

Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*

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Abstract: It is generally assumed that belowground starch reserves are consumed partially and gradually after successive resprouting events in resprouter woody plants. We have explored the aboveground (biomass) and belowground (root starch) response of three species of *Erica*, *Erica australis* L., *Erica scoparia* L., and *Erica arborea* L., after different histories of disturbance intensity to test the existence of a gradual decrease in (i) the final biomass of the aboveground regrowth and (ii) the relative amount of root starch across increasing levels of disturbance frequency. Increasing clipping frequency produced a progressive reduction in the final regrowth in the three species. By contrast, root starch levels dropped markedly in plants of all clipping treatments when compared with root starch of unclipped plants, but significant differences were not detected among clipping frequencies. This pattern was consistent across the three species of *Erica*. This study highlights a crucial role of belowground (root) starch reserves for postdisturbance regrowth in resprouter species of *Erica*. It also shows a consistent pattern of rapid, not conservative, consumption of starch reserves after the complete removal of the aboveground part, nearly irrespective of the previous history of disturbance frequency.

Key words: belowground reserves, *Erica arborea*, *Erica australis*, *Erica scoparia*, postdisturbance regrowth, postdisturbance starch mobilization.

Résumé : On assume généralement que les réserves d'amidon hypogées sont partiellement et graduellement consommées après des événements successifs de rejets chez les espèces ligneuses drageonnantes. Les auteurs ont exploré la réaction épigée (biomasse) et hypogée (amidon racinaire) chez trois espèces d'*Erica*, *Erica australis* L., *Erica scoparia* L. et *E. arborea* L., après différents historiques d'intensités de perturbation, afin de vérifier l'existence d'une diminution graduelle (i) de la biomasse finale du rejet épigé et (ii) de la quantité relative d'amidon racinaire, avec une augmentation graduelle de la fréquences des perturbations. Une augmentation de la fréquence des coupes entraîne une réduction progressive de la repousse finale chez les trois espèces. Au contraire, les teneurs en amidon racinaire des plantes non coupées chutent nettement chez les plantes ayant subi tous les traitements de coupe, comparativement à l'amidon racinaire des plantes non coupées, mais on n'observe pas de différences significatives entre les fréquences de coupe. Ce patron se retrouve chez les trois espèces d'*Erica*. Cette étude met en lumière un rôle crucial des réserves d'amidon racinaire pour le rejet post-perturbation des tiges chez les espèces drageonnantes d'*Erica*. Elle montre également un patron congru de consommation rapide, non conservateur, des réserves d'amidon après une ablation complète des parties épigées, presque indépendamment de l'historique antécédent des fréquences de perturbation.

Mots-clés : réserves hypogées, *Erica arborea*, *Erica australis*, *Erica scoparia*, rejet post-perturbation, mobilisation de l'amidon post-perturbation.

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Introduction

The ability of plants to survive the complete removal of their aboveground photosynthetic parts, and regenerate by the activation and growth of dormant buds is a widespread feature among Mediterranean shrub and tree species (Keeley 1986; Del Tredici 2001). These dormant buds are concealed near the surface of modified underground parts, such as lignotubers, root crowns, or shallow woody roots (James 1984). Growth of dormant buds is supported by carbohy-

drate reserves stored primarily in the secondary xylem tissue of underground organs (Loescher et al. 1990; Pate et al. 1990). Starch, which is often used as the sole indicator of the carbohydrate reserve status of a plant (Kozlowski 1992), is the most abundant reserve polysaccharide in resprouter woody plants (Bowen and Pate 1993; Kozlowski and Pallardy 1997).

The capacity of resprouter plants to overcome severe disturbance depends not only on the intensity, but also, and more markedly, on the frequency of recurrent disturbance events (Zammit 1988; Moreno and Oechel 1991; Riba 1998). Short intervals between severe disturbance events, such as fire or slashing, reduce the ability of resprouter plants to recover (Zedler et al. 1983; Trabaud 1991; Riba 1997; Díaz-Delgado et al. 2002), probably as a result of a depletion of belowground carbohydrate reserves. It is generally assumed that frequent, successive disturbance events

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cause a progressive decline of belowground starch reserves in plants (e.g., Chapin et al. 1990), gradually driving resprouter plants to reserve exhaustion and, ultimately, to death (Miyanishi and Kellman 1986; Bell and Pate 1996; Canadell and López-Soria 1998). However, since some studies have shown an apparent failure in resprouter plants to use all their stored starch before death after recurrent disturbance, it has been suggested that factors other than belowground reserves, such as number of dormant buds, or soil nutrient and water conditions, may limit the resprouting response (Bilbrough and Richards 1993; Van der Heyden and Stocks 1995; Cruz et al. 2003). Partial decline of starch reserves has been used to argue that belowground starch storage may be an adaptive feature for other functions apart from supplying carbon for postdisturbance regrowth (Cruz and Moreno 2001; Cruz et al. 2003).

The lignotuber has been traditionally considered the organ for the presence of dormant buds ("bud bank") and storage of starch reserves so as to enable postdisturbance regrowth in resprouter woody plants (James 1984). Nevertheless, the role of the lignotuber as a specialized organ for starch storage in resprouter woody plants has been questioned by some authors (e.g., Carrodus and Blake 1970; Cruz and Moreno 2001; Wildy and Pate 2002), with its selective advantage being mainly related to the enlargement of the bud bank (Carrodus and Blake 1970; Kummerow 1989). In contrast, numerous studies have highlighted the xylem parenchyma of woody roots as the major location for belowground starch storage (Carrodus and Blake 1970; Loescher et al. 1990; Pate et al. 1990; Bell et al. 1996; Bell and Ojeda 1999; Wildy and Pate 2002).

Erica australis L., *Erica scoparia* L., and *Erica arborea* L. (Ericaceae) are three common heath species in Mediterranean heathlands and heath-scrub understoreys of cork oak (*Quercus suber* L.) woodlands from the Strait of Gibraltar region, at the western end of the Mediterranean Basin (Ojeda et al. 2000). Wildfire, forest thinning, scrub slashing, and browsing by free-range cattle and game (mainly red and roe deer) are the main disturbance agents on these heathlands (Ojeda et al. 1996). Forest thinning and scrub slashing in this region are common management practices used to optimize cork production, to facilitate cork harvesting, and to avoid forest wildfires (Ceballos and Martín-Bolaños 1930; Torres and Montero 2000). The three species of *Erica* have similar aboveground morphology and a thick lignotuber from which they readily resprout after slashing or burning. However, these species show a progressive decline in the vigour of the aboveground regrowth following successive, highly frequent disturbance events (Paula and Ojeda 2006).

Here we present a field study to explore the aboveground (resprouted biomass) and belowground (root starch) response of three species of *Erica* after different histories of disturbance intensity. Specifically, we test for each of the three species the existence of a gradual decrease in (i) the final biomass of the aboveground regrowth and (ii) the level of belowground (root) starch storage across increasing levels of disturbance frequency. We believe that this study provides valuable insights to improve the understanding of the dynamics of belowground starch reserve consumption in resprouter woody plants after severe disturbance.

Materials and methods

Study site

The experiment was conducted in Monte Murta, within the Aljibe Mountains, in the northern side of the Strait of Gibraltar, South Spain (36°19'35"N; 5°33'25"W). The climate is mild mediterranean, with a mean annual rainfall of ca. 1300 mm. The altitude in Monte Murta ranges from 350 to 450 m above sea level. The soil is a mixture of sandstone and clay, except on ridges and upper slopes, where acid, nutrient-poor, sandstone soil emerges. Dominant vegetation is a *Quercus suber* (cork oak) woodland with medium to sparse tree cover and a heath-scrub understorey. Open heathlands, with virtually no trees, cover the sandstone crests and upper slopes.

Field experiment

Because of the contrasting ecological optima between *E. arborea* and *E. australis* in this region (Ojeda et al. 2000), it was not possible to find the three species of *Erica* occurring at the same location. Hence, two neighbouring sites (ca. 200 m apart) were initially chosen in this study. Site 1 consisted of a heathland on mixed soil in a cleared patch of a sparse cork oak woodland, where *E. arborea* and *E. scoparia* co-occurred, the latter one being less abundant. Site 2 was an open heathland on sandstone, where both *E. scoparia* and *E. australis* were abundant. Forty-five adult, healthy-looking plants of *E. arborea*, 70 of *E. scoparia* (25 from site 1 and 45 from site 2), and 45 of *E. australis* were initially selected. They were chosen randomly, although very small or very big plants were disregarded, as well as plants that had undergone any major disturbance, by wildfire or slashing, within 10 years prior to this study (which was done by counting growth rings of the three thickest basal branches of each plant). Also, care was taken that there was a minimum distance of 10 m between individual plants.

Plants of each species were randomly designated to one of four disturbance frequency treatments: clipped every 6 months, clipped every year, clipped every 2 years, and clipped only once (hereinafter, 6-month, 1-year, 2-year and once-clipped treatments, respectively). At the beginning of the experiment (February 1998), all selected plants, except the ones of the once-clipped treatment, were clipped to ground level and caged individually with 1 cm × 1 cm wire mesh to exclude vertebrate herbivory. Unfortunately, several cages were broken, and resprouts were browsed heavily by free-range cattle and (or) game. These plants were removed from the experiment, thus changing the initial number of 160 selected plants to 138 plants, distributed among the different treatments as reflected in Table 1. These plants were subsequently clipped to the ground according to their different frequency treatments until February 2000, when once-clipped plants were also clipped. In so doing, aboveground regrowth harvested at the end of the experiment (August 2000) was 6 months old across all frequency treatments. This final regrowth of all plants was collected, oven-dried, and weighed to the nearest 0.1 g. After the first clipping, the upper surface area of the lignotuber of all plants was estimated by measuring the two main perpendicular diameters and assuming elliptic shape. Since plant size is strongly cor-

Table 1. Number of individuals of the three species of *Erica* employed in every clipping treatment.

	Site	6 months	1 year	2 years	Once clipped	Never clipped
<i>E. arborea</i>	1	11 (5)	5 (5)	7 (3)	9 (5)	(4)
<i>E. scoparia</i>	1	7 (5)	4 (4)	4 (4)	6 (5)	(5)
<i>E. scoparia</i>	2	16 (6)	10 (5)	9 (6)	9 (5)	(5)
<i>E. australis</i>	2	16 (8)	8 (4)	9 (5)	8 (5)	(6)

Note: The numbers of extra individuals of the three species employed in root sampling in August 2000 are indicated in parentheses.

related with the lignotuber upper surface area in these species (Canadell et al. 1991; Riba 1997; Moreno et al. 1999), we used lignotuber surface area as a covariate for the comparison of resprouted biomass between species and clipping treatments (see below).

At the conclusion of the experiment (August 2000), one segment of woody root (ca. 1 cm width and 5 cm length) from above the point of lateral branching of the root was collected from a subsample of plants of each species and clipping treatment for root starch determination (Table 1). Root material from additional unclipped plants of the three species was collected in August 2000, following the same criteria as plants chosen for the clipping experiment (see above) and used as a control for starch content in mature undisturbed plants (hereinafter, never-clipped treatment; see Table 1). Numbers of individuals sampled per species and treatment are not even in Table 1, since many roots had to be discarded after processing in the laboratory (see below) because they had high tannin content, which interfered with starch viewing under the microscope.

Determination of root starch

Root samples were softened by soaking in glycerine-ethanol 1:1 v/v (O'Brien and McCully 1981) for 5 d, and thin (20–30 μm) transverse sections were obtained using a Leica SM 2000 R sliding microtome (Leica Microsystems, Nussloch, Germany). Sections were washed in a decreasing ethanol gradient, stained with 2% iodine solution (I_2KI) for the detection of starch granules, dehydrated in an increasing ethanol gradient, and mounted on glass slides.

For quantitative estimation of starch, 10 images per root section (5 located in the outer, and 5 in the inner areas of xylem) were obtained using a digital camera (DKC-CM30, Sony, Tokyo, Japan) connected to a light microscope. The relative amount of starch stored in root xylem tissue was calculated as the percentage area of xylem tissue containing starch granules (see Pate et al. 1990). This was determined manually by superimposing a 1 cm \times 1 cm grid over each image (1 cm = 57.5 μm). A previous study using *E. scoparia* and *E. australis* (Paula 2004) showed a very strong relationship between this method and the classical chemical method (Pucher et al. 1948; Dubois et al. 1956) for quantifying starch concentration in root tissue ($R^2 = 0.83$; $\text{df} = 25$; $P < 0.0001$ in *E. scoparia* and $R^2 = 0.76$; $\text{df} = 28$; $P < 0.0001$ in *E. australis*). Moreover, the intercept did not differ significantly from zero ($t_{25} = 0.65$, $P = 0.521$ in *E. scoparia*; and $t_{28} = 0.50$, $P = 0.619$ in *E. australis*). Therefore, this histological method was deemed to have similar accuracy as the chemical method, particularly for very low starch content.

Statistical analyses

To detect differences in resprouting vigour among clipping treatments across species, we used the 6-month-old regrowth (dry mass) harvested in August 2000 as the dependent variable in statistical analyses. This variable was log-transformed to meet normality and homoscedasticity requirements. As we were concerned with the possibility that plants of *E. scoparia* might respond differently under the two sites or edaphic conditions, we first tested the existence of differences in the disturbance frequency treatments between both sites in this species by means of a two-way ANCOVA. The covariate, surface area of lignotuber (also log-transformed), was nested within the interaction of the two factors ("clipping treatment" and "site") because of the lack of homogeneity among slopes for the different combinations of factor levels (Verdú 2002). This statistical analysis highlighted significant differences between clipping frequency levels ($F_{[3,53]} = 5.6$; $P = 0.026$), with the effect of the covariate, surface area of lignotuber, being statistically significant ($F_{[7,53]} = 2.8$; $P = 0.014$). However, no significant differences were found in the resprouted biomass between sites ($F_{[1,53]} = 0.1$; $P = 0.762$) nor in the response patterns to the clipping treatments between sites (clipping treatment \times site: $F_{[1,53]} = 0.1$; $P = 0.76$). This allowed us to pool data for the plants of *E. scoparia* from both sites.

For each species, the existence of differences in the biomass of the final 6-month-old regrowth harvested in August 2000 (log-transformed) was tested among clipping frequency levels by means of independent one-way ANCOVAs, with the surface area of lignotuber (log-transformed) used as a covariate.

Analogously, differences in relative abundance of root starch 6 months after the last clipping across clipping treatments were tested for each species by means of independent one-way ANOVAs. The response variable was the mean value of the percentage area occupied by starch in the 10 images per plant's root cross-section (arcsin-transformed). For these comparisons, the surface area of lignotubers was not included in the statistical analysis because of the absence of correlation with root starch abundance (see also Cruz et al. 2003). As with resprouter biomass, we previously tested for differences in the root starch content in *E. scoparia* between clipping treatments and sites by means of a two-way ANOVA. We did not detect differences between sites ($F_{[1,40]} = 6.96$; $P = 0.093$), nor in the interaction between clipping treatment and site ($F_{[4,40]} = 0.62$; $P = 0.651$) in the relative amount of starch in roots of *E. scoparia*. Hence, we pooled data for belowground (root) starch of *E. scoparia* from both sites.

When necessary, post-hoc multiple comparisons were performed by means of both Tukey's HSD and Fisher's LSD

Table 2. One-way ANCOVA results for the comparison of the 6-month-old resprouted biomass (g dry mass; log-transformed) harvested in August 2000 among the four clipping treatments in the three species of *Erica*.

Source	<i>Erica arborea</i>				<i>Erica scoparia</i>				<i>Erica australis</i>			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Clipping treatment	3	4.21	34.6	0.000	3	2.18	20.4	0.000	3	1.51	3.9	0.02
Lignotuber	1	0.38	3.1	0.087	1	3.35	31.2	0.000	1	0.16	0.4	0.525
Error	27	0.12			60	0.11			36	0.39		

Note: The upper surface area of the lignotuber (cm²; log-transformed) was the covariate.

tests, to balance the risks of type I and type II errors. While Tukey's HSD post-hoc test is highly conservative to detect significant differences between means (i.e., high type II error rate), Fisher's LSD is more sensitive to small differences (i.e., high type I error rate) (Sokal and Rohlf 1998).

Results

Overall 10.9% mortality occurred among the 138 plants at the end of the experiment. Of the 15 dead plants, 8 were *E. australis* (19.5% mortality), 5 were *E. arborea* (15.1% mortality), and 2 were *E. scoparia* (3.1% mortality). Except for two plants of *E. australis* from the 2-year clipping treatment, all this mortality was concentrated in the 6-month clipping treatment.

For the three species of *Erica*, the final 6-month-old regrowth was significantly different across treatments (Table 2), decreasing gradually with increasing clipping frequency (Fig. 1). This pattern was particularly noticeable in *E. arborea* and, to a lesser extent, in *E. australis*, as inferred from the Tukey's HSD post-hoc comparisons (see Fig. 1). In *E. scoparia*, by comparison, the final 6-month-old regrowth remained somewhat similar across clipping frequencies until the 6-month treatment, where it dropped substantially (Fig. 1).

Control plants (nonclipped) of the three species possessed considerable amounts of starch in the root xylem, whereas there was a sharp reduction in root starch in once-clipped plants (77% in *E. arborea*, 87% in *E. scoparia*, and 85% in *E. australis*; Table 3). The post-hoc analyses detected significant differences in root starch content between never-clipped plants and the plants subjected to the four clipping frequency treatments (Fig. 1), except for *E. australis* after the Tukey's HSD test, where comparisons of the never-clipped with the 1-year and the 2-year treatments were non-significant. Nevertheless, no significant differences in root starch were found in the three species between once-clipped plants and plants from any of the other clipping frequencies, even after the more sensitive Fisher's LSD multiple-comparison test (see Fig. 1).

Discussion

Short intervals between severe disturbance events such as fire have been reported to reduce the ability of resprouter plants to recover (Zedler et al. 1983; Trabaud 1991; Díaz-Delgado et al. 2002), probably as a result of a progressive decrease in belowground carbohydrate reserves (Miyaniishi and Kellman 1986; Trabaud 1991; Bell and Pate 1996; Canadell and López-Soria 1998). However, Cruz et al. (2003) have recently challenged the relevance of belowground (lignotuber) stored reserves in *Erica australis*, suggesting

Fig. 1. Dry mass (mean \pm SE) of the 6-month-old resprouted biomass (regrowth; open circles) after the last harvest (August 2000) from the four clipping treatments and percentage (mean \pm SE) of xylem tissue filled with starch in cross-sections of roots (solid circles) of plants from the four clipping treatments and "never-clipped" (control) plants in the three species of *Erica*. Different upper-case letters indicate post-hoc significant differences (Tukey's HSD test, at $\alpha = 0.05$ significance level) in aboveground regrowth and different lower-case letters indicate post-hoc significant differences (Fisher's LSD test, at $\alpha = 0.05$ significance level) in root starch.

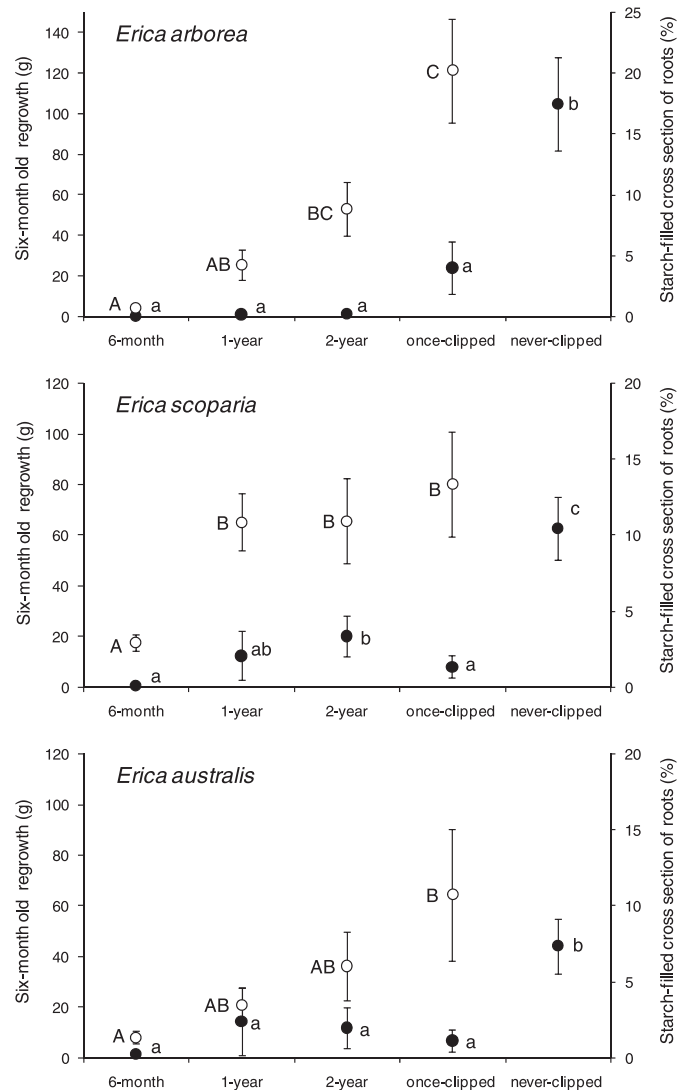


Table 3. One-way ANOVA results for the comparison of the percentage root section filled with starch in plants whose resprouted biomass was harvested in August 2000 (plus not-clipped, control plants) across clipping treatments in the three species of *Erica*.

Source	<i>Erica arborea</i>				<i>Erica scoparia</i>				<i>Erica australis</i>			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Clipping treatment	3	224.6	13.5	0.000	3	2.18	20.4	0.000	3	1.51	3.9	0.02
Error	27	16.6			60	0.11			36	0.39		

the role of other factors, such as bud-bank size (see also Bell and Pate 1996) and soil nutrient and (or) water availability, as crucial for limiting postdisturbance regrowth in this species (Cruz et al. 2002, 2003).

Results presented in this study show a small, progressive decrease in the final 6-month-old aboveground regrowth after increasing clipping frequency in the three species of *Erica*. On the other hand, there was a marked drop in root starch reserves between never-clipped and once-clipped plants in the three species, but no significant differences were detected between this once-clipped treatment and any of the other clipping frequency ones. Therefore, a progressive decrease in the final 6-month-old aboveground resprouted biomass across the different clipping treatments in the three species of *Erica* is not paralleled by a similarly progressive decrease in belowground (root) starch levels. Contrary to what might be expected, a marked drop in root starch from never-clipped to clipped plants, nearly irrespective of the previous frequency of clipping events, has been found in the three species. These two contrasting aboveground (regrowth) and belowground (starch) patterns cannot be due to a possible decrease in soil water (cf. Cruz et al. 2002), since cumulative rainfall in the 6-month periods March–August and September–February increased steadily from 1998 to 2000 (Paula and Ojeda 2006), that is, for the duration of the experiment.

The lack of significant differences in root starch levels between once-clipped resprouting plants and resprouting plants coming from an intense history of recurrent clipping allows us to infer that these resprouter plants would use belowground (root) carbon reserves (starch) rapidly, not conservatively, after any severe disturbance event. This nonconservative dynamic of belowground starch consumption would most likely boost a large first pulse of photosynthetic regrowth, large enough to support and maintain respiration costs (Noble 2001; Wildy and Pate 2002) and to maximize subsequent plant regrowth. In so doing, resprouting plants may potentially assimilate more carbon, which would then be allocated to replenishing depleted reserves of root starch and to sustain regrowth (Iwasa and Kubo 1997).

Our results are in apparent conflict with Cruz et al.'s (2003) arguments of underestimating the role of belowground carbon reserves in aboveground resprouting of *E. australis*, although it should be noted that Cruz et al. (2003) focused on the lignotuber (see also Canadell and López-Soria 1998), while we focused on roots. However, albeit focusing on roots instead of on the lignotuber, this study strongly supports a crucial role of belowground starch in boosting postdisturbance regrowth in the three species of *Erica* tested.

Bell and Pate (1996) reported that the lignotuber bud bank could become exhausted after a number of postdisturbance

recoveries in the resprouter *Leucopogon verticillatus* (Ericaceae) from SW Australia, and suggested that the number of buds might limit the resprouting response after recurrent disturbance in this species. In this regard, although the possible role of bud bank was not considered in this study, we detected a higher mortality of individuals of *E. australis* with larger lignotubers (see Paula and Ojeda 2006). Larger lignotubers may be assumed to correspond with older plants and, therefore, to have suffered more disturbance events, thus having fewer dormant buds left. In fact, we observed that new shoots in some large lignotubers of *E. australis* were confined to one or few small sections of the upper lignotuber area. However, this presumable bud-bank limitation was not evident for *E. arborea* nor *E. scoparia* (Paula and Ojeda 2006; see also Riba 1998 for *E. arborea*). A possible bud-bank limitation effect might contribute to explain the progressive decrease in the aboveground regrowth across frequency clipping treatments in the three species of *Erica*. Nevertheless, they would not affect results highlighted here of a marked drop in root starch of resprouting plants after severe disturbance, irrespective of the previous frequency of disturbance events.

In conclusion, this study highlights a crucial role of belowground (root) starch reserves for resprouting in the three resprouter species of *Erica*. It also shows a consistent pattern across the three species of profuse, not conservative, consumption of the starch reserves after the complete removal of the aboveground part, regardless of the previous history of disturbance frequency. We interpret this intense mobilization of belowground starch reserves as a means for resprouting plants to maximize the first postdisturbance pulse of photosynthetically active regrowth to endure recurrent severe disturbance (Iwasa and Kubo 1997).

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