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To resprout or not to resprout: factors driving intraspecific variability in resprouting

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Resprouting is a mechanism that allows individual plants to persist in disturbance-prone ecosystems. It is often considered a binary trait, defining species as resprouters or non-resprouters. Although this dichotomous classification accounts for a high proportion of the interspecific variability in resprouting, it does not account for the intraspecific variability, as not all individuals of resprouting species successfully resprout, even if they are subject to a similar disturbance. To ascertain the causes of the intraspecific variability in resprouting we propose a conceptual model that disaggregates the process of resprouting into three sequential steps: initial ability to resprout, resprouting vigour and post-resprouting survival. To test this model, we clipped 151 plants of three resprouting species (*Anthyllis cytisoides*, *Globularia alypum* and *Linum suffruticosum*) and, for each individual, we analysed the carbohydrate (starch and soluble sugars) and nutrient (N and P) concentrations in the roots at the moment of the disturbance (clipping all aboveground biomass). We then monitored initial ability to resprout, resprouting vigour and post-resprouting survival in each individual during a one-year period. *Anthyllis* showed high initial ability to resprout and high post-resprouting survival. *Globularia* and *Linum* had low final resprouting success, mainly due to their low post-resprouting survival, but also to the low initial ability to resprout in *Linum*. All three species showed variable resprouting vigour. Our results suggest that resprouting success is limited by different phases of the process of resprouting, depending on the species. Intraspecific variability in resprouting supported the importance of: a) the pre-disturbance state of the plant (i.e. plant size and stored resources) on the initial ability to resprout and on the resprouting vigour, and b) the initial post-disturbance capacity to acquire resources (i.e. resprouting vigour) on the post-resprouting survival. The proposed three-step model of resprouting provides a mechanistic description of the factors driving intraspecific variability in resprouting.

Resprouting is a mechanism that allows individual plants to regenerate after the elimination of the aboveground biomass and persist in ecosystems with recurrent disturbances (Bond and Midgley 2001). In such ecosystems, intraspecific variability in resprouting might affect the dynamics of the community by determining to what extent species persist or decline under high disturbance recurrence. Thus, understanding this persistence mechanism is essential for explaining species diversity and evolution (Bond and Midgley 2003) and for predicting vegetation shifts in the framework of global change (Bond et al. 2003, Bradley and Pregitzer 2007).

Resprouting has often been considered a binary trait and used to separate species as resprouters or non-resprouters (Pausas et al. 2004, Vesk et al. 2004). However, after a disturbance that eliminates all aboveground plant parts, neither do all individuals of resprouting species survive, nor do all individuals of non-resprouting species unavoidably die. That is, even if this dichotomous classification of species accounts for a high proportion of the interspecific variability in resprouting, it does not account for the intraspecific variability observed in this trait (Gill and Bradstock 1992, Vesk et al. 2004, Paula et al. 2009). Thus, in many cases, a semi-quantitative classification (e.g. no, weak, strong resprouters) could be more adequate than a binary classification (Vesk and Westoby 2004a). While most studies on resprouting have focused on the response of plants to different disturbance regimes (i.e. different disturbance type, recurrence and intensity; Moreno and Oechel 1991, Lloret and López-Soria 1993, Cruz et al. 2003a, Vesk et al. 2004), few have focused on the response of different individuals (of the same species) to a similar disturbance. However, the fact that intraspecific variability in resprouting is observed under disturbances with similar characteristics (Lloret and López-Soria 1993, Canadell and López-Soria 1998, Kabeya and Sakai 2005, Paula and Ojeda 2006) suggests that this variability may be driven by factors related to the state of the individual plants (e.g. non-structural carbohydrates and nutrients levels; Iwasa and Kubo 1997, Canadell and López-Soria 1998). Thus, studying the factors driving the intraspecific variability in resprouting, for a given disturbance, may provide clues for a mechanistic understanding of the process of resprouting.

A model for the resprouting process

Resprouting might be limited by different phases in the resprouting process, depending on the species. Thus, to ascertain the causes of the intraspecific variability in resprouting, we propose a conceptual model that disaggregates the process of resprouting into three sequential steps: initial ability to resprout, resprouting vigour and post-resprouting survival (Fig. 1).

The initial ability to resprout (i.e. whether or not resprouting is initiated after the elimination of aboveground biomass) does not necessarily correspond to the final resprouting success, as many plants do not survive after resprouting is initiated (Moreno and Oechel 1991, Lloret and López-Soria 1993, Cruz et al. 2003a, Catry et al. 2010). A plant can initiate resprouting after its aboveground biomass has been eliminated only if it has a stock of surviving dormant buds (i.e. bud bank; Vesk and Westoby 2004b) from which new sprouts can grow. Moreover, as disturbed plants lose photosynthetic capacity, they need to have sufficient carbohydrates and nutrients stored in their belowground organs to maintain respiration demands and to initiate resprouting (Pate et al. 1990, Bowen and Pate 1993, Canadell and López-Soria 1998, Kabeya and Sakai 2005). Indeed, resprouting species exhibit significantly higher starch levels in their belowground organs than non-resprouting ones (Pate et al. 1990, Bell et al. 1996, Bell and Ojeda 1999, Verdaguer and Ojeda 2002), and these levels decrease during post-disturbance resprouting (Bowen and Pate 1993, Canadell and López-Soria 1998, Kabeya and Sakai 2005). The bud bank should be coordinated with the stored reserves (carbohydrates and nutrients) so that it does not limit resprouting; stored resources would be of limited importance in the absence of buds. Only in severe disturbances (e.g. extremely intense fires) the bud bank might be destroyed preventing plants from initiating the resprouting response regardless of the level of stored reserves (Vesk and Westoby 2004b).

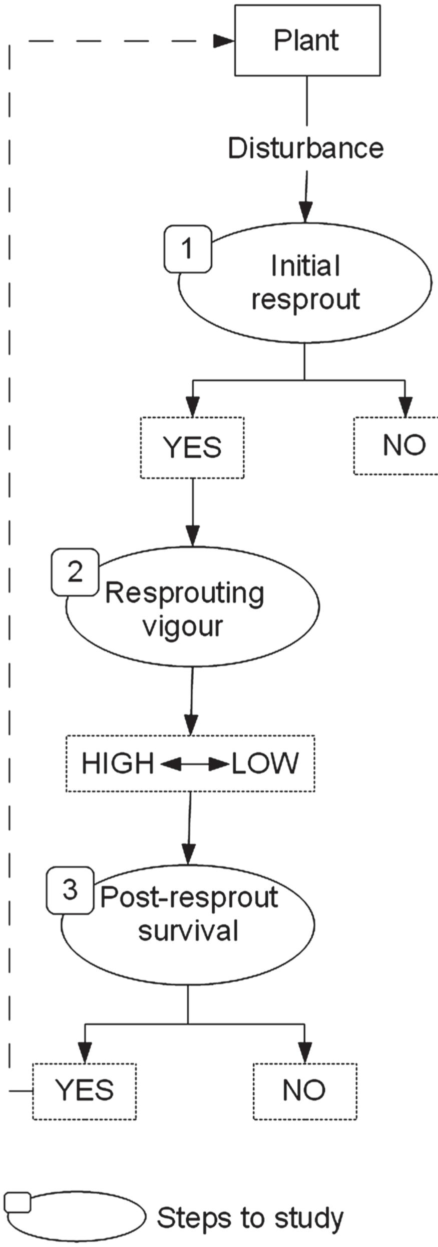

Figure 1. The three-step model of the process of resprouting (step 1: initial resprouting ability, step 2: resprouting vigour, and step 3: post-resprouting survival).

Individuals that resprout can differ quantitatively in their resprouting vigour (e.g. resprouted biomass; Stohlgren et al. 1984, Lloret and López-Soria 1993, Paula and Ojeda 2006). In many cases resprouting vigour is positively correlated with pre-disturbance plant size (Stohlgren et al. 1984, Lloret and López-Soria 1993, Pausas 1997, Vesk et al. 2004, Paula and Ojeda 2006, Vesk 2006) and with the concentration of carbohydrates and nutrients stored in the belowground organs of the plant (Chapin III et al. 1990, Avice et al. 1996, Kabeya and Sakai 2005). However, resprouting vigour is not always correlated with carbohydrates, either because they may be stored in excess (Cruz et al. 2003a, b) or because, once the plant produces photosynthetic biomass, the carbon fixed by the resprouts is used to continue growth (Richards and Caldwell 1985, Chapin III et al. 1990, Avice et al. 1996).

Post-resprouting mortality (i.e. failure to survive after resprouting is initiated) is commonly observed in many species (Moreno and Oechel 1991, Lloret and López-Soria 1993, Cruz et al. 2003a, Catry et al. 2010) and it is not necessarily controlled by the same factors that drive the initial ability to resprout (Lloret and López-Soria 1993), although both processes are often lumped together in a single response (Paula et al. 2009). Resprouting vigour is related to the capacity of plants to quickly acquire resources for sustaining the maintenance costs and avoiding reserve depletion (Chapin III et al. 1990, Iwasa and Kubo 1997), and thus it should be positively correlated with the probability of plant survival (Moreno and Oechel 1991). Nevertheless, the role of resprouting vigour as a key factor for post-resprouting survival has never been addressed in detail.

To the best of our knowledge, no study has related a plant's resprouting response at individual level to the pre-disturbance stored resources measured in the same individual. Most studies compare levels of stored resources between disturbed and undisturbed individuals (Canadell and López-Soria 1998, Cruz et al. 2003a, b). Thus, the examination of a plant's pre-disturbance state (measured in each individual) should provide a better understanding of the intraspecific variability in the process of resprouting.

Our hypothesis is that there are different steps in the process of resprouting and that each of these steps is limited by different factors. We propose that resprouting can be viewed as a three-step sequential process (Fig. 1) and that studying each of these steps should provide important clues to understand the intraspecific variability and the mechanisms behind resprouting. Specifically, we predict that a plant's initial ability to resprout and its resprouting vigour are determined by the pre-disturbance state of the plant (e.g. plant size and stored reserves), and that post-resprouting survival is related to the plant's resprouting vigour (indicative of the plant's capacity to acquire resources). We tested this model using three species living in fire-prone ecosystems of the eastern Iberian Peninsula (western Mediterranean Basin).

Methods

Species and study area

We selected three shrub species common in eastern Spain: *Anthyllis cytisoides* (Fabaceae), *Globularia alypum* (Plantaginaceae) and *Linum suffruticosum* (Linaceae). These species are relatively short (< 1 m tall) and most aboveground biomass is composed by fine fuel that is consumed during the passage of a fire. *Anthyllis* and *Globularia* typically resprout from the root crown, while *Linum* can also resprout from rhizomes or roots. None of them has a lignotuber (Paula et al. 2009). The three species are facultative resprouters (R + P + sensu Pausas et al. 2004), that is, after fire they are able to regenerate by resprouting and by recruiting new individuals from seed. We selected facultative resprouters because of the high observed intraspecific variability in resprouting (Paula et al. 2009), as species possessing the two post-fire regeneration mechanisms might be less efficient in each of them when compared with species that only present one of the mechanisms (Paula and Pausas 2008). Because of the different local abundance, two species (*Linum* and *Globularia*) were sampled at Barranc de la Casella (Alzira, Valencia, Spain; 39°09′N, 00°29′W) and the third (*Anthyllis*) in Serra Calderona (Gàtova, Valencia, Spain; 39°74′N, 00°51′W). Barranc de la Casella is located at 700 m a.s.l., the bedrock type is limestone, mean annual precipitation is 633 mm and mean annual temperature is 17.4°C. It is a shrubland dominated by *Linum suffruticosum*, *Globularia alypum*, *Lithodora fruticosa*, *Ulex parviflorus* and *Erica* sp. pl. with an herbaceous layer of *Brachypodium retusum* and with scattered *Pinus halepensis* trees. Serra Calderona is located at 600 m a.s.l., the bedrock type is sandstone, mean annual precipitation is 584 mm and mean annual temperature is 17.7°C. It is an open *Pinus halepensis* stand with a shrubland dominated by *Anthyllis cytisoides*, *Cistus monspeliensis* and *Ulex parviflorus* and an herbaceous layer of *Brachypodium retusum*. In both study areas, precipitation falls mainly in two peaks, a more prominent one in autumn and a weaker one in spring. Summers are warm and dry and wildfires are frequent (Pausas 2004), although they have not affected the study sites for the last 30 years.

Sampling

All plants were clipped in August 2008, i.e. in summer, when physiological activity is low and most fires occur (severe disturbance). For each species we selected ca 50 adult plants, separated by a minimum distance of 10 m, which lacked any sign of recent disturbance (Table 1). For each individual of each species we measured its height, clipped the aboveground biomass and then fenced it to avoid mammal herbivory. All individuals were clipped at ca 10 mm aboveground without damaging buds below this point (i.e. no variability in the severity of the disturbance) during the same week (i.e. no seasonal variability) and, for each species, on the same site (i.e. low spatial variability). Clipped biomass was oven-dried at 80°C for eight days to obtain the total dry weight. We carefully excavated a few centimetres of the soil close to each individual and extracted a lateral root sample (less than 1 cm in diameter) for carbohydrate and nutrient analyses. The length of the root samples ranged from 13 to 67 cm and was not significantly different between resprouting and non-resprouting plants (*Linum* $p = 0.11$, *Anthyllis* $p = 0.75$, *Globularia* $p = 0.83$). To minimize respiration and lost of carbohydrates during transport, root samples were placed individually in

Table 1. Total number of plants studied, plant biomass (in g), concentration of stored resources in the roots and responses to clipping for each of the three species studied. Stored resources include concentration (mean and standard deviation; in mg g^{-1}) of nitrogen (N), phosphorus (P), starch and soluble sugars (SS). Responses are the number of plants that failed to resprout, that initiated resprouting but died, or that initiated resprouting and survived, for each of the three species (in parentheses the % of the total plants studied). Different letters (in rows) indicate significant differences among species at $p < 0.03$.

	Linum suffruticosum	*Anthyllis cytisoides*	*Globularia alypum*
Number of plants	51	52	48
Plant biomass (g)	46.64 ± 40.82^{c}	121.44 ± 65.04^{b}	142.54 ± 84.72^{a}
Plant stored resources			
N (mg g^{-1})	10.21 ± 3.12^{a}	11.55 ± 3.66^{a}	5.34 ± 1.43^{b}
P (mg g^{-1})	0.24 ± 0.10^{b}	0.62 ± 0.28^{a}	0.16 ± 0.07^{c}
Starch (mg g^{-1})	8.86 ± 5.50^{b}	16.72 ± 10.97^{a}	8.66 ± 7.38^{b}
SS (mg g^{-1})	53.26 ± 34.82^{a}	31.80 ± 11.10^{b}	19.96 ± 10.92^{c}
Plant responses			
Failed to resprout	13 (25.5%)	1 (2.0%)	3 (6.0%)
Resprouted and died	25 (49.0%)	4 (8.0%)	33 (69.0%)
Resprouted and survived	13 (25.5%)	47 (90.0%)	12 (25.0%)

a hermetic bag with silica gel and transported in a cooler (at 0°C) to the laboratory. Root samples were oven-dried at 80°C for 24 h and because of the high surface/volume ratio of the roots sampled, root temperature was expected to increase very quickly stopping respiration immediately. Samples were conserved frozen at −18°C in hermetic bags with silica gel until analysed (ca one year) for determination of soluble sugars (SS; i.e. sucrose, glucose and fructose), starch, nitrogen (N) and phosphorus (P) concentrations (Agrolab Analítica SL). Soluble sugars and phosphorus were measured through calorimetric reaction and spectrometric analysis (Bertramson 1942, Green et al. 1989). Nitrogen was analyzed following the Kjeldahl method (Nelson and Sommers 1973); and starch was determined by an enzymatic procedure and measured calorimetrically using a coupled glucose oxidase/peroxidase reaction and spectrometric analysis (Rasmussen and Henry 1990). Total amount of carbohydrate and nutrients (i.e. pool size) was estimated multiplying the concentration values by the plant pre-clipping dry weight biomass. Carbohydrate and nutrient were determined in 41, 42 and 35 of the individuals clipped, for *Linum*, *Anthyllis* and *Globularia*, respectively.

Initial ability to resprout, resprouting vigour and post-resprouting survival were monitored 4 and 12 months after clipping (i.e. December 2008 and August 2009). The first survey was after the autumn precipitation peak (213 mm during October 2008, Valencia, AEMET, Spanish Meteorological Service). Plants that initiated resprouting, even if they died later on, were considered to have the initial ability to resprout. Plants that had resprouted and died before the first survey or between surveys were detected by the presence of dead sprouts. Post-resprouting mortality was considered to have occurred when all resprout shoots within an individual were dead. Final resprouting success refers to plants that initiated resprouting and survived during the study period (one year). In each survey we counted the number of resprouts and measured the maximum height. In the final survey (i.e. 12 months after clipping) we also clipped all resprouted biomass to obtain the dry weight. Although the survival to 12 months might not entirely correspond to the long term success, mortality (attributable to the applied disturbance) in subsequent years is generally low and declines through time (Lloret and López-Soria 1993, Paciorek et al. 2000).

Statistical analysis

For the individuals that resprouted and survived, resprouting vigour was calculated as the product of the number of resprouts and the maximum height four months after clipping (scaled between 0 and 1). This proxy of resprouting vigour was probed to be more closely related to resprout biomass than using resprout mean length obtained from multiple measurements (Cruz et al. 2003a). There was a significant linear correlation between this measure of resprouting vigour and resprouted biomass for the 12-month sampling (*Anthyllis*: $r = 0.59$, $p < 0.001$, $n = 47$; *Globularia*: $r = 0.89$, $p < 0.001$, $n = 12$; *Linum*: $r = 0.59$, $p = 0.032$, $n = 13$), suggesting that it is a good indicator of resprouting vigour. For individuals that resprouted and died by the fourth month, resprouting vigour was not calculated and these individuals were not included either in the analysis of initial resprouting vigour or in the analysis of post-resprouting survival.

In order to evaluate the role of the pre-disturbance state of the plant on its initial ability to resprout (step 1) we studied the probability of resprouting after clipping, in relation to pre-clipping plant biomass (used as a surrogate of plant size) and plant stored reserves (N, P, starch and SS; considering both the concentration and the amount of reserves). Because the resprouting data was binary (yes/no), we used a generalized linear model (GLM) assuming a binomial error distribution. For the individuals that initiated resprouting, we analyzed the role of pre-clipping plant biomass and plant stored reserves in determining resprouting vigour four months after clipping (step 2) using a standard regression model. We also tested the role of pre-clipping plant biomass, plant stored reserves and resprouting vigour in the probability of post-resprouting survival (one year after clipping; step 3) using a GLM with a binomial error distribution (binary data). In the three steps, variables were tested independently and then a multivariate model was built following a forward stepwise procedure and tested with the F-test for Normal distributed data and the χ^2-test for binomial data. Previous to the analysis, variables were standardized (subtracted the mean and divided by the standard deviation) for allowing the comparison of regression coefficients as effect sizes. In all cases, interactions between variables were tested and only variables that explained a significant proportion of the variance were retained.

Results

Initial ability to resprout (step 1)

Most individuals of *Anthyllis* and *Globularia* initiated resprouting (98% and 94% of the total individuals, respectively, Table 1). *Linum* showed high intraspecific variability in this step: of the 51 individuals clipped, 38 resprouted while 13 showed no evidence of resprouting. In *Linum*, the probability of initial resprouting after clipping was independent of plant biomass or SS concentration ($p > 0.05$). Similarly, we did not detect any significant effect of the total amount of carbohydrates and nutrients (i.e. pool size). On the other hand, the initial ability to resprout was significantly related to the concentration of nutrients (N and P) and starch both if the three variables were tested independently (nitrogen: $p = 0.006$; phosphorus: $p = 0.012$; starch: $p = 0.008$) or if they were added sequentially (Table 2, Fig. 2); interactions were not significant.

Resprouting vigour (step 2)

Resprouting vigour at four months after clipping was positively related to pre-clipping plant biomass in *Linum* ($F_{1,14} = 20.44$, $p = 0.0005$) and *Anthyllis* ($F_{1,38} = 8.66$, $p = 0.0055$), but not in *Globularia* ($F_{1,15} = 0.04$, $p = 0.848$). Moreover, for *Anthyllis,* resprouting vigour was also positively related to the concentration of starch and P when tested after plant biomass (Table 3, Fig. 3). The interaction between plant biomass and concentration of reserves was not significant.

Table 2. Summary of the stepwise regression for the probability of initiating resprouting after clipping for *Linum*, in relation to the concentration (mg g^{-1}) of nitrogen (N), phosphorus (P) and starch in the roots. The final column includes the standardized coefficient (and standard error) of each variable, for the final model. Only variables that explain a significant proportion of the variance are included. Fitted values of this model are presented in Fig. 2.

	Deviance	Resid. DF	Resid. dev	p	Coef. (SE)
NULL		40	51.22		
N	7.68	39	43.54	0.006	1.20 (0.59)
+ P	6.78	38	36.76	0.009	1.48 (0.60)
+ Starch	7.24	37	29.52	0.007	1.76 (0.83)

Post-resprouting survival (step 3)

At the end of the experiment most of the *Anthyllis* individuals that had initially resprouted (step 1) were found to have survived (47 of the 51 individuals that initiated resprouting; Table 1). In contrast, of the 38 individuals of *Linum* that resprouted (step 1), 25 failed to survive (Table 1). Individuals of *Globularia* exhibited the lowest values of post-resprouting survival; only 12 from the 45 plants that initiated resprouting finally survived (Table 1). The probability of post-resprouting survival was not related to any of the variables associated to the pre-clipping state of the plant (in all cases $p > 0.05$); however, it was positively related to the resprouting vigour in all three species (Fig. 4).

Final resprouting success

The three studied species showed different responses to the elimination of their aboveground biomass. Most individuals (> 90%) of *Anthyllis* and *Globularia* exhibited initial ability to resprout, while only 74% of *Linum* individuals were able to initiate resprouting (step 1). Of the individuals presenting an initial ability to resprout, 65% of *Linum* and 73% of *Globularia* died during the first year after the disturbance (step 3, Table 1). Thus, considering all the plants clipped, the total number of plants that successfully resprouted (i.e., that initiated resprouting and survived for the year) after the disturbance was 47 in *Anthyllis* (90% of total), 13 in *Linum* (25% of total) and 12 in *Globularia* (25% of total, Table 1).

Discussion

Our results suggest that the overall resprouting success is the outcome of the variability in different steps of the resprouting process (i.e. initial resprouting ability, resprouting vigour and post-resprouting survival) and that, depending on the species, each of the steps might limit the overall resprouting success differently. Resprouting success might be limited by the initial ability to resprout (step 1; e.g. 26% of *Linum* plants failed to initiate resprouting). Moreover, resprouted plants exhibit variable resprouting vigour (step 2), which drives the probability of post-resprouting survival (step 3). Indeed, post-resprouting survival might be even more important for the overall resprouting success than the initial ability to resprout (e.g. post-resprouting mortality was 49% in *Linum* and 69% in *Globularia)*.

The 3-step model (Fig. 1) provides a mechanistic description of the process of resprouting and suggests that the limiting step for resprouting success differs among species. Our results support that the initial ability to resprout (step 1) might be related to the pre-disturbance state of the plant (e.g. *Linum*). That is, plants with higher levels of starch and nutrients have a higher probability of initiating resprouting. The initial resprouting vigour (step 2) might be driven by the pre-disturbance state of the plant with respect to plant biomass (e.g. *Linum* and *Anthyllis*) or to the concentration of starch and nutrients (e.g. *Anthyllis*). Of a total of 33 plants of *Globularia* that resprouted and died (Table 1), 14 died before the four-month sampling and thus were not used in the analysis of resprouting vigour. These individuals had lower starch concentration ($p = 0.08$), lower SS ($p = 0.01$) and thus lower TNC ($p < 0.01$) than the individuals that survived the first 4 months. Giving the influence of initial resprouting vigour in the probability of survival, it is plausible to consider that these individuals had low resprouting vigour. Thus the lack of a significant predictor for resprouting vigour in *Globularia* might be due to this early death.

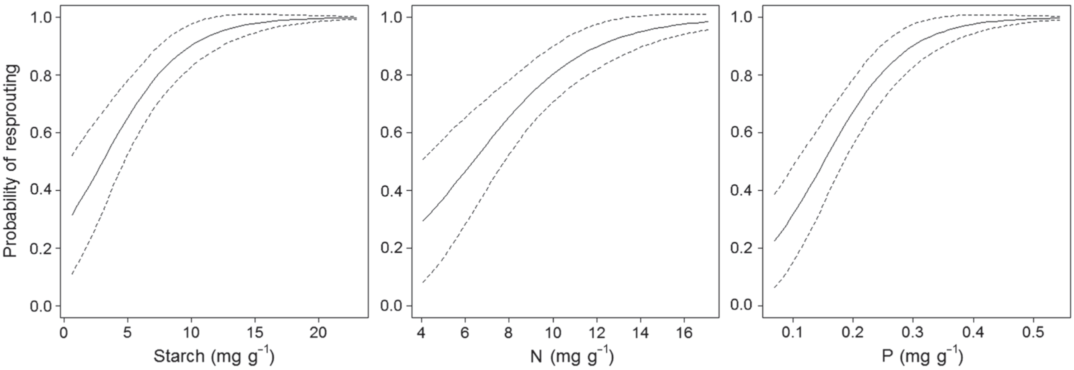

Figure 2. Probability of initiating resprouting (step 1) after clipping for *Linum* in relation to the concentration (mg g^{-1}) of starch, nitrogen (N) and phosphorus (P) in the roots, based on the model presented in Table 2 (using for each variable the median values of the other two variables). Dotted lines refer to SEs.

Table 3. Summary of the stepwise regression for the analysis of resprouting vigour at 4 months after clipping. Only variables that explain a significant proportion of the variance are included. For *Linum* the significant variable is the pre-clipping plant biomass (in g); and for *Anthyllis* the variables are the pre-clipping plant biomass (g) and the concentration (mg g^{-1}) of phosphorus (P) and starch. The final column is the standardized coefficient (and standard error) of each variable for the final model. Fitted values of these models are presented in Fig. 3.

		SS	Resid. DF	RSS	F	p	Coef. (SE)
Linum	NULL		15	255 699			
	Plant biomass	151 766	14	103 933	20.44	<0.001	100.59 (22.25)
Anthyllis	NULL		39	102 549			
	Plant biomass	19 042	38	83 507	12.52	0.001	22.63 (6.2)
	+ P	9589	37	73 918	6.31	0.017	8.30 (6.6)
	+ Starch	19 189	36	54 729	12.62	0.001	23.38 (6.6)

Our results emphasize the importance of plant size (Stohlgren et al. 1984, Lloret and López-Soria 1993, Pausas 1997) and stored reserves (Bowen and Pate 1993, Canadell and López-Soria 1998, Kabeya and Sakai 2005) for initiating resprouting vigorously. The effect of plant size (i.e. larger plants resprouted more vigorously than smaller ones) on resprouting vigour may be explained by the positive correlation between size and the capacity of the belowground parts of the plant to mobilize resources after the disturbance; i.e. to use stored resources and uptake water and nutrients from the soil (Rundel et al. 1987, Lloret and López-Soria 1993). Although larger plants might have higher total amount of reserves, they also have higher maintenance costs (the absolute of respiration increases with the amount of root). Thus, for the range of plant sizes considered, we can speculate that the gain resulting from the higher storage capacity and the increase in the volume of soil explored by larger plants (and thus the increased capacity of resource acquisition) is greater than the higher maintenance costs associated with the increase in biomass. Post-resprouting survival (step 3) was not directly related to the pre-disturbance state of the plant but to the initial amount of biomass that resprouting plants could produce in the early stages of regeneration (i.e. resprouting vigour). Higher resprouting vigour allows plants

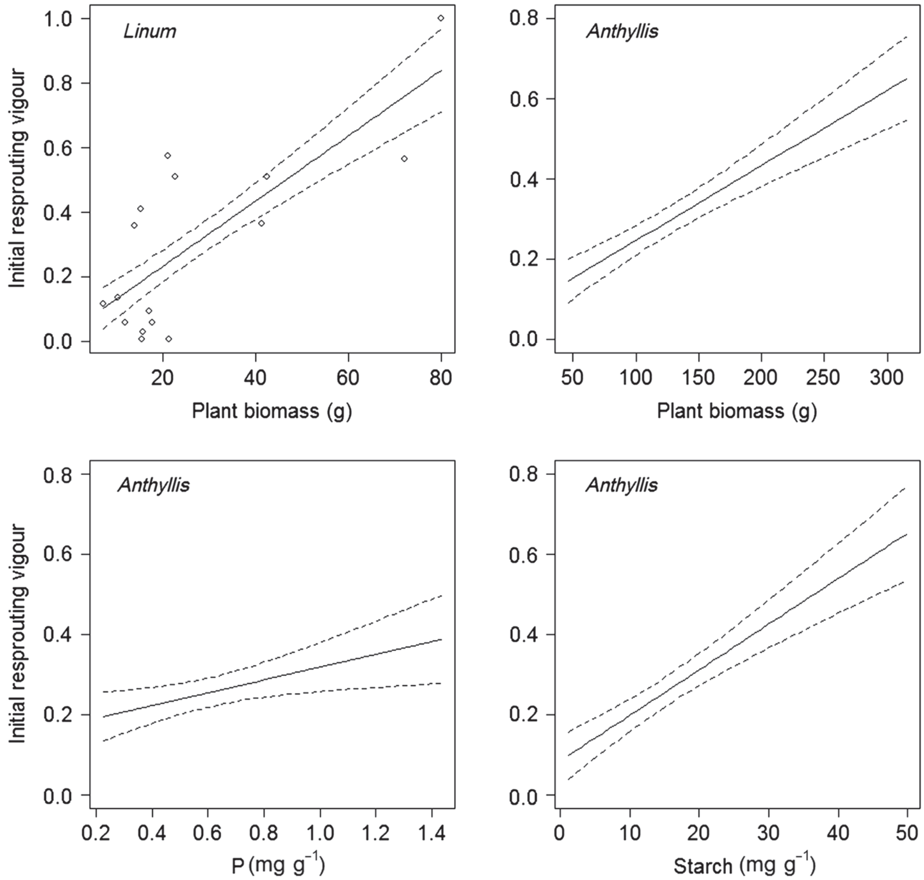

Figure 3. Resprouting vigour at 4 months after clipping (scaled between 0 and 1) for *Linum* in relation to pre-clipping plant biomass (g), and for *Anthyllis* in relation to pre-clipping plant biomass (g), concentration of phosphorus (P, mg g^{-1}) and concentration of starch (mg g^{-1}). For *Anthyllis* we used for each variable in the model the median values of the other two variables (see Table 3 for details). Dotted lines refer to SEs.

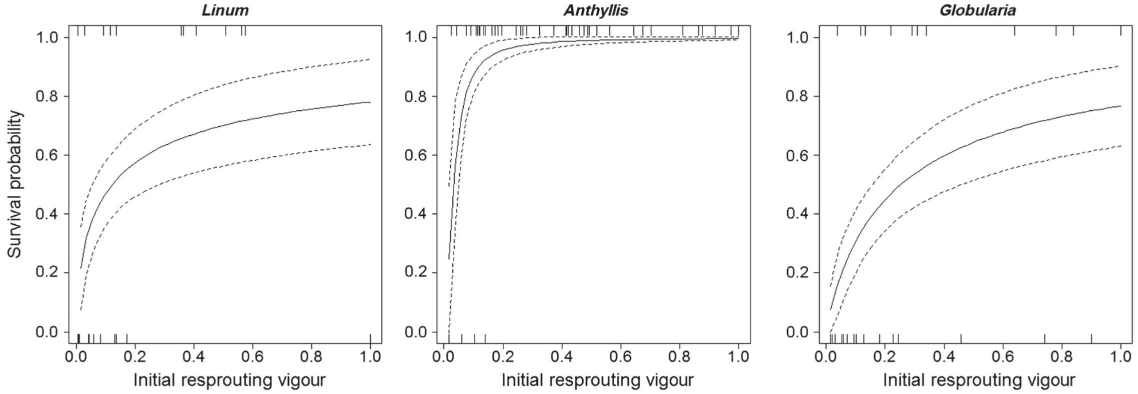

Figure 4. Probability of post-resprouting survival (step 3) one year after clipping in relation to the resprouting vigour at 4 months after clipping (scaled between 0 and 1), considering only the plants that initiated resprouting and had survived in the first survey (GLM, *Linum* p = 0.0463, *Anthyllis* p = 0.0034, *Globularia* p = 0.0102). Dotted lines refer to SEs. Ticks on the top and bottom axis indicate the values on post-resprouting survival and mortality, respectively.

to obtain more resources that can be allocated to sustain plant requirements (for respiration and growth) and restore reserves, thus increasing the probability of post-resprouting survival. This suggests that in resprouting plants living in disturbance-prone ecosystems, the photosynthetic capacity of resprouts must be under strong selective pressure towards high photosynthetic efficiency and/or high photosynthetic biomass. Indeed, leaves on resprouting shoots tend: (a) to be larger than leaves on normal shoots, (b) to have more chlorophyll on a leaf dry weight basis and, consequently, (c) to have increased photosynthesis efficiency (Arianoutsou and Margaris 1981, Castell et al. 1994, Fleck et al. 1995, Schutz et al. 2009).

It should be pointed out that our model is based on shrubs subject to clipping, that is, the disturbance applied eliminates of all above ground biomass without the destruction of buds. Applying our model to post-fire resprouting, and especially under high intensity fires, one should consider that the bud bank might also be affected by the disturbance (Vesk and Westoby 2004b). For other growth forms (e.g. trees), other traits like protective structures (e.g. bark thickness) might also become relevant (Pausas 1997).

Despite the fact that the dichotomous classification of species into resprouters and non-resprouters accounts for a high proportion of the interspecific variability in resprouting, it overrides the great intraspecific variability in this trait. Different studies have related resprouting variability to factors such as disturbance regime, and spatial, environmental or ecotypic variability (Keith 2002, Cruz et al. 2003a). However, for a given disturbance and environmental condition, we found that intraspecific variability in resprouting is determined by both the stored (pre-disturbance) resources, and the initial (post-disturbance) resource acquisition capacity. Stored reserves are important for initiating resprout and for the initial growth (first for maintaining root and buds alive and subsequently for producing new leaves and shoots). However, once plants have resprouted (using the stored reserves), they rely on the initial post-disturbance capacity to acquire resources (i.e. resprouting vigour) for surviving.

Intraspecific variability is of paramount importance for predicting species dynamics (Bolnick et al. 2011, Moreira et al. in press) and the response to environmental changes (Ramírez-Valiente et al. 2010), as well as to understand evolutionary processes (Pausas et al. 2012). This is especially evident in fire-prone environments where the regime of a strong disturbance such as fire is very sensitive to global change drivers (Dubinin et al. 2011, Pausas and Fernández-Muñoz 2012). In such ecosystems, intraspecific variability in resprouting might play a key role in determining the fate of plant species in a world with continuous changes in the disturbance regime. Thus we argue that studying individual resprouting variability in disturbance-prone ecosystems should be encouraged.

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