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Abstract Seed sowing may be a cheap and efficient reforestation method that can yield high-quality seedlings for many woody species, but this option is usually discarded against seedling planting due to the high seed losses to mammal predators. The search for methods to reduce seed predation is therefore a key issue to broaden reforestation options and restoration success. In this study we tested (1) the effectiveness of a new device to prevent small mammals from consuming large seeds such as acorns and (2) its effect on initial seedling performance. The device consists of a capsule made of two truncated pyramids joined at the bases, with two small openings at the top and the bottom where the stem and root can exit but rodents cannot enter. We conducted a field seed-predation experiment using fenced plots (only rodents present) and unfenced plots (rodents + wild boar present) and a nursery experiment to check seedling emergence and growth. Acorn predation by rodents was almost nil when protected by the device (1.1 vs. 53.4 % without seed shelter), whereas predation by wild boar in the unfenced plots was not reduced by the device (12.4 %). In the nursery experiment there was no effect of the device on seedling emergence or growth. These results suggest that physical protectors like the one used in this study could represent a cheap method to foster the restoration of tree cover via seed sowing, especially if used in combination with fences or habitat features to reduce predation by large animals.

Keywords Seed predation · Innovation · Technology · Forestry · Direct seeding

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Introduction

Forest restoration is a major challenge worldwide, and it has enormous ecological and societal implications (Egan et al. 2011; Lamb and Gilmour 2003). Besides compensating for the ongoing loss and degradation of ecosystems, forest restoration can enhance biodiversity and recover the functioning of important ecosystem services such as water retention, atmospheric regulation, and the provision of forest goods and spiritual values (CBD 2001; Lamb and Gilmour 2003; MA 2005; Rey-Benayas et al. 2009). Forest restoration also has substantial economic implications, arising both from the large investments in these activities and the value of the restored ecosystem services (MA 2005; Mansourian et al. 2005). The success of forest restoration is thus paramount to meet ecological and societal targets, and innovation can play an essential role in achieving this in an economically efficient way.

Besides natural regeneration, active restoration of tree cover is usually addressed in one of two ways: planting nursery-grown seedlings (either with bare-rooted seedlings or enclosed in root containers) or seed sowing (Savill et al. 1997; Allen et al. 2001; Lamb and Gilmour 2003; Dey et al. 2008). Seedling planting has several advantages over sowing, such as generally faster seedling growth (Allen et al. 2001; Löf et al. 2004; Fields-Johnson et al. 2010), higher survival rates (Dey et al. 2008; Fields-Johnson et al. 2010; Valkonen 2008; but see González-Rodríguez et al. 2011; Löf et al. 2004), promotion of habitat heterogeneity and diversity (Twedt and Wilson 2002), and the avoidance of seed predation (Stewart et al. 2000). However, seed sowing potentially generates a much lower impact on soil and vegetation during working operations, which in turn are easier to carry out, have more flexibility in terms of timing, and allow restoration in areas where seedling planting is too costly or difficult (Allen et al. 2001). Sowing also reduces the risk of transferring plant diseases from nurseries to the field (Sánchez et al. 2005). And, in particular, the economic cost of sowing is far lower than that of planting (Bullard et al. 1992; King and Keeland 1999; Madsen and Löf 2005; Farlee 2013). The net balance between seedling planting and seed sowing, whenever the target species offers both possibilities, is thus context-dependent.

In addition to the above considerations, many plant species develop a tap root—a large, central dominant root growing directly downward from which the rest of the root system sprouts laterally– whose morphology may be affected by the choice of reforestation method (Savill et al. 1997). This is particularly the case of oak species (genus *Quercus*), which constitute a major component of forest ecosystems in the Holarctic and are a frequent target in restoration and reforestation programs (e.g. EEC Regulation no. 2080/92). In the case of nursery-grown oak seedlings, the tap root may be damaged or anomalously-shaped when grown in containers, or pruned in the case of bare-root transplanted seedlings (Allen et al. 2001; Tsakaldimi et al. 2009; Farlee 2013). This may lead to a shallower root system with less access to soil moisture (McCreary 2009; Tsakaldimi et al. 2009), and ultimately to an abnormal development and lower performance of the seedling, particularly in areas with marked water stress during the growing season such as Mediterranean-type ecosystems (Pemán et al. 2006; McCreary 2009; Tsakaldimi et al. 2009; González-Rodríguez et al. 2011). By contrast, oak seedlings regenerated via seed sowing show a normal tap-root development (Tsakaldimi et al. 2009; Zadworny et al. 2014). In addition, acorn sowing usually renders high emergence (usually 50–90 %; Fuchs et al. 2000; Gómez 2004; Valkonen 2008) and survival rates (usually above 50 % and up to 100 % during the first growing seasons; Gómez 2004; Navarro et al. 2006). All this suggests that acorn sowing could be an effective method to restore oak forests. However, acorn sowing is largely discarded due to the high losses to vertebrate seed predators, mainly rodents and, to a lesser extent, larger animals such as wild boars (Dey et al. 2008; McCreary 2009; Farlee 2013). Thus, acorn sowing could be regarded as an effective restoration method provided that seed predation is controlled. Under these premises, the search for methods to reduce seed predation has long been recognized as a key issue to improve the effectiveness while reducing the cost of reforestation efforts (Allen et al. 2001; Dey et al. 2008; Farlee 2013), and the discovery of an effective protection could represent a landmark in the science and practice of forestry and restoration ecology.

Non-lethal methods to control acorn predation have been investigated for decades. Several types of protection have been suggested, such as using or creating habitat types that negatively affect seed predators (McCreary 2009; Birkedal et al. 2010; Leverkus et al. 2013), adding perches to attract birds of prey (Farlee 2013), increasing burial depth (Fuchs et al. 2000; Leverkus et al. 2013), sowing at times of high food availability or providing alternate food sources to satiate predators (Sullivan 1979; Dey et al. 2008), applying non-harmful chemical repellents (Williams and Funk 1979; Nolte and Barnett 2000; Leverkus et al. 2013), and employing physical protectors ranging from large-scale fencing to small wire mesh screens, perforated cans, or buried tubes (Schmidt and Timm 1991; Löf et al. 2004; Madsen and Löf 2005; Dey et al. 2008; McCreary 2009; Farlee 2013). None of them have, however, shown satisfactory results to date for large-scale restoration. Devices that offer physical protection, in particular, are generally ineffective, alter the normal development of roots, are difficult and expensive to produce, are large and uncomfortable to carry in the field, and/or require excessive post-sowing management (see references above). Consequently, sowing is still often not used in reforestation largely because of the unresolved problem of seed predation.

In this study, we tested the effectiveness of a new, simple device to protect seeds from predators. The seeds were inserted into the device (named seed shelter), which was later buried. Due to its small size, the seed shelter is designed to protect seeds primarily from rodents, but it might also be effective against larger predators such as wild boars. To test the effectiveness of the seed shelter against predators we conducted an acorn predation experiment under field conditions using fenced (allowing only rodent predation) and unfenced plots (allowing predation by both rodents and ungulates). We also performed a nursery experiment to detect any effect of the seed shelter on seedling emergence or development. We hypothesized that (1) the seed shelter would reduce acorn predation by rodents and possibly by larger animals such as wild boars, and (2) the seed shelter would not affect plant development or growth. Overall, we expected to find a way to turn acorn sowing into an effective, reliable, and low-cost method to restore oak forests. If confirmed effective, the use of this protective device or any other similar physical structure could help to boost the efficiency of forestation activities and potentially increase their extent by greatly reducing reforestation costs.

Materials and methods

The seed protector

In this study we tested a prototype of a new device named seed shelter (patent number 201331441, University of Granada). The prototype consisted of a capsule made of two truncated quadrangular pyramids joined at the bases (Fig. 1). These pyramids were

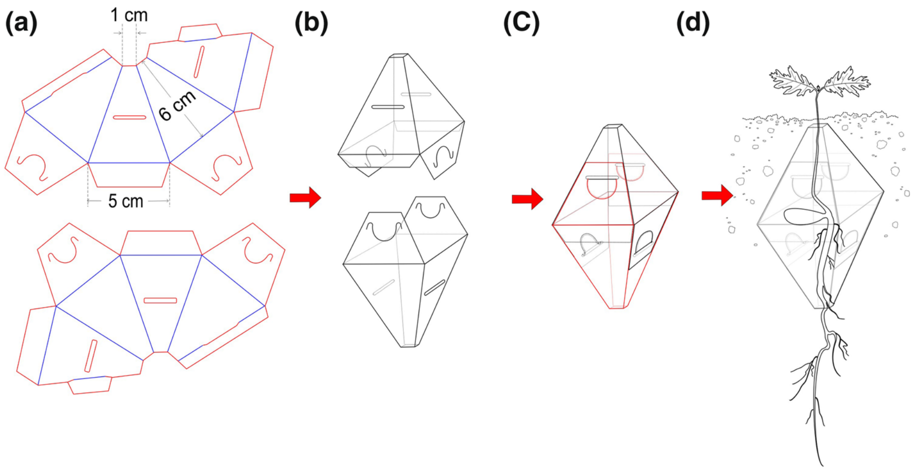

Fig. 1 Design of the seed shelter used for this study. It consists of two truncated pyramids punched out of a plastic sheet of 0.8 mm thick polypropylene (**a**). Two identical pyramids (**b**) were interlocked at the base to form the capsule (**c**), which was filled with soil and an acorn and buried (**d**)

manufactured from flattened shapes punched out of 0.8 mm-thick polypropylene sheets and then assembled with a series of crimped folds and tabs interlocked into slots. Two identical pyramids are then filled with soil [33.3 % sand and 66.6 % peat (Kekkilä Garden Brown 025W)] plus an acorn, and then interlocked bottom-to-bottom to form the 10.5 cm-high capsule (Fig. 1). The capsule is then buried vertically with its upper opening at 2 cm below ground. The rationale is that while the openings at the upper and lower ends are too tiny for a small mammal to penetrate, they are large enough to allow the shoot and root to exit. The design of this prototype was chosen because of the ease of the punch-out system for manufacturing a few hundred homemade units. The material used for this prototype is not biodegradable, so that all the units used in the experiments were finally removed and brought back to the laboratory.

Seed predation experiment

The experiment for seed predation was conducted under field conditions at the Loma de los Panaderos (La Cortijuela Botanical Garden, Sierra Nevada National Park, SE Spain; 37°5′N, 3°28′W). Previous studies have documented high rates of acorn predation in this area, both by rodents and wild boars (Gómez et al. 2008; Puerta-Piñero 2010). We used three fenced plots of ca. 3000 m^2 (approximately 200 m apart from each other) built in 1997 where ungulates were excluded (Castro et al. 2004), as well as three unfenced plots located just beside the fenced plots. This allowed an experiment with two levels of predators (ungulates plus rodents, using the unfenced areas; and only rodents, using the fenced areas). The site, located at 1800 m a.s.l., has Mediterranean-type climate with a mean rainfall of 830 l m^{-2} y^{-1}, mean temperature of the coldest month (January) of 3.5 °C, and mean temperature of the hottest month (August) of 21.6 °C. Vegetation in the area is dominated by successional shrubs intermingled with interspaces of bare ground and some scattered trees (Castro et al. 2002). The acorns used for this experiment were from *Quercus suber* L. (a widely distributed oak species in the Mediterranean region) and had an average weight of 6.77 ± 1.16 g (50 acorns weighed). The acorns were harvested 3 weeks before the experiment and stored under cold conditions (4 °C) until the time of sowing.

We randomly placed 30 sowing stations in each plot and sowed two acorns (≈50 cm apart) at each station: one acorn with a seed shelter and one without, rendering a total of 360 monitored acorns (6 plots × 30 sowing stations × 2 acorns per station). Sowing stations were at least 10 m apart from each other. Acorns with seed shelter were placed inside the device as described above, and the whole structure was buried in the soil (Fig. 1), resulting in seeds sown at a depth of ca. 7 cm. Acorns without seed shelter were buried at a similar depth. Sowing was conducted in February 2014, and acorn predation was monitored after 15, 30 and 90 days of sowing, noting the state (depredated or not) of each acorn and the predator responsible. Predator identity was ascribed to wild boars when the sowing point was completely unearthed by boar rooting, to mice (*Apodemus sylvaticus* in the study area) when there was a narrow hole excavated from the surface to reach the acorn, and to voles (*Microtus duodecimcostatus*) when there were apparent tunnels reaching the sowing point (predator attribution was based on previous works in the area and authors' personal experience; Puerta-Piñero et al. 2010; Leverkus et al. 2013). The first and second samplings were non-destructive, and thus we noted the state (depredated/non-depredated) according to visual inspections. In the last sampling, conducted at the time of acorn germination (in May 2014), we additionally unearthed all the sowing points to confirm the presence of the acorn. We considered removed acorns as depredated because previous studies found that >98 % of acorns found by rodents are finally depredated and that there is no secondary caching by the main acorn dispersers in the area (Gómez et al. 2008). The cases where the seed shelter was unearthed by an animal but without acorn consumption were considered as depredated in the analyses, as these acorns desiccated inside the devices and were unlikely to render viable seedlings (pers. obs.). In the last sampling we also noted whether the non-depredated acorns had germinated. Two sowing stations (thus two acorns with and two without seed shelter) were not relocated and were removed from the analyses.

Seedling development experiment

To assess the potential effects of the seed shelter on seedling emergence and initial development we conducted a nursery experiment under outdoor conditions in a nursery located close (1 km) to the University of Granada campus, at 735 m a.s.l. The acorns used for this experiment were from *Quercus ilex* L. (similarly a widely distributed oak species in the Mediterranean region) and had an average weight of 6.20 ± 1.14 g (50 acorns weighed). They were harvested 4 weeks before the experiment and stored under cold conditions (4 °C) until the time of sowing. We sowed each of 30 acorns with and 30 without seed shelter inside 50 cm length, 9 cm diameter PVC tubes, which were buried with their upper opening at ground level. The tubes were positioned 3 cm apart, and were used to ensure that roots of different seedlings did not overlap, guaranteeing the individuality of each sample. Inside the tubes, the upper 25 cm were filled with the same soil mixture as the seed shelter, and the lower 25 cm with local soil. Local soil is deep, of alluvial nature, with average values up to 1 m deep of 44.8 % sand, 41.8 % silt, 13.3 % clay, and 0.8 % organic matter [measurements performed at *Laboratorio Agroalimentario de la Junta de Andalucía,* Atarfe, Granada (official laboratory of the Regional Agricultural Service)].

Sowing was conducted on 3 March, randomly distributing acorns with and without seed shelter among the tubes. The experiment was monitored regularly for seedling emergence and survival. On 27 July (almost 5 months after sowing), seedlings were uprooted and examined for root and shoot length and biomass, number of shoots produced, shoot diameter (measured at root collar level and values obtained by averaging two perpendicular measurements) and root-to-shoot ratio. The site was irrigated by soil flooding every 10 days from the onset of summer drought (mid June).

Data analyses

To test the effect of fencing and the seed shelter on final acorn predation and acorn germination, we fitted a generalized linear mixed model with binomial errors, using the lmer function from the lme4 package (Bates et al. 2012) in R (version 3.1.1; R Development Core Team 2014). In these models we specified the spatial structure of the experiment (sowing stations located within plots) in the random effects part of the model, and we used *Fencing*, *Seed shelter* (its presence or absence), and the *Fencing* × *Seed shelter* interaction as fixed effects. To analyze predation by the individual predator guilds (wild boars or rodents) we considered the acorns depredated by the other guild as not being depredated and repeated the analysis. For computational reasons we had to simplify the specification of the experiment's spatial structure with only plot as a random effect in these models. *P* values for the mixed models were calculated with the "mixed" function of the "afex" package (Singmann 2014).

The effect of the seed shelters on seedling emergence in the nursery experiment was analyzed with a GLM with binomial errors, and the number of shoots with a GLM with Poisson errors (there was no overdispersion in these models). All other growth parameters were analyzed with an ANOVA.

Results

Seed predation experiment

Acorn predation was affected by the *Seed shelter* but not by *Fencing* (Table 1), with an overall value of 33.4 % (all treatments pooled). Predation by small rodents (mice and voles) happened exclusively on acorns without seed shelters (52.8 vs. 0.0 % with seed shelter; Fig. 2) and was not significantly affected by *Fencing* ($\chi^2 = 1.29$, $P = 0.26$; analysis for acorns without seed shelters only). On the contrary, predation by boars happened exclusively

Table 1 Summary of the generalized linear mixed model for overall acorn predation and germination (all factors considered simultaneously) in the field experiment

Variable	Source	*df*[a]	F	*P*
Acorn predation	Fencing (F)	1, 7.53	0.02	0.88
	Seed shelter (S)	1, 176	112.31	<0.0001
	F × S	1, 176	2.61	0.11
Acorn germination	Fencing (F)	1, 33.19	0.01	0.92
	Seed shelter (S)	1, 230.12	17.34	<0.0001
	F × S	1, 232.99	1.57	0.21

[a] Numerator and denominator, respectively

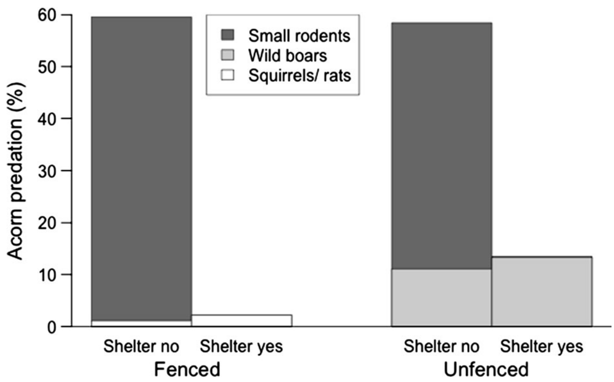

Fig. 2 Percentage of acorn predation by the different predator guilds relative to fencing and the use of seed shelters. Small rodents included mice and voles

in the unfenced areas (12.4 vs. 0.0 % inside fences; Fig. 2) and was not affected by *Seed shelter* ($\chi^2 = 0.22$, $P = 0.64$; analysis for acorns outside the fences only).

From the seed shelters dug up by boars (thus considered depredated), 33.3 % were cracked open and had the acorns inside depredated, whereas the remaining 66.7 % were lying intact on the ground with the acorn untouched but desiccated in most of the cases. Two acorns with seed shelter and one without were depredated within the fenced plots, presumably by a large rodent such as a rat or squirrel (because of the tracks left and the seed shelters being unburied—the whole seed shelter is presumably too heavy for a mouse or vole); other than these, all the acorns with seed shelter within the fences survived (see above). Germination of non-depredated acorns was significantly higher for acorns with seed shelters (93.9 %) than without (72.6 %; Table 1).

Seedling development experiment

None of the parameters regarding seedling emergence and initial performance differed among treatments (Table 2; Online Resource 1). Nonetheless, a further examination of the non-emerged seedlings showed that 50 % of the failed seedlings within a seed shelter had a clear spiraling of the root whereas this happened in only 14 % of the failed seedlings without seed shelter. On the other hand, in 13 % of the seedlings emerged in a seed shelter, the shoot or the root protruded through the assembly slots.

Discussion

Effectiveness of the seed shelter

Our results show that the seed shelter was 100 % effective against predation by mice and voles and, in addition, it did not affect seed germination, seedling emergence, or initial seedling growth. As predation by small rodents is a major reason for the failure of re-forestation with acorns (Dey et al. 2008; Farlee 2013), the new device could in many cases be considered sufficient to boost the effectiveness of direct sowing.

Larger rodents such as rats and squirrels, as well as rabbits, may depredate sown acorns also (Crawley and Long 1995; Herrera 1995; Farlee 2013), although their effect on

Table 2 Summary of the growth parameters recorded for seedlings in the nursery experiment after 5 months

Variable	Measured values[a]		Test statistic[b]	P value
	With seed shelter	Without seed shelter		
Seedling emergence (%)	80.0	76.7	0.313	0.75
Number of shoots	3.39 ± 0.40	3.08 ± 0.39	0.573	0.57
Root length (cm)	37.93 ± 1.74	36.56 ± 1.23	0.410	0.53
Shoot length (cm)	23.01 ± 1.26	24.07 ± 1.08	0.408	0.53
Shoot diameter (mm)	3.25 ± 0.13	3.33 ± 0.18	0.113	0.74
Root mass (g)	1.39 ± 0.13	1.49 ± 0.14	0.293	0.59
Shoot mass (g)	2.34 ± 0.21	2.46 ± 0.19	0.208	0.65
Root:shoot ratio	0.63 ± 0.04	0.59 ± 0.03	0.477	0.49

[a] Values are mean ± 1 SE of the mean (except for seedling emergence, which are percentages)

[b] z value for emergence and number of shoots; F for the rest of variables. The test for germination is based on 1 and 58 degrees of freedom and all the rest on 1 and 44

reforestation is possibly minor, judging by the few references to them in the literature. In our study, three acorns (out of the 360 sown, thus <1 %) were considered likely to have been consumed by one of these animals. The loss of these acorns was inconsequential in this case, but careful consideration of potential predators in a particular area might be necessary to ensure the efficacy of the seed shelter. For cases where large rodents are feared to jeopardize the success of sowing, the mass of the seed shelter could be increased by means of modifications to its volume, substrate type, or both, thereby enabling a reduction of their impact. Thus, we expect that the potential detrimental effect of small mammals could be minimized.

In contrast to rodents, wild boars generated acorn losses irrespective of the seed shelters, although they had a low overall impact (≈12 % predation on unfenced plots). The commonly reported lower impact of ungulates respect to rodents is often explained by the frequently observed high and fast acorn predation by the latter (e.g. Herrera 1995; Leverkus et al. 2013). However, this did not seem to be the case in our study, as predation by rodents was lower than commonly recorded in the study area (Puerta-Piñero et al. 2010; Gómez et al. 2003) and left more than half of the seeds in unfenced areas potentially available for ungulates. In addition, only one-third of the seed shelters uplifted by boars were broken and had the acorn consumed. Although this has little implication for the protective effect of the seed shelter (though present, these acorns had little possibility of yielding a healthy seedling), it could suggest that the nutritional benefit obtained by the animal from the acorn may not compensate for the effort involved in extracting it from the seed shelter, according to optimal foraging theory (MacArthur and Pianka 1966). Adding thorns, spikes, or other elements to dissuade large predators might enhance this effect and generate more effective protection (Online Resource 2).

Implications for management

High levels of seed predation by rodents and ungulates have long been considered a major argument to avoid seeding as a method to regain forest cover. Although several factors are known to affect the degree to which these mammals depredate seeds, and despite the extensive search of methods to control seed predation (Stewart et al. 2000; Madsen and Löf 2005; Dey et al. 2008; McCreary 2009; Leverkus et al. 2013), we are not aware of any method that may yet turn the balance in favor of sowing as an alternative to planting in situations with high risk of seed predation. Our results show that the seed shelter tested in this study could represent such a method, at least in cases of low activity of large seed predators. In cases of high abundance of large acorn predators, other solutions would be necessary because the seed shelter proved ineffective against wild boars. Several methods exist to control predation by large animals, such as fencing (as in the present study), managing ecosystems so as to increase habitat complexity and impede their foraging (Leverkus et al. 2013), or sowing under certain shrubs (Perea and Gil 2014). However, our results also show that merely addressing predation by ungulates is not enough if their effect is synergistically combined with that of rodents. In fact, rodent activity can be even greater inside exclusions (Gómez and Hódar 2008; Pérez-Ramos and Marañón 2008), in habitats with a complex structure (Leverkus et al. 2013), and under shrubs (Fuchs et al. 2000; Gómez 2004) due to habitat requirements different from those of large animals and to lower competition and/or predation pressure by ungulates. Our results show that the effect of reducing or eliminating predation by large animals in combination with the protection conferred by the seed shelter against rodents may offer a solution to this enduring problem.

The main concept of the physical protector used in this study (a capsule containing the seed and the substrate) enables the use of any particular combination of substratum, water-retention gels, slow-release fertilizers, mycorrhizal inoculation, or compounds intended to improve seedling germination and plant growth (Savill et al. 1997). Furthermore, in cases of high risk of herbivory on the established seedling, the (underground) seed shelter could also be coupled with aboveground protectors such as tree shelters (for more on this technique, see McCreary 2009). The structure of the seed shelter may also be improved to reduce the risk of root spiraling or the protrusion of shoot or root through the assembly slots (Online Resource 2). In summary, either the seed shelter presented here or similar physical protectors have high potential for reforestation via seed sowing due to its simple design, feasibility for low-cost mass industrial production, ease of use, and possibilities for combination with other elements to foster seedling success (Online Resource 2).

Conclusions

Our study has demonstrated that a physical structure such as the one tested here may effectively protect seeds from predation by small animals, partially providing a solution to a persistent problem. We expect these results, combined with the lack of effect of the seed shelter on germination and plant development, its potential for mass production, and its low expected production cost, to bring sowing back to the foreground in the restoration of woody plant species. Despite the need for improvements in its design and production, the marked success of this device highlights the fact that simple, low-tech innovations have the potential to solve enduring problems in the applied fields of ecology and forestry and can aid in successfully meeting the formidable challenges for ecosystem restoration in the twenty-first century.

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Conflict of interest JC and AL are the inventors of the seed shelter. The device is patented by the University of Granada (a public academic institution), who funded this study. However, besides the authors (JC is Professor, FF Master student, and AL Ph.D. student) no one else participated in any way in the design of the experiment, the analysis and interpretation of the data, or the writing of the manuscript.

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