# Seeding acorns for montane cloud forest restoration in central Veracruz, Mexico: practical experiences

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## Abstract

Tropical montane cloud forests in Mexico, though rich in unique species, cover less than 1% of the country and face severe deforestation and ongoing threats, especially to oaks (*Quercus* spp.). Our study in the montane cloud forests in the Jamapa and La Antigua River basins of central Veracruz tested acorn seeding for forest restoration. Field trials were conducted across peri-urban and rural secondary forests, employing a range of acorn protection devices (e.g., wire mesh cages, chili pepper (*Capsicum* spp.) covering) and site preparation techniques to mitigate predation by rodents (Order Rodentia) and other fauna. The study also assessed the influence of microsite selection and pre-germination treatments on seedling emergence. Various rodents were the main obstacle to seeding success, exclusion devices like wire mesh cages greatly improved outcomes. Effectiveness depended on species, site, and year. Chili pepper coverings did not deter birds, and they exposed the acorns to seed predators. Successful restoration requires careful microsite selection; acorns are less preyed upon by rodents in areas with low to moderate vegetative cover. Seeds should be collected from multiple mother trees during peak fall and inspected for viability. When storage is needed, acorns should be stored under controlled conditions to maintain moisture and prevent fungal contamination. Acorn masting leads to variable seed availability modulating seed predation patterns; mast years are optimal for seeding projects. These findings underscore the need for adaptive, site-specific restoration protocols, including rapid pilot trials and monitoring of acorn production cycles.

## Keywords

*Quercus*, acorn seeding, seed predation, mast years, rodent exclusion devices

## Contents

# 1 The forest

## 1.1 Physiographic region

Our study area is in the mountainous regions of the Jamapa and La Antigua River basins in central Veracruz, Mexico (Figure 1a, area ≈ 1600 km$^2$). These river basins are considered priorities for urgent conservation and restoration actions, and the region is a biodiversity hotspot due to the convergence of the Nearctic and Neotropical regions (Cotler et al. 2010; Gómez-Díaz et al. 2023; Toledo-Aceves et al. 2011). Land use in the region is comprised of agricultural crops, shade coffee (*Coffea arabica* L.) plantations, cattle (*Bos taurus*) pastures, secondary cloud forests, and remnants of conserved tropical montane cloud forest (TMCF) (CONABIO 2010). The TMCF fragments in this area are distributed mainly along an elevational gradient from 1000 to 2400 masl. At the lower and upper extremes of this gradient, the mean annual temperatures are 18 and 12 °C, and annual precipitation is 1700 and 1200 mm, respectively, with the highest precipitation (2200 mm) occurring at the middle of the gradient (Williams-Linera et al. 2013). Soils are mainly Andosols with abundant organic matter and Luvisols at the lower elevations in the landscape (Williams-Linera 2012; Williams-Linera et al. 2013). Three well-defined seasons occur in the region: a cold dry season from late October–November to March, a hot dry season from April to May, and a hot wet season from June to September–October (Williams-Linera 2012; Williams-Linera et al. 2013). Global climate models suggest higher temperatures at higher elevations in the next century, and uncertainty remains regarding the effects of temperature and moisture changes on cloud formation in mountainous regions because the cloud base could lift in response to higher temperatures (Foster 2001; Salinas et al. 2021).

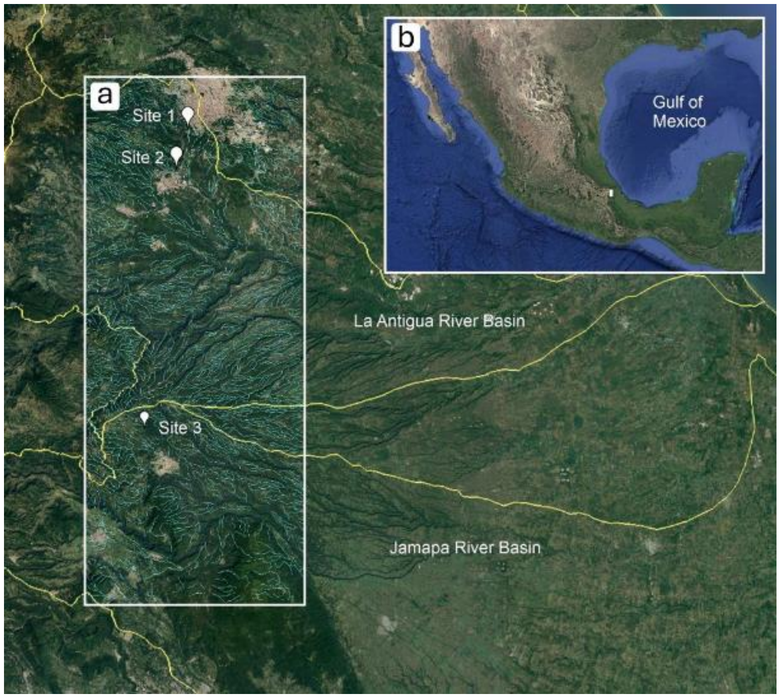



Figure 1. (a) Location of the mountainous regions in the Jamapa and La Antigua River basins in central Veracruz, Mexico (rivers are delineated as ephemeral (light blue) and permanent (dark blue). (b) Location of the study area relative to Veracruz State and the Gulf of Mexico. (Photo credits: (a–b) Google Earth, Images from 2024).

## 1.2 Forest type

The TMCF has a fragmentary distribution and occupies only 0.5 to 1% of Mexican territory. This forest type is present in mountainous areas with steep topography, particularly in areas protected from solar radiation and strong winds. It is characterized by the frequent presence of clouds and fog (Rzedowski 1996). In Mexico, TMCF is the forest type with the highest floristic richness per unit area, the estimated habitat of more than 3000 species of vascular plants (about 10–12% of plant richness in the country), of which about 30% are endemic (Rzedowski 1996; Williams-Linera 2012). In central Veracruz, Williams-Linera et al. (2013) recorded two groups of forests defined by elevation and tree species composition: lower (1250 to 1630 masl) and upper (1800 to 2550 masl) montane forest. The canopy and overstory of lower montane forests are dominated by *Quercus lancifolia* Schltdl. & Cham., *Q. sartorii* Liebm., *Q. xalapensis* Bonpl., *Carpinus tropicalis* (Donn.Sm.) Lundell, *Clethra macrophylla* M. Martens & Galeotti, *Liquidambar styraciflua* L., and *Turpinia insignis* (Kunth) Tul., whereas the canopy of the upper montane forest is dominated by *Q. corrugata* Hook., *Prunus rhamnoides* Koehne, *Cleyera theaeoides* (Sw.) Choisy, *Ternstroemia sylvatica* Schltdl. & Cham., and *Weinmannia pinnata* L. TMCF fragments are highly diverse and heterogeneous in structure. Trujillo-Miranda et al. (2018) evaluated a mature forest fragment and 21-year-old secondary forests, documenting average tree heights of 25 and 14 m, mature tree densities of 614 and 350 trees $ha^{-1}$, and basal areas of 44 and 12 $m^2$ $ha^{-1}$, respectively. Commercially valuable tree species include *Juglans pyriformis* Liebm., *Oreomunnea mexicana* (Standl.) J.-F.Leroy, *Quercus spp., Trema micrantha* (L.) Blume, and *L. styraciflua* (Toledo-Aceves et al. 2021a).

### 1.3 Deforestation and degradation of the forest

In central Veracruz, TMCF has been deforested and converted mainly into coffee, sugarcane (*Saccharum officinarum* L.) plantations, and pastures, while the main recent threat is the conversion of remnant forest patches to urban and suburban housing (Toledo-Aceves et al. 2011). In this region, an annual TMCF cover change of −0.44% was estimated for the period from 1993 to 2000, although a low positive rate of forest cover gain (0.11%) was recorded in 2000–2014 (Gómez-Díaz et al. 2018). In addition to forest conversion, there are other causes of degradation, including selective illegal logging and hunting, environmental contamination, and climate change. Climate change is projected to cause the loss of populations of threatened and endangered cloud forest trees (Jiménez-García and Peterson 2019). The genus projected to undergo the most serious negative effects is *Quercus*, which is also the most important genus in this biome. Land use change could exacerbate the negative impacts of climate change (Gómez-Díaz et al. 2018; Rojas-Soto et al. 2012).

## 2 Impacts of deforestation and degradation on candidate restoration sites

### 2.1 Site degradation

Three sites illustrate the degradation history and high heterogeneity in their areas. Site 1 is a 30-ha peri-urban forest (old-secondary forest; 1250 masl) bordering the city of Xalapa and comprised of a vegetation mosaic that includes preserved TMCF patches and regenerating secondary and degraded forests (Williams-Linera et al. 2013). In the 1940s, some patches were plantations of coffee or citrus (*Citrus* spp. L.), and featured a canopy formed by exotic species planted to provide shade, together with native species. These plantations were abandoned in the 1980s, but patches with some exotic fruit species (such as *Citrus* spp. and loquat, *Eriobotrya japonica* (Thunb.) Lindl.) can still be found.

Site 2 is a 2.5 ha young secondary forest located northeast of Coatepec, Veracruz (5 km from Site 1), at an elevation of 1200 masl. Cattle were excluded from this site from 2019 onward, and the mosaic of secondary vegetation consists of areas dominated by exotic grasses such as *Cynodon dactilon* (L.) Pers. and *Paspalum spp*. L. and woody pioneer species including *Vernonia patens* Kunth. *Heliocarpus appendiculatus* Turcz., *H. donnellsmithii* Rose, and *Cnidoscolus multilobus* (Pax) I.M.Johnst. among others. Active restoration has been implemented at this site since 2020.

Site 3 is a mosaic of passively and actively restored secondary forest fragments (around 61 and 37 ha, respectively) located in the municipality of Huatusco (1500 masl). This TMCF site was deforested and transformed into cattle pastures in 1950; exotic grasses were introduced (e.g., *Cynodon plectostachyus* (K.Schum.) Pilg., *Brachiaria decumbens* Stapf, *Setaria sphacelata* (Schumach.) Stapf & CE Hubb. ex Moss, and *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs). Livestock were excluded from the grazing areas in 1995, and passive and active restoration interventions have since taken place.

### 2.2 Damaging agents

Despite the different disturbance regimes of the restoration sites, common factors limit tree regeneration (seed and seedling survival and sapling establishment). At study Site 3, there is low regeneration of late-successional trees dispersed by gravity and animals (barochory and zoochory) compared to regeneration in the adjacent mature forest fragment (Toledo-Aceves et al. 2021b). Bird and mammal seed dispersers in the landscape are affected by habitat loss, forest isolation, edge effects, urban roads, illegal hunting, and feral fauna. In the defaunated secondary forest fragments, some small rodents (Order Rodentia), such as squirrels (Family Sciuridae), sustain their populations mainly through seed predation, especially acorns.

Seedling emergence and establishment are limited by abiotic microhabitat constraints, competition from patches of exotic grasses, vines, shrubs (e.g. *Rubus* spp. L., *Piper* spp. L.), and especially the fern *Pteridium arachnoideum* (Kaulf.) Maxon (Toledo-Aceves et al. 2022). Herbivory of seedlings by gophers (*Heterogeomys hispidus* Le Conte) and rabbits (*Sylvilagus floridanus* J.A. Allen) is another important but less evaluated limiting factor at all the restoration sites (Ortega-Pieck et al. 2011). At some sites, cattle foraging also impacts seedling survival, particularly along forest edges. Seedlings and saplings are exposed to physical and physiological damage due to extreme weather events such as wind and rainstorms, heat waves, and flooding and landslides.

## 3 Mitigating impacts for acorn seeding

### 3.1 Damage

Oaks are key tree species for forest restoration in the region because they are forest foundational species and exhibit relatively high survival and growth on degraded sites. However, acorn predation is widely documented as the most important filter for the feasibility of seeding as a restoration strategy (Löf et al. 2019). Acorns are consumed by insects, birds, and mammals (Bartlow et al. 2018). In the study areas, squirrels and mice (Family Muridae) are the main active removers of acorns. Some buried, superficial, or mixed devices have been developed to prevent acorn removal and *in situ* predation (Figure 2a–d). Castro et al. (2015) developed an effective plastic device that is half buried, with two small openings at the top and bottom where the stem and root can emerge, and limits rodent access to the acorn held in the interior (Figure 2a). Wire mesh devices have also been developed, with relative success at preventing acorn removal by small mammals. Some of these devices are designed to prevent underground acorn removal (Figure 2b; Reque and Martin 2015). At Site 1, wire mesh cages fixed to the ground were used to protect acorns of four oak species, and this technique was found to be highly effective because it prevented access by vertebrates for 184 days, allowing 22.5% of the seeded acorns to establish a seedling (Figure 2c; García-Hernández and López-Barrera 2024). Although wire cages are easily produced and reusable, these types of devices must be removed before they interfere with seedling development (Figure 2c), thereby increasing their cost, especially when utilized on a large scale (Löf et al. 2019).

The best acorn protection technique should effectively reduce predation with no effect on germination (radicle extension), seedling emergence (plumule extension), or plant development, maintain the cost advantage of seeding over planting seedlings, and be environmentally sustainable. One method to deter seed predators is coating acorns with capsaicin, a compound found in chili peppers (*Capsicum* spp. L.) that irritates some animals. However, this method can affect seedling emergence because high capsaicin concentrations can affect plumule emergence (Leverkus et al. 2013). At Site 2, Brewster-Salmones et al. (2024) evaluated the protection provided by chili peppers (*C. annuum* L. and *C. pubescens* Ruiz & Pav.) to acorns of *Q. germana* Schltdl. & Cham., an endangered endemic oak tree of the cloud forest. This technique did not affect germination or seedling emergence (Figure 2d); however, the peppers did not result in protecting acorns because birds consumed the chili peppers.

Germination rate could influence acorn fate, depending on seed predator type and population size. Buried and pre-germinated acorns confer the advantage of reducing predation and accelerating the transition from seed to seedling (Figure 2d). However, when seed predator populations are abundant, even buried and germinated acorns can be found and consumed. For instance, acorns of white oak (Section Quercus) species germinate immediately upon seed fall, but squirrels detect them by their odor, removing the embryos before the seeds are cached. In the case of red oak (Section Lobatae) acorns that show dormancy, squirrels prefer to cache intact acorns for subsequent consumption (Steele et al. 2001). At Site 1, *Q. pinnativenulosa* C.H. Mull. acorns were buried 1 to 2 cm below the forest litter (Rodríguez-Zambrano 2024). Pre-germinated acorns had lower predation than non-germinated seeds (Table 1). The high level of acorn predation can be attributed to the high populations of squirrels and mice and the constant acorn production in this peri-urban secondary forest fragment. However, at Site 2, a pilot study by Vivar-Vázquez (unpublished data) showed that burying pre-germinated acorns of *Q. xalapensis* successfully avoided acorn removal during a cold winter (Figure 2d, Figure 4e, Table 1). Rodent activity can be modulated by climatic variability with cold winters reducing rodent metabolism and activity. At this site, however, rodent populations seemed to be highly variable and there were no mast-producing oaks in the canopy.

Table 1. Field evaluations of germination and emergence of oak (*Quercus* spp.) species of tropical montane cloud forests in Mexico.

| Species | Year | Acorn removal/predation (%) | | | | Acorn germination (%) | | | Seedling emergence (%) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | A | B | C | D | A | B | D | A | B | C | D |
| *Q. germana* Schltdl. & Cham.[a,b] | M | 56 | 22–0 | – | – | 20 | 58–78 | – | 4 | 8–20 | – | – |
| | NM | 68.3 | – | – | 77.5–80.8 | 30.8 | – | 36.6–42.9 | – | – | – | – |
| *Q. insignis* M.Martens & Galeotti[c] | M | 97.0 | – | – | – | 25.3 | – | – | 1.0 | – | – | – |
| | NM | 88.3 | – | – | – | 1.7 | – | – | 0.0 | – | – | – |
| *Q. lancifolia* Schltdl. & Cham.[a] | M | 74 | 46–0 | – | – | 14.0 | 28–54 | – | 4.0 | 16–32 | – | – |
| Q. *pinnativenulosa* C.H.Mull.[d] | M | 44.7 | – | 25.8 | – | – | – | – | 2 | – | 14.7 | – |
| *Q. sartorii* Liebm.[a] | M | 50 | 34–0 | – | – | 0.0 | 4–22 | – | 0.0 | 2–4 | – | – |
| *Q. xalapensis* Bonpl.[a] | M | 72 | 58–0 | – | – | 14.0 | 12–62 | – | 6.0 | 4–34 | – | – |

[a] García-Hernández and López-Barrera 2024. [b] Brewster-Salmones et al. 2024. [c] García-Hernández et al. 2025. [d] Rodríguez-Zambrano 2024. M = mast year. NM = Non-mast year. Treatments: A = Seed not pre-germinated and sown without protection. B = Partial - total exclusion. C = Pre-germinated acorns. D = Chili pepper protection.

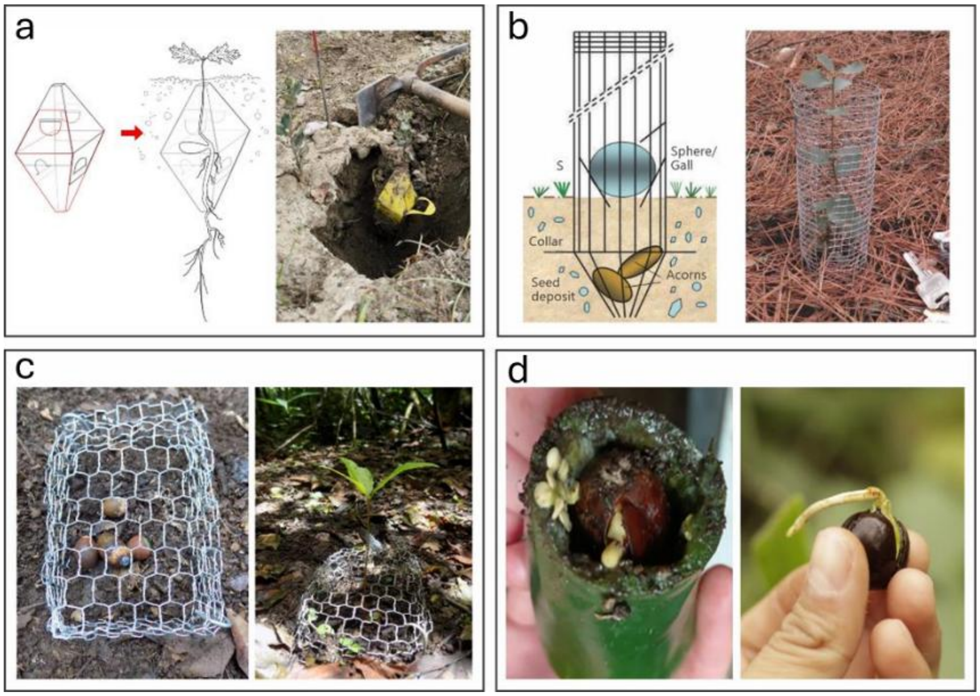



Figure 2. Devices and strategies used to reduce acorn predation. (a) Seed shelter (total protector). (b) Seed total protector. (c) Wire cages implemented at Site 1 (total protections). (d) Examples of partial protection, *Q. germana* Schltdl. & Cham. acorns inserted in *Capsicum annum* L. fruit implemented at Site 2) and pre-germinated acorns of *Q. xalapensis* Bonpl. to reduce acorn predation at Site 2 (Photo credits: (a) Castro et al. (2015), (b) Reque and Martin (2015), (c) García-Hernández and López-Barrera (2024), (d) Brewster et al. (2024) and Dulce C. Vivar-Vázquez).

## 3.2 Site preparation

In degraded areas, seeding microsite types should be considered as they influence presence and foraging patterns of rodents. Acorns are at greater risk of predation by rodents that prefer to forage in microsites with high vegetative cover from various strata, such as herbaceous plants, shrubs, small and large trees, under and near shelterwoods, and woody debris and slash piles. Thus, it is advisable to bury acorns at sites with low to moderate vegetative cover and avoid log piles that can provide shelter for rodents (García-Hernández et al. 2016; García-Hernández and López-Barrera 2024). Nevertheless, vegetative cover helps maintain acorn moisture, acting to promote germination and emergence.

Striking a balance is necessary between the microenvironmental requirements for seedling establishment and the risk of acorn predation. The different foraging patterns of the faunal assemblage should also be considered, even when using acorn protection to deter rodent predation. For example, Leverkus et al. (2015) reported that a protective device was effective in preventing rodent predation in the Mediterranean region, but its effectiveness against wild boar (*Sus scrofa*) predation was dictated by microhabitat complexity.

# 4 Seed procurement and preparation

## 4.1 Collection

Masting, the episodic production of seed crops in some years, followed by one or more years of low or no mast (Steele 2021), has been reported for some oak species. In central Veracruz, the studied oak species alternate their production with heavy mast in one year followed by another year with low or very low acorn production. This has also been reported for two oak species in the highlands of Chiapas, Mexico, where acorn production can be 8 to 9 times greater in a mast year than in the following non-mast year (161 ± 19 vs. 21 ± 3 acorns $m^{-2}$, respectively; López-Barrera et al. 2007). The oak having the largest seed at Site 3, *Quercus insignis* M. Martens & Galeotti presented an even higher difference of 25 times greater acorn production in the mast year than in non-mast year (García-Hernández et al. 2025).

Low production and high predation rates could delay or impede the implementation of an enrichment restoration project in degraded or secondary forests. It is also crucial to consider the variation in seed production for each species for the purposes of project planning and implementation because this affects acorn quantity and quality. Acorn availability in relation to the seeding field trials from our study sites is shown in Table 1. For secondary forests in a non-mast year (Sites 1 and 3), a large part of the crop was predated while still on the tree; the acorns that survived to mature and fall to the forest floor were quickly removed by fauna (García-Hernández et al. 2025; López-Barrera et al. 2007).

Although it is advisable to collect seed from many individuals to guarantee high genetic variability (Vander Mijnsbrugge et al. 2010), in the case of species that have restricted distribution or drastically reduced populations, it is not always possible to include a large number of mother trees. For our study sites, the number of mother trees sampled for acorn collections ranged from three to 10 individuals per species. A particular oak species can exhibit a different fruiting period depending on the region in which it is found, and it is therefore important that planning includes the monitoring of potential mother trees to determine the appropriate time for acorn collection.

Collecting acorns during peak fall increases the probability of suitable seed quality and viability. A mature acorn is partially or completely brown (Figure 3h–i) and heavier than the immature, damaged, or non-viable seeds when it falls from the tree (Rodríguez-Acosta and Coombes 2020). In central Veracruz, acorn fall occurs mainly in autumn, from mid-October to mid-December. Acorns used in this research were collected in late October and early November. However, in recent years, some species have released their seed in early September or delayed their release until mid-winter.

Acorns are typically collected directly from the ground, although this can be done using seed traps or, where possible, directly from the tree (Figure 3a–c). Although it has been reported for different species that large seeds produce individuals with greater growth and biomass acquisition (Baraloto et al. 2005; García-Hernández et al. 2023), size selection could inadvertently reduce genetic variability. Thus, given the low number of mother trees for some species, seeds of all sizes encountered were included in our studies, and only fully developed (mature) and healthy (no bite marks or weevil (*Curculio* spp. L.) larvae exit holes) seed were collected (Figure 3d–i). Acorns having evidence of partial predation are generally considered to have poor performance and are discarded. However, one study showed that acorns of *Q. insignis*, the largest-seeded oak species in the world, can lose up to 30% of its total size (Figure 3f) with no reduction in germination and emergence values (García-Hernández et al. 2023).

Figure 3. (a–b) Collecting acorns of *Q. lancifolia* Schltdl. & Cham. directly from the ground. (c) Seed trap placed in the forest (Site 3). (d) Transversal cut of a healthy *Q. insignis* M. Martens & Galeotti acorn. (e) Non-viable acorn with exit holes left by the emergence of weevil larvae. (f) Acorn partially damaged by rodents. (g) Float method to discard non-viable acorns. (h–i) Mature and healthy acorns of *Q. xalapensis* Bonpl. and *Q. insignis* M. Martens & Galeotti. (j) Acorns prepared for cold storage. (Photo credits: (a–e) Ma. de los Ángeles García-Hernández, (f) Fabiola López-Barrera, (g–h) Dulce C. Vivar-Vázquez, (i) Ma. de los Ángeles García-Hernández, (j) Dulce C. Vivar-Vázquez).

After collection, in addition to visual inspection to identify dried or damaged seed (Figure 3e and 3f), all seed were subjected to the buoyancy test to eliminate apparently non-viable seed (Gribko and Jones 1995). It is important to note that this technique is not 100% effective in detecting seed having weevil larvae that have yet to emerge (Figure 3g). For this reason, a second acorn inspection should also be conducted at the time of sowing. Seed of each studied species were stored in labeled (collection site, date, species, tree number) plastic (polyethylene) bags (Figure 3j) and transported to the Functional Ecology Laboratory of The Institute of Ecology A.C. (INECOL).

## 4.2 Handling

Where necessary, each acorn was separated from its cupule and dirty seed were cleaned, inspected again to discard damaged individuals, and buoyancy tested. Prior to storage, excess moisture was removed with a dry cloth to prevent fungal contamination. Studies indicate that acorn moisture content below 30 to 40% affects viability (Liu et al. 2024; Schroeder and Walker 1987). Acorns are recalcitrant and sensitive to desiccation, which will affect their viability, so care must be taken to avoid drying the seed too much when handling. Oak species mainly distributed in humid montane forests typically have desiccation sensitive acorns because rain and high humidity are present most of the year (Kang et al. 2023). However, exposure to excessive moisture for extended periods can reduce germination due to fungal decomposition.

### 4.3 Storage and stratification

All viable seeds of each species were stored in labeled plastic bags and refrigerated at 4 to 7 °C until sowing in the field (in our studies a maximum of three weeks). Seed (particularly white oaks) can germinate or mold when stored in a dark refrigerator if there is sufficient humidity, so they must be checked at least every third day. Maximum storage time will depend on species (oaks with rapid germination vs. oaks with dormancy), seed lot quality, humidity at the time of collection, and temperature (Liu et al. 2024; Rodríguez-Acosta and Coombes 2020; Schroeder and Walker 1987).

### 4.4 Preparing seeds for the field environment

Soaking acorns for a few hours prior to sowing could promote germination (Rodríguez-Acosta and Coombes 2020) and hydrated seed brought to the field might be more able to withstand climatic variability on degraded sites. Pre-germinated seed (radicle of 1 to 3 cm) can be transported to the field; this practice is particularly beneficial for red oak species that show dormancy. There are several techniques to pre-germinate acorns, such as using a germination chamber at a temperature of 26 to 28 °C (Rodríguez-Acosta and Coombes 2020; Vivar-Vázquez unpublished data). Sowing pre-germinated seed of *Q. pinnativenulosa* resulted in faster seedling emergence compared to untreated seed (Rodríguez-Zambrano 2024). At Sites 1 and 3, acorns that were not pre-germinated were used in our study and marked with a wax pencil to distinguish individuals in the field (Figure 2c). At Site 2, acorns inserted in chili peppers were used as part of a study to determine the protective effect of the peppers for predation prevention and facilitation of germination (Figure 2d; Brewster et al. 2024).

## 5 Plantation establishment

### 5.1 Plantation design

Oak species in sections Quercus (*Q. germana*, *Q. insignis*, and *Q. lancifolia*) and Lobatae (*Q. xalapensis* and *Q. sartorii*) have been used in seeding experiments (Table 1). Rodríguez-Zambrano (2024) also introduced *Q. pinnativenulosa* (Section Lobatae) at Site 1. Seeding practices with oaks are directed plantings in terms of sowing density and selected microsites (see above, Site Preparation). For example, in the case of Site 1, one acorn of each species (*Q. germana*, *Q. lancifolia*, *Q. xalapensis*, and *Q. sartorii*) was sown at each sowing spot (Figure 4d). In each selected microsite, sowing a single or few seeds (2 to 4) may increase their survival because predators have less chance of discovering small seed groups. In some cases, as in Site 3, 15 *Q. insignis* acorns were sown per microsite (Figure 4c) to benefit identification of seed predators captured with camera traps. Sowing density can therefore be modified according to objectives. Distance between microsites can vary according to site size and distribution of the best microsites for sowing. Examples from our work includes minimum distances between sowing microsites of 10 to 15 m (Brewster-Salmones et al. 2024), 15 to 20 m (García-Hernández and López-Barrera 2024), and up to 40 m at larger sites such as Site 3 (García-Hernández et al. 2025).

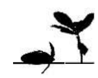
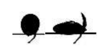
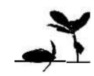
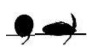
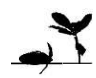

Figure 4. (a) Sowing acorns at Site 1. (b) Total protection using metal stakes to fix the wire cage to the ground. (c) Sowing unprotected *Q. insignis* M. Martens & Galeotti acorns at Site 3. (d) Comparing two wire-cage types (total protection) and unprotected acorns from four oak species at the same seeding microsite. (e) Emerged seedlings (*Q. xalapensis* Bonpl.) at Site 2 from partially protected (*Capsicum* spp. L. fruits) and unprotected acorns illustrating for this site and year (cold winter) that there was no need to protect acorns (Photo credits: (a–d) Ma. de los Ángeles García-Hernández, (e) Dulce C. Vivar-Vázquez).

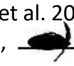
## 5.2 Sowing practices

In our studies, seed were sown at selected microsites during the natural period of acorn fall and seedling recruitment (autumn). Monitoring was extended up to 184 days depending on the time required for germination and emergence of seedlings of each species (Table 2). Whether or not to bury acorns with soil, leaf litter, or plant debris from each site depends on several factors. If the seed are protected and the restoration site has tree cover with low microclimate variation at the forest floor, acorns can be sown on leaf litter, left unburied to avoid rotting. If acorn protection is not planned for use due to a low density of predators or deployment of pre-germinated seed, it is advisable to bury acorns 2 to 4 cm deep to avoid detection and predation. Likewise, if acorns are protected but the site is open, such as a recently abandoned pasture, they can be buried under plant litter to avoid desiccation. Because acorn removal and predation patterns were known for some species at Site 1 (García-Hernández et al.

2016), different rodent exclusion treatments were applied: total exclusion, partial exclusion (access by mice only), and no exclusion (Figure 4d). Cages made with mesh wire of various mesh sizes were used. The cages covered the seed but allowed water and light to enter. Each cage was fixed to the ground with metal stakes to prevent lifting by squirrels (Figure 4b). At Site 2, seeds were embedded in chili peppers (*C. pubescens* or *C. annum*), which were placed above ground and accessible to all predators (Figure 2d). At Site 2, Vivar-Vázquez (unpublished data) placed intact pre-germinated acorns under plant debris and grass litter, while all *Q. insignis* seed at Site 3 were exposed with no protection (Figure 4c). Given that this species has the largest acorns, varying from 10 to 86 g, its size may modulate acorn removal, predation and dispersal by small mammals (García-Hernández et al. 2025).

Table 2. Greenhouse evaluation of germination and emergence of oak (*Quercus* spp.) species of tropical montane cloud forests in Mexico.

| Section | Species | Mean acorn mass ± SE | Acorn germination (%) | Seedling emergence (%) | 1-2 weeks | 2-4 weeks | 1-2 months | 2-4 months | 4-6 months |
|---|---|---|---|---|---|---|---|---|---|
| *Quercus* | *Q. germana* Schltdl. & Cham. | 14.5 ± 4.8[a] | 80.0 | 31.4 |  |  |  |  |  |
| | | 10.6 ± 0.2[b] | 66.0 | – | | | | | |
| | | 11.7 ± 0.5[c] | 85 | 67.5 | | | | | |
| | | 18.1[d] | 18.1 | – | | | | | |
| | *Q. insignis* M.Martens & Galeotti | 34.5 ± 0.4[b] | 55.0 | 37.7 |  |  |  |  |  |
| | | 45.2 ± 0.70[e] | 46.7 | 38.5 | | | | | |
| | *Q. lancifolia* Schltdl. & Cham. | 4.82±0.15[c] | 83.3 | 78.3 | | | |  |  |
| *Lobatae* | *Q. pinnativenulosa* C.H.Mull. | 1.20±0.05[g] | 42 | 29 | |  |  |  |  |
| | *Q. sartorii* Liebm. | 3.05±0.03[b] | 70.3 | 53.7 |  |  |  | |  |
| | | 2.24±0.05[c] | 15.8 | 13.3 | | | | | |
| | *Q. xalapensis* Bonpl. | 2.77± 0.04[b] | 60.0 | 60.0 | | | |  |  |
| | | 3.2 ± 0.1[c] | 48.0 | 46.7 | | | | | |
| | | 3.1 ± 0.1[f] | 47.5 | 37.5 | | | | | |

[a] Brewster-Salmones et al. 2024. [b] García-de la Cruz et al. 2016. [c] García-Hernández and López-Barrera 2024. [d] Toledo-Aceves et al. 2017. [e] García-Hernández et al. 2023. [f] Vivar-Vázquez (unpublished data). [g] Rodríguez-Zambrano 2024.  = acorn germination,  = seedling emergence,  = seedling > 15 cm tall.

## 6 Post-sowing practices and maintenance

Most restoration ecology studies of acorn seeding are concluded after measurement of seedling emergence (Figure 5). In our case, monitoring for more than 100 days allowed us to determine the time required for each species to transition from germination to plumule emergence, to establishment of vigorous and competitive seedlings that exceeded 15 cm tall (Table 2). Many of the experiments at our three sites have evaluated the factors that limit early seedling establishment. Some practices that increased seedling survival included seeding in open areas but under partial shade from isolated trees (*Q. insignis*; Montes-Hernández and López-Barrera 2013) or performing 3 to 4 annual releases from exotic grass competition until the seedlings outgrew the weeds (Williams-Linera et al. 2015). No additional measures have been used to protect seedlings, although cattle have been excluded from the sites. Herbivory events have been observed sporadically but the resprouting capacity of some oaks allows them to persist. Additionally, it is still necessary to evaluate whether established seedlings may be favored in their growth by releasing them from the understory in different microhabitats within the degraded areas.

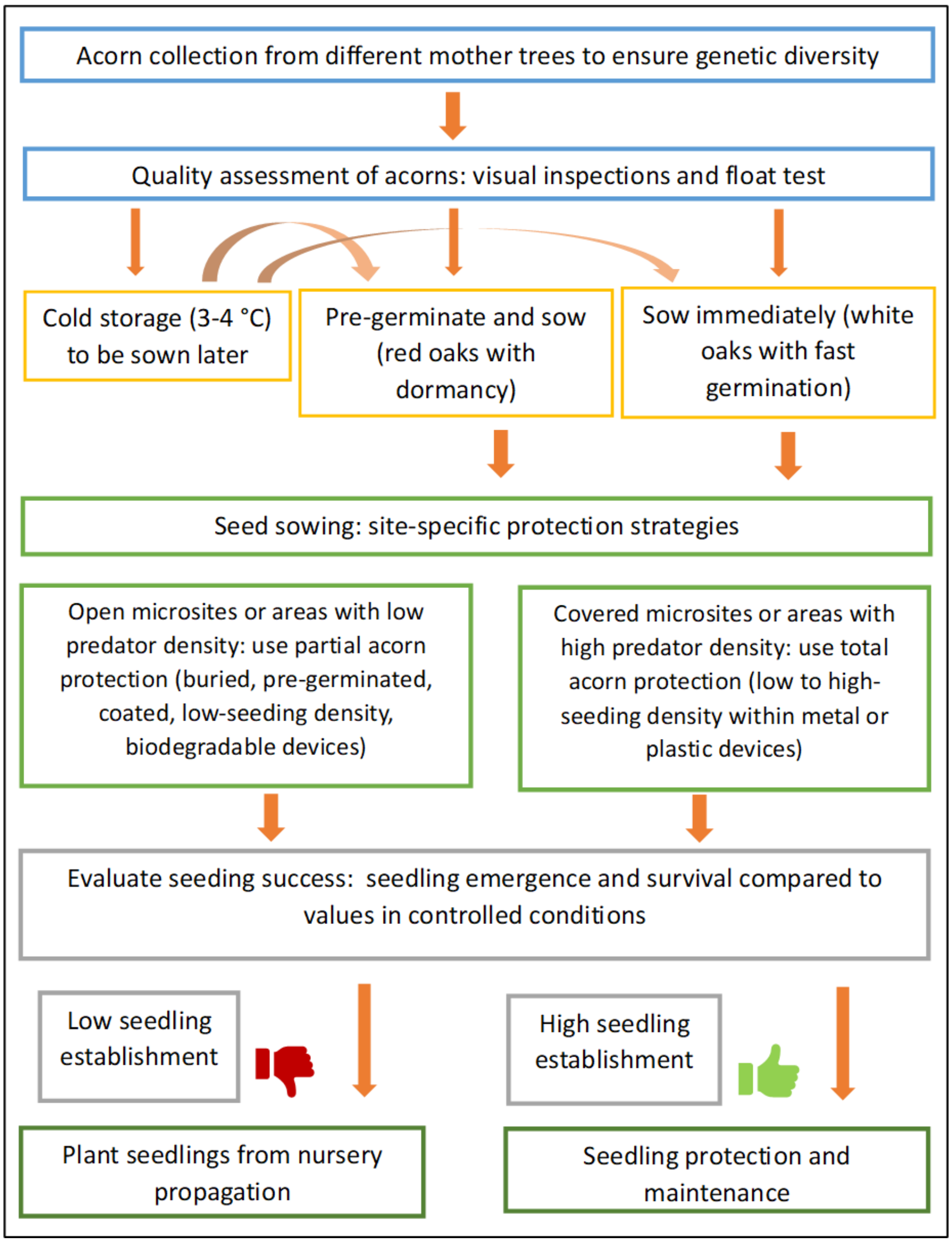



Figure 5. Diagram showing progression of the general steps for seeding acorns. For acorn collection, a minimum of five mother trees is recommended. Figures 2 and 4 show examples of total and partial protection of acorns. Low seeding density or seeding a single acorn per sowing spot and covered by plant litter reduce the probability of encounter by predators.

# 7 Successful seeding

## 7.1 Defining success

We measured seeding success by evaluating germination percentage and seedling emergence in the field (Figure 6b and 6c) relative to values recorded under controlled conditions in the nursery (Figure 6a). Results from various studies at the prior mentioned study sites are summarized in Tables 1 and 2. As general trends, we found that: (1) microsites with lower vegetative cover reduce acorn predation without affecting germination and seedling emergence; (2) when acorns are completely protected (total exclusion), germination and seedling emergence are highest (54% and 22.5%, respectively), while unprotected seed had the lowest values of these variables (12.5% and 3.5%, respectively); (3) higher acorn predation (and therefore lower germination) was recorded during non-mast years when seeding was conducted in secondary forests having canopy oaks; and (4) there is high intra- and interspecific variability in acorn mass, and also germination and seedling emergence even under controlled conditions.

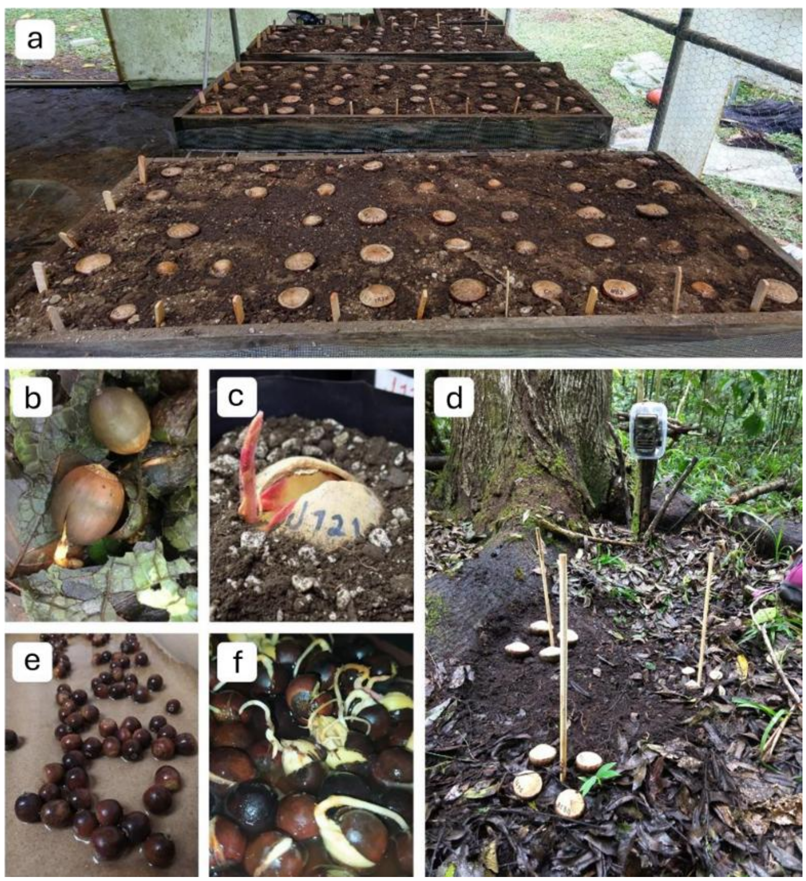



Figure 6. (a) *Quercus insignis* M. Martens & Galeotti acorns sown in a greenhouse to evaluate viability under controlled conditions. (b) Germinated acorns of *Q. sartorii* Liebm. on the forest floor. (c) *Q. insignis* seedling emergence. (d) Installation of camera trap to identify the fauna that consume *Q. insignis* acorns. (e-f) Pre-germination process for acorns of *Q. xalapensis* Bonpl. before sowing (burying) in the field (Photo credits: (a–d) Ma. de los Ángeles García-Hernández, (e–f) Dulce C. Vivar-Vázquez).

In addition, species differ in viability (acorn germination and seedling emergence) and rodent selection pressure (Tables 1 and 2). For instance, at Site 1, *Q. germana* exhibited the highest germination percentage in the field, followed by *Q. lancifolia*, *Q. xalapensis*, and *Q. sartorii*; while emergence was highest in *Q. lancifolia*, followed by *Q. xalapensis*, *Q. germana*, and *Q. sartorii*. For some species, these values were between 8 to 38.5 times lower than those recorded in greenhouse studies (Table 2). These differences could be due to species-specific removal preferences of rodents (García-Hernández et al. 2024). *Q. insignis* is highly variable in acorn mass (10 to 86 g), but these heavy acorns were also removed and consumed (Table 1); only 13.5% germinated and 0.5% emerged as seedlings in a mast year. The large size of its seed indicates a high nutrient content, so they are frequently removed by seed predators (mainly squirrels) and their establishment at planting microsites was low (García-Hernández et al. 2025). This emphasizes a regeneration bottleneck in degraded forests for some oak species and the need to plant seedlings or saplings rather than sow seed in some restoration settings.

### 7.2 Limiting factors and risks

We identified the bottlenecks to seedling establishment. We have also observed intra- and interspecific variability in the responses of the *Quercus* genus, as well as spatial (sowing microsites and predator assemblage) and temporal (mast years, predator population size, climatic events) heterogeneity. This variability limits the possibility of creating universally applicable protocols to successfully restore TMCF through seeding. Establishing rapid, small-scale pilot experiments and acorn availability surveys in forested areas can provide insight and reduce risk prior to implementing a large-scale program. Mast years will provide a sufficient quantity and quality of acorns to evaluate the use of pre-germinated buried acorns of different species (highest diversity) at open microsites (Figure 5). These rapid surveys allow the practitioner to decide if total or partial seed protection is needed to prevent acorn predation and seedling herbivory. Moreover, seeding density can be assessed experimentally, using 1 to 5 acorns per sowing spot to help determine and measure the probability of seed predation. Camera traps set at seeding microsites can inform the practitioner of likely seed predators (Figure 6d), which will contribute to selection of appropriate protection devices for seed and seedlings, at least for the first (establishment) year. We found that sowing unprotected seed limited establishment, with only 2.5% or fewer exposed seed reaching the seedling stage. In contrast, completely protecting seed increased seedling emergence by up to 20%.

### 7.3 Key elements contributing to success

Knowing the time required for germination and emergence of the various red and white oak species and the particular threats that seeds are exposed to at each site are vital for the effective design and implementation of seeding projects. Where information is not available, probable germination rates can be inferred from Section (red or white oaks) and from rapid greenhouse tests of viability. Another strategy could be to collect seed germinating in the field under mother trees (Figure 6b) because many of the seedlings in this situation will be unable to establish under the dense shade of the canopy. However, such extractions should not remove all mast because of the value of the cohort to regeneration and local fauna.

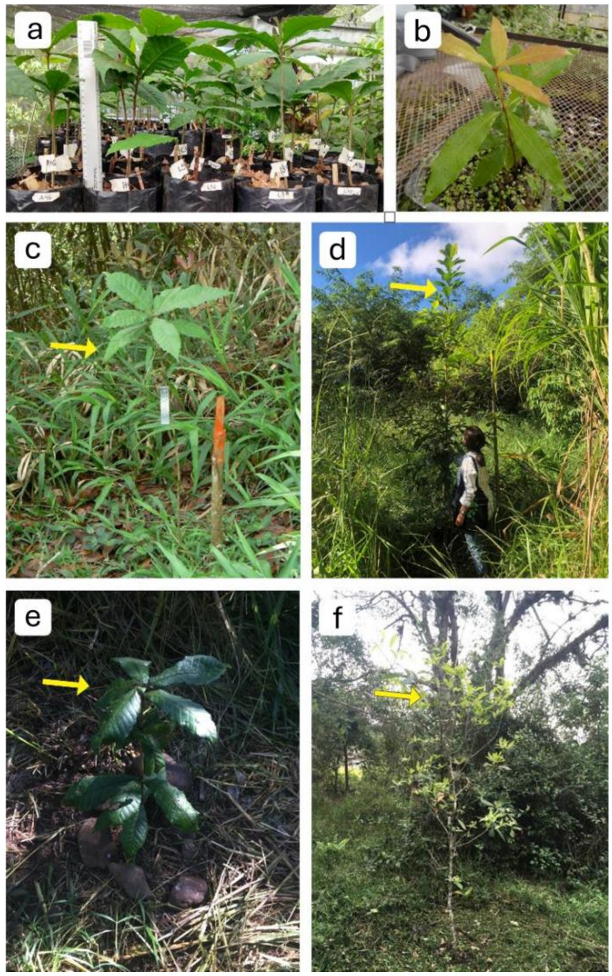



Figure 7. (a–b) Seedlings of *Q. insignis* M. Martens & Galeotti and *Q. lancifolia* Schltdl. & Cham. six months after being sown under nursery conditions. (c) 2-year-old sapling of *Q. insignis* at Site 3. (d) 4-year-old sapling of *Q. germana* Schltdl. & Cham. at Site 2. (e) 1-year-old seedling of *Q. germana* at Site 2. (f) 4-year-old sapling of *Q. pinnativenulosa* C.H.Mull. at Site 2. (Photo credits: (a–b) Ma. de los Ángeles García-Hernández, (c–f) Fabiola López-Barrera).

The five species we studied differed in the amount of time required for germination and emergence and would thus require different periods of seed protection (Table 2). The acorns of *Q. lancifolia* and *Q. xalapensis* presented late germination and emergence, and their seeds remained viable until the end of the experiment (184 days), with removal by predators resultantly continuing through this period. For these species, it is necessary that seed is sown with some type of protection or that it is pre-germinated prior to sowing (Rodríguez-Zambrano 2024). Acorns of *Q. sartorii* and *Q. germana* showed rapid germination; however, it was observed that their seeds quickly lose moisture when exposed to field conditions. Moisture loss has been related to acorn size (large cotyledons typically dry slower), acorn moisture at the time of dispersal, and pericarp condition following dispersal. Once cracked, the pericarp facilitates the process of water absorption and loss (Kang et al. 2023). In the case of *Q. insignis*, acorns presented rapid germination and emergence, but rodents were observed to cut the radicles, which prevented seedling development. It is important to consider that germination and emergence, even within the same species and regardless of Section, may vary each year due to provenance and genetic characteristics of mother trees, climatic conditions (temperature, wind, precipitation, etc.), and environmental conditions (vegetation characteristics, competition, soil nutrition, etc.) of the restoration site.

It is necessary to reverse the degradation and loss of TMCF and sustain the great diversity of foundational oaks in the region. Restoration of oaks, because of their favorable acorn characteristics, are generally quite suited to establishment with seeding. Primary issues with oak seeding in the TMCF stem from seed predation. Opportunities exist for innovating acorn protection with local materials that are inexpensive, easily installed, and biodegradable. To be successful, the design of innovative protection devices will need to account for the behaviors of main seed predators active in the region and the length of time protection is required to obtain seedling establishment.

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Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

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