Journal of
Plant Ecology

VOLUME 5, NUMBER 3,
PAGES 287–293

JULY 2012

doi:10.1093/jpe/rtr030

Advanced Access published
on 27 October 2011

available online at
www.jpe.oxfordjournals.org

Responses of five woody species to burial by marly sediment: the role of biomass allocation pattern flexibility

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Abstract

Aims

In eroded lands of the French Southern Alps, burial of early established seedlings under marly sediment weakens the effect of vegetation on soil stabilization and sediment trapping. Therefore, this protective role is largely dependent on species' resistance to burial, and the understanding of species' tolerance to this environmental disturbance is highly valuable for basic knowledge on plant succession and for ecological restoration purposes.

Methods

The response of five woody species with contrasting ecological requirements and natural habitats—three tree species, *Pinus nigra*, *Robinia pseudoacacia* and *Acer campestre*, and two shrubs, *Ononis fruticosa* and *Hippophae rhamnoides*—to experimental burial under marly sediment was studied. Seedlings were exposed to three burial levels: no burial (control), partial burial (50% of seedling height) and complete burial (100% of seedling height). Burial tolerance was evaluated based on seedling survival, height and biomass. Biomass allocation to shoots and roots and soluble sugar and starch contents in roots and stems were measured to identify plant traits that determine species response to burial.

Important Findings

All species survived partial burial but only *A. campestre* seedlings emerged from complete burial. Tree species were more tolerant to burial and buried plants showed no significant differences with control. The two shrubs were found less tolerant and buried plants showed slower growth than controls. The results showed that species response was not related to initial soluble and starch content in roots and stems, but instead to biomass allocation pattern flexibility.

Keywords: burial • sediment • marls • response to burial • plant traits

Received: 6 September 2011 Revised: 6 September 2011 Accepted: 6 September 2011

INTRODUCTION

In some eroded areas of the French Southern Alps, the presence of plants growing in areas stabilized by ecological restoration (Rey 2009) is determinant for long-term erosion control (Rey *et al.* 2004). After restoration, vegetation cover is partially composed of seedlings of tree and shrubby species (Burylo *et al.* 2007; Rey *et al.* 2005) subjected to extreme environmental stresses such as burial under sediment due to concentrated flow erosion and shallow landslides (Oostwoud Wijdenes and Ergenzinger 1998).

Vegetation plays a crucial role in preventing soil erosion by influencing both abiotic and biotic conditions. Plants affect soil mechanical and hydrological characteristics by intercepting raindrops and increasing water infiltration (Morgan 1995), modifying soil chemical properties (Angers and Caron 1998) or reinforcing soil cohesion (Gyssels *et al.* 2005). Some species can facilitate the recruitment of other species (Callaway 1995) and act as nurse plants by protecting seedlings, buffering microclimatic conditions and enhancing vegetation cover development (Castro *et al.* 2004; Padilla and Pugnaire 2006). By influencing vegetation succession, resistant species can also modify communities, ecosystems and landscapes, as was observed during the past 130 years following massive ecological restoration operations in the marly badlands of the French

Southern Alps (Vallauri *et al.* 2002). Therefore, the evaluation and prediction of species' tolerance to burial are of major importance for ecological restoration purposes.

Species response to burial has been extensively studied in the past few years for herbaceous and woody dune species. It has been demonstrated that burial by sand can stimulate physiological activity and growth (Disraeli 1984; Maun *et al.* 1996; Langlois *et al.* 2001; Perumal and Maun 2006; Shi *et al.* 2004), a shift in biomass allocation (Brown 1997; Dech and Maun 2006; Harris and Davy 1988; Martinez and Moreno-Casasola 1996) and adventitious root production (Dech and Maun 2006; McLeod and Murphy 1983). Nevertheless, many of the above-mentioned studies have focused on species growing in areas where sand accretion is a frequent and constant feature of the environment, producing a spatial pattern in plant communities (Dech and Maun 2004; Maun and Perumal 1999). Many of these species are thus adapted and possess particular survival traits (Dech and Maun 2006).

Apart from morphological plasticity and flexibility in resource allocation patterns, it has been suggested that the amount of energy contained in below-ground organs such as roots, rhizomes or underground stems, could be related to the probability of survival after burial in perennial species (Maun 1998; Perumal and Maun 2006). Indeed, following burial, recovery may result from a reversion of the source-to-sink relationship, resulting in a reallocation of the energy reserves from the buried parts to the unburied parts of plants. In particular, carbohydrates, such as soluble sugar and starch, might be important for quick recycling and support after an environmental stress (Chapin *et al.* 1990).

Much of our knowledge comes from studies on the effect of burial by sand, while few reports have been published on the response of plants to burial under a different material (e.g. volcanic tephra: Antos and Zobel 1985; sediment in wetlands: Ewing 1996; sand and silt in intertidal sand flats: Mills and Fonseca 2003; Cabaço and Santos 2007). Moreover, in marly badlands, it is particularly valuable to know species' response to erosion at the seedling stage, when plants are the most vulnerable.

The present study was designed (a) to examine the responses to burial by sediment of the seedlings of species growing in the eroded lands of the French Southern Alps and (b) to investigate whether differences in species tolerance to burial can be related to plant traits such as energy reserves and biomass allocation patterns. To accomplish this goal, seedlings of five woody species, prevalent in marly badlands of the Southern Alps, were grown under controlled conditions and buried experimentally under marly sediment. Survival, growth, biomass as well as soluble sugar and starch content were measured to evaluate and explain species' response to burial.

MATERIALS AND METHODS

Study area and species

The study was conducted in a common garden at the Cemagref institute (Agricultural and Environmental Engineering Research Institute) in Grenoble (France). In Grenoble (210 m a.s.l.; 45°10′N, 5°45′E), the climate is oceanic with continental influences. The mean annual precipitation is 1300 mm, evenly distributed throughout the year. Mean annual temperature ranges from 2.8°C in December to 21.8°C in July (Météo-France, 1971–2000).

Five woody species, all pioneer species prevalent in the marly lands of the French Southern Alps, were selected for the study. There were three tree species, *Pinus nigra* Arn. ssp. *nigra*, *Robinia pseudoacacia* L. and *Acer campestre* L. and two shrubs, *Ononis fruticosa* L. and *Hippophae rhamnoides* L. *P. nigra* and *R. pseudoacacia* are exotic species native to the Balkans and North America, respectively. *Robinia pseudoacacia* is invasive in many regions, but this behaviour has not been observed in marly lands where its development has remained similar to native species since it was introduced. *Acer campestre* also shows a pioneer behaviour on unstable soils. *Ononis fruticosa* and *H. rhamnoides* are both heliophytes commonly found in Mediterranean and perialpine regions, capable of nitrogen fixation because of its symbiotic relationships with *Rhizobia* and *Frankia* bacteria, respectively.

Growth conditions and burial treatments

In early May, commercial seeds of the five species were germinated in vermiculite, a chemically inert mineral substrate and allowed to grow for 3–4 weeks in a growth chamber at 25/15°C day/night temperature and 70% relative humidity. After germination, forty seedlings of each species, similar in size and shape, were selected and transplanted into plastic pots (14 cm in diameter × 17 cm deep) filled with marly substrate collected from the field (Draix experimental site, Alpes de Haute Provence Department, France, 44°8′N, 6°20′E). The plants were then placed in the common garden in a randomized block design. After acclimation (5 weeks), the plants were buried under marly sediment using polyvinyl chloride (PVC) drainage pipes (12 cm in diameter). Three burial treatments were tested: no burial (control), partial burial (50% of plant height) and complete burial (100% of plant height). Plant height ranged from 5.5 to 10.2 cm on average (Table 1) and average burial depth ranged from 2.9 to 5.2 cm for partial burial and from 5.7 to 10.6 cm for complete burial. These burial depth values are on similar order of magnitude as the sediment deposit heights observed in the field, which are approximately 10 cm per year (Rey 2009). At the same time, another sample of seedlings was harvested to measure carbohydrate content

Table 1: **mean plant heights and burial depths (cm ± SE) at the time of burial**

	Height	Partial burial depth	Complete burial depth
Acer campestre	8.4 ± 0.5	4.5 ± 0.3	8.5 ± 0.4
Hippophae rhamnoides	5.5 ± 0.4	3 ± 0.2	6 ± 0.4
Ononis fruticosa	5.6 ± 0.6	2.9 ± 0.2	5.7 ± 0.4
Pinus nigra	5.9 ± 0.4	3.2 ± 0.2	5.7 ± 0.3
Robinia pseudoacacia	10.2 ± 0.6	5.2 ± 0.4	10.6 ± 0.5

at the time of burial and preserved at −80°C until analysis. There were 10 replicates per treatment per species. The pots were watered when natural precipitations were not sufficient but no fertilizer was applied. During the experiment, which was carried out from June to August 2007, total rainfall reached 325 mm and the mean temperature was 21.2°C. Eight weeks after burial, all plants were harvested.

Measurements and data analysis

To evaluate species' responses to burial, survival and plant height were recorded every 2 weeks during the experiment. At the end of the experiment, PVC pipes were gently removed and the entire plant was harvested. Seedlings were carefully cleaned of the remaining soil particles and separated into shoots and roots for biomass measurements. Plant fractions were then dried at 60°C for 48 h and weighed, and the shoot-root ratio was calculated. Samples harvested at the time of burial were used to measure soluble sugar and starch content in roots and stems of plants following the protocol described in Dreywood (1946).

A repeated-measures analysis of variance (ANOVA) was used to analyse species' response for plant height. One-way ANOVAs were used to investigate differences in shoot and root biomass and the shoot–root ratio among treatments as well as differences in soluble sugar and starch content among species [Tukey's HSD (Honestly significant difference) test]. The assumption of normal distribution was checked before analysis (Shapiro–Wilks test). All the analyses were carried out with STATISTICA (version 7.1 for Windows).

RESULTS

Species response to burial

Survival of seedlings

All individuals survived in the control treatment and only a few individuals died after partial burial with survival rates varying between 90 and 100% (Table 2). On the other hand, only *A. campestre* survived complete burial, with 40% of the seedlings that had emerged from sediment 6 weeks after burial. This percentage fell to 20% at 8 weeks after a violent hail storm. For the rest of the analyses, only the data resulting from control and partial burial treatments were used since no plant material was available for measurement after complete burial.

Plant height

Both control and partially buried seedlings had positive growth in height during the experiment (Table 3, effect of burial duration). The two shrubby species, *H. rhamnoides* and *O. fruticosa*, had the highest growth rates, with an average 150 and 115% increase in seedling height, respectively. Tree species, *A. campestre*, *P. nigra* and *R. pseudoacacia*, exhibited smaller increases, respectively, 37, 7 and 37% (Fig. 1). Burial had a significant effect on the height of the shrub *H. rhamnoides* (Table 3, effect of burial), resulting in lower height values in buried seedlings. Differences between buried and unburied individuals became significant 6 weeks after burial and height values were found 44% higher in control seedlings at the end of the experiment. For the remaining four species, burial had no significant effect on plant growth.

Table 2: percentages of seedlings emerged from sediment through time under the different Burial treatments

Burial treatment	Species	2 Weeks	4 Weeks	6 Weeks	8 Weeks
Control	All species	100	100	100	100
	Acer campestre	100	100	100	100
	Hippophae rhamnoides	100	100	100	100
50%	*Ononis fruticosa*	90	90	90	90
	Pinus nigra	100	100	100	100
	Robinia pseudoacacia	100	90	90	90
100%	*Acer campestre*	0	10	40	20
	Other species	0	0	0	0

Table 3: *F* values and significant levels of the effect of burial duration, burial and their interaction on seedlings height determined by the repeated-measures ANOVA

Species	Burial duration	Burial	Time × burial
Acer campestre	20.4***	0.002, ns	0.3, ns
Hippophae rhamnoides	72.4***	5.4*	5.6***
Ononis fruticosa	69.4***	1.88, ns	2.06, ns
Pinus nigra	4.5*	1.2, ns	0.9, ns
Robinia pseudoacacia	9.5***	0.1, ns	0.1, ns

Significance levels are ns, non-significant, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Biomass

Biomass of *H. rhamnoides* was negatively affected by burial and was found significantly lower in buried individuals, for both above- and below-ground parts (Table 4). The root biomass of *P. nigra* also decreased following burial. For the remaining treatments, burial had no significant effect on species' biomass.

Biomass allocation pattern

Biomass allocation patterns were also affected by burial. At the end of the experiment, the shoot–root ratio was significantly higher in partially buried seedlings of the tree species (Table 4). Biomass allocation patterns were not significantly different between control and buried seedlings of the shrubby species.

Energy reserves

There were significant differences in initial soluble sugar and starch content in plant stems and roots among species (Fig. 2). For sugar content in roots, *A. campestre* had the lowest mean concentration, while *P. nigra* had concentrations almost three times

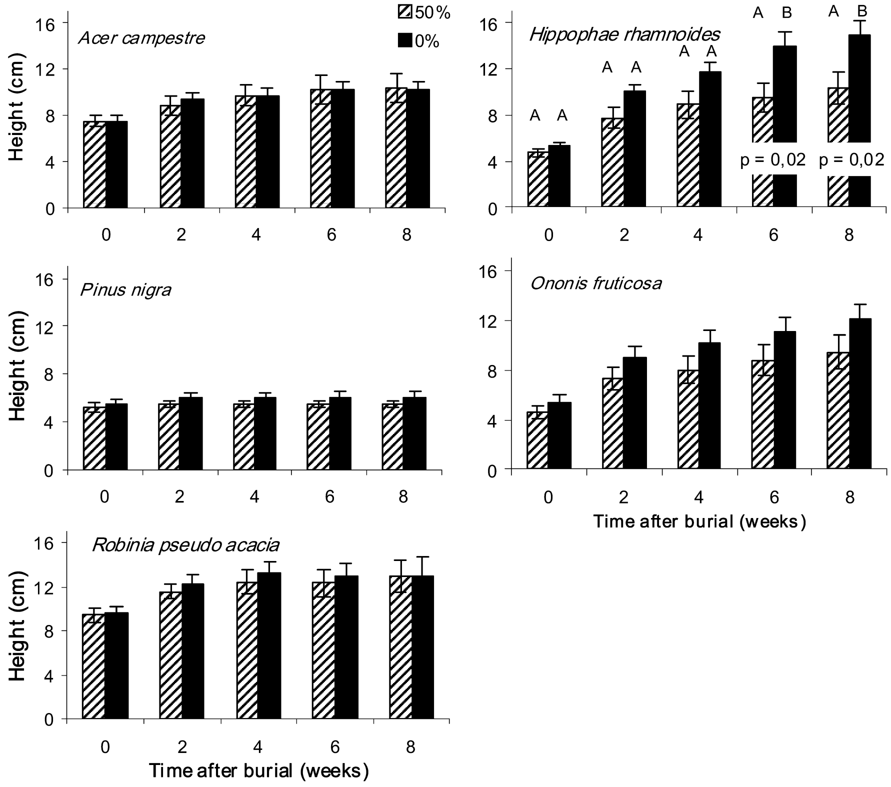

Figure 1: species growth after burial. Values are mean height (cm) ± SE. Letters indicate significant differences between treatments when burial effect was found significant in Table 3.

Table 4: mean values ± of shoot biomass, root biomass and shoot:root ratios of five woody species in two burial treatments (control and partial burial), *F* statistics and significant levels of ANOVA for the effect of burial

	Shoot biomass			Root biomass			Shoot:root ratio		
	Control	Burial	*F*	Control	Burial	*F*	Control	Burial	*F*
Acer campestre	0.34 ± 0.07	0.40 ± 0.09	0.10, ns	0.56 ± 0.09	0.45 ± 0.06	1.84, ns	**0.60 ± 0.03**	**0.83 ± 0.08**	**6.36***
Hippophae rhamnoides	**0.26 ± 0.05**	**0.10 ± 0.02**	**5.65***	**0.12 ± 0.03**	**0.04 ± 0.01**	**4.95***	2.32 ± 0.45	2.37 ± 0.23	0.06, ns
Ononis fruticosa	0.16 ± 0.02	0.13 ± 0.02	0.33, ns	0.09 ± 0.02	0.07 ± 0.01	0.24, ns	1.93 ± 0.19	1.92 ± 0.15	0.005, ns
Pinus nigra	0.13 ± 0.01	0.11 ± 0.01	1.87, ns	**0.12 ± 0.01**	**0.07 ± 0.01**	**14.02****	**1.04 ± 0.05**	**1.61 ± 0.13**	**9.08****
Robinia pseudoacacia	0.37 ± 0.11	0.38 ± 0.14	0.43, ns	0.25 ± 0.06	0.17 ± 0.04	0.32, ns	**1.40 ± 0.12**	**2.09 ± 0.34**	**5.05***

Significance levels are ns, non-significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Significant effects are highlighted in bold.

higher. *Hippophae rhamnoides*, *O. fruticosa* and *R. pseudoacacia* had intermediate mean concentrations. As for starch content, variations between species were even more contrasted. The starch concentration in the stems of *P. nigra* was more than six times lower than in *H. rhamnoides*, and in its roots, it was five times lower than the concentration in the roots of *O. fruticosa*.

DISCUSSION

The present study examined the response of individual plant species to experimental partial and complete burial. The results of this experiment showed that plant survival after burial differs among the five species. Complete burial (100% of plant height) caused high seedling mortality rates and only *A. campestre* seedlings survived. Seedlings of all the species survived partial burial. These results corroborate the findings of several authors who reported that certain species were unable to emerge from complete burial while other could (Shi *et al.* 2004; Zhang and Maun 1992; Zhang *et al.* 2002).

The tolerance to burial was also found to differ according to species' growth form. Following burial in sediment, the two shrubby species, *O. fruticosa* and *H. rhamnoides*, exhibited a decrease in height growth, and *H. rhamnoides* also showed a decrease in shoot and root biomass. These observations are typical of the negative response described by Maun (1998). The three remaining tree species, *P. nigra*, *R. pseudoacacia* and *A. campestre*, showed

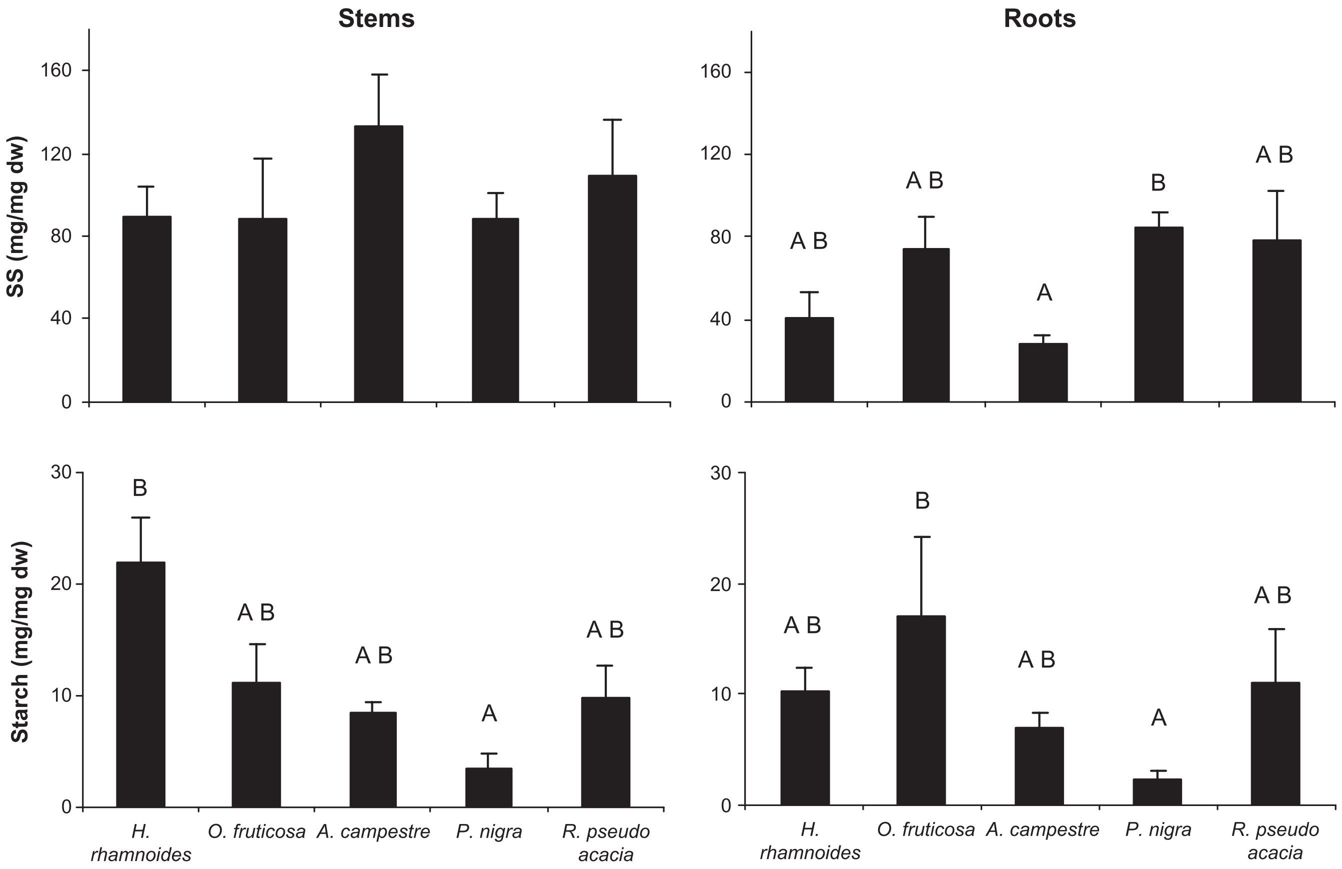

Figure 2: soluble sugar (SS) and starch concentrations (in mg/mg of plant dry weight) in the stems and roots of the five species studied at the beginning of the experiment. Bars are means ± SE. Letters indicate significant differences between species (Tukey HSD test, $P = 0.05$).

a rather neutral response. In these species, height and shoot biomass in buried plants remained similar to control but root biomass was found slightly lower for *P. nigra*. However, none of the species studied had a positive response. The results of this experiment suggest that early established seedlings of tree species have a greater ability to withstand burial than shrubby species.

Plants' response to burial has been related to adventitious root production (Dech and Maun 2006; Langlois *et al.* 2001; McLeod and Murphy 1983) and shifting in biomass allocation patterns (Brown 1997; Dech and Maun 2006; Martinez and Moreno-Casasola 1996). In the present experiment, no adventitious roots were observed, but, as expected, the shoot–root ratio increased in the buried tree species identified as more tolerant to burial, whereas it remained constant in the two shrubby species. This reversal of the source–sink relationship is assumed to support the maintenance and the growth of shoots after burial (Brown 1997; Dech and Maun 2006; Harris and Davy 1988).

We hypothesized that species' response to burial could also be determined by carbohydrate reserves in plant stems and roots. The results on soluble sugar and starch concentrations show no trend supporting this hypothesis. However, nutrient concentrations (N, P and K), which can also influence species' response (Chapin *et al.* 1990), were not measured. In particular, nitrogen and nitrogen compound concentrations could be important factors in the nitrogen-fixing species, *O. fruticosa*, *H. rhamnoides* and *R. pseudoacacia*.

The species studied in this experiment are pioneer species in plant successional series capable of withstanding severe climatic conditions such as drought, warm temperatures and poor and poorly structured soils. The results reported herein show that, at the early stages of plant development, tree species seem more tolerant to burial in sediment than shrubby species. Surprisingly, *O. fruticosa* and *H. rhamnoides* presented a negative response to burial whereas they are known for their robustness and resistance to erosive constraints (Barrouillet 1982; Burylo *et al.* 2009). The decrease in oxygen concentration in the root zone due to soil deposition (Maun 1998), reducing the activity of symbiotic bacteria, might explain the lower level of activity of these two species.

This experiment was designed to test for species tolerance to burial in terms of vertical growth, whereas species' response to disturbance is typically classified into three processes: tolerance, avoidance and regeneration (Lavorel and Garnier 2002). Regeneration through resprouting may be an alternative survival strategy for plant species after burial in sediment. Indeed, after the whole above-ground biomass has been removed by environmental disturbances (e.g. erosion, fire, herbivory), many species have the ability to resprout from axillary or adventitious buds and persist (Bellingham and Sparrow 2000; Guerrero-Campo *et al.* 2006, 2008; Pausas *et al.* 2004). Clonal integration can also enhance survival after burial. Yu *et al.* (2001) observed that unburied parts of plants can support the buried parts using stolon connection and thus improve the capacity of the plant to withstand burial. In particular, *O. fruticosa* and *H. rhamnoides* are species known to invest a substantial part of their biomass into vegetative structures (Barrouillet 1982; personal observations through field prospects). However, none of the data confirm vegetative regeneration as a means to enhance the performance of these species in the field. Further investigations into species' strategy to resist burial would contribute useful new information and extend our understanding of species resistance to burial. In particular, more partial burial treatments, e.g. 75% of plant height, should be tested to better discriminate species responses.

CONCLUSION

The present study has shown that woody species can tolerate burial in marly sediment up to a certain height in the early stages of development and thereafter, which may have important implications for degraded land management and the evaluation of ecosystem resistance to erosive constraints. The results highlighted that tree species (*P. nigra*, *R. pseudoacacia* and *A. campestre*) tend to be more resistant than shrubby species (*O. fruticosa* and *H. rhamnoides*), which exhibited lower growth after burial. Species' response was not related to initial soluble and starch content in roots and stems, but instead to biomass allocation pattern flexibility, consistent with previous studies.

FUNDING

This work resulted from the project 'Génie biologique sur la Durance', funded by EDF (Electricité de France), Agence de l'eau Rhône Méditerranée et Corse, Région Provence Alpes Côte d'Azur and the European Union with FEDER funds.

ACKNOWLEDGEMENTS

We thank Damien Lemoine for his help in preparing root samples and measuring soluble sugar and starch content and for valuable comments on the experiment. We would like to thank Sophie Labonne for assistance in collecting and analysing root samples and help in the laboratory.

Conflict of interest statement. None declared.

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