reserves to regrowth *vs* that from current photosynthesis, could not be assessed in this work. The capacity to mobilize repeatedly reserves can be important to cope with multiple disturbance events, such as fire followed by intense grazing.

Our results also suggest that in addition to the carbon supply, nutrients can potentially limit regrowth following above-ground damage. Phosphorus for *Arbutus* was depleted by 29% and most of the other lignotuber nutrient concentrations exhibited slight depletion by the end of the first growing season after a single clipping. Phosphorus is a rather immobile nutrient in the soil (Yeo & Flowers 1994) so it is expected to be readily depleted when it is suddenly required for regrowth following disturbances. This can be especially critical in soils with low P contents, like those derived from granite and granodiorite in north-east Spain where our study was located (Canadell & Vilà 1992). Hence, we concur with Chapin *et al.* (1990) that factors other than the carbon source possibly limit the resprout process.

The relative importance of the depletion of nutrient reserves *vs* starch reserves is strongly influenced by the type of chemical analyses performed in our study. The starch analysis is a measure of storage carbon, and therefore available carbon, whereas we analysed the total content of nitrogen, phosphorus, potassium, magnesium and calcium which includes both available and structural forms. Therefore, the measures of starch depletion were much more representative of storage pools and, thus, they were more sensitive to depletion than those of nutrients. This reinforces the critical role that some nutrients stored in the lignotuber may have in the regrowth process. Some studies present evidence that mineral nutrients are potentially regrowth limiting after disturbances. Thus, Miyanishi & Kellman (1986) found that 1 year after fire, root phosphorous concentration was depressed in *Banksia* *oblongifolia*, a savannah shrub species, growing on soils with low phosphorus content. Other authors have reported foliar analyses of resprouts showing evidence of possible mineral deficiencies. For instance, DeSouza *et al.* (1986) suggested that some mineral nutrients other than nitrogen may become limiting to plant regrowth, as shown by chlorotic leaves found one growing season after a fire. Rundel & Parsons (1980) found foliar magnesium concentrations depressed in post-fire resprouts of *Adenostoma fasciculatum* and *Ceanothus leucodermis.*

Multiple-disturbance scenarios bring an important ecological consideration to understanding the evolutionary origin of the lignotuber whose acquisition is thought to be mediated by disturbances as a selective pressure. Multiple disturbances are particularly significant in fire-prone ecosystems (Zedler, Gautier & McMaster 1983; Christensen 1985) and in environments where fire events are followed by herbivory on the highly palatable new resprouts (Davis 1967; Wimbush & Forrester 1988; Thomas & Davis 1989; Moreno & Oechel 1991). In our study, all lignotuber resources (starch and nutrients) were heavily depleted after multiple clippings. This shows, indeed, the critical importance of lignotuber reserves in sustaining continuous resprouting in environments with high frequency disturbances and suggests that multiple-disturbance scenarios may have been important in the formation and selection of the lignotubers in the past.

Failure to resprout after disturbances is commonly associated with meristematic tissue damage, bud-bank size, tolerance to drought in post-disturbance conditions and availability of below-ground reserves (Noble 1984; Miyanishi & Kellman 1986; Canadell *et al.* 1991; López-Soria & Castell 1992; Mazzoleni & Esposito 1993). In our study, very low starch levels in the lignotuber (5 $\mathrm{mg\,g^{-1}}$, 4% of that of unclipped plants) probably caused plant mortality when plants were subjected to multiple clippings. The interpretation of this result is that low production of current photosynthate is not enough to support new tissue growth as well as keep up with the root respiratory demands of an extensive root system. Because growth of new meristematic tissue did occur during the 27 month period of multiple disturbances, mortality probably did not result from bud primordia limitation (Zammit 1988).

We conclude that the lignotubers of *Arbutus* and *Erica* have a dual function. The first, which is morphological related, is to store concealed buds that will resprout after disturbances. The lignotuber provides a very large bud store that enables plants to regrow repeatedly in environments subjected to multiple disturbances. The second function is to store non-structural carbohydrates and nutrients which will support regrowth after disturbances. The pools of lignotuber resources seem to be large enough to sustain regrowth in environments where multiple-disturbance events occur and before the most limiting resources may cause plant mortality. However, sustained high frequencies of disturbances (< 2 years) may lead to plant death. Our study indicates that complete depletion of starch reserves is probably one of the causes of plant mortality.

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