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The following article appeared in *Archives of Biological Sciences*, 64(4): 1543-1554 (2012); and may be found at <https://doi.org/10.2298/ABS1204543C>

EFFECTS OF BURIAL DEPTH ON SEED GERMINATION AND SEEDLING EMERGENCE OF MEXICAN OAKS: A GLASSHOUSE EXPERIMENT

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Abstract - Despite the interest in restoring oak forests in Mexico, very little is known about their regeneration ecology. We assessed the influence of acorn burial depth on seed germination and seedling emergence for eight Mexican oak species (*Q. affinis*, *Q. castanea*, *Q. coccolobifolia*, *Q. laeta*, *Q. mexicana*, *Q. polymorpha*, *Q. tinkhamii* and *Q. viminea*). We performed a glasshouse experiment in which acorns were buried at five soil depths (0, 2, 4, 6 and 8 cm). After four months, acorn germination and seedling emergence were recorded. Buried acorns showed higher germination and seedling emergence than unburied ones, but burial depth also influenced these responses. The optimum burial depth for seedling emergence of each species was 2, 4, 6 and 8 cm depth for four species (*Q. castanea*, *Q. mexicana*, *Q. tinkhamii*, and *Q. viminea*); 2 and 4 cm for *Q. laeta*; as well as 2, 4 and 8 cm for *Q. coccolobifolia*.

Key words: Acorns, *Erythrobalanus*, *Lepidobalanus*, North American forests, *Quercus*, regeneration ecology

INTRODUCTION

The first stages of plant life cycles strongly influence recruitment patterns in natural plant populations (Grubb, 1977). One of the most obvious factors influencing germination and seedling emergence is the seed burial depth in the soil (Fuchs et al., 2000; Traba et al., 2004). Seed burial may be promoted by abiotic-driven soil disturbances, such as those caused by wind and water, as well as by biotic factors, including earthworm activity and the foraging behavior of seed dispersers (Vander-Wall 1990, 1993; Chambers and MacMahon, 1994; Renard et al., 2010). Seed burial helps seeds to escape from post-dispersal predation and prevents the death of the embryo by desiccation or extreme temperatures during the unfavorable season (Borchert et al., 1989; Vander-Wall, 1990; Seiwa et al., 2002; Cheng et al., 2007). On the other hand, the presence of buried viable seeds has been related

to earlier successional species (Livingston and Alessio, 1968).

Moreover, as most seeds on the soil surface need light to germinate, burial is an essential prelude to dormancy in several species (Thompson et al., 1993; Grime, 2001). From this point of view, burial may provide safe sites for seeds until germination occurs, although other processes such as seed predation, fungal attack, etc. can also be operating (Borchert et al., 1989; Vander-Wall, 1993; Seiwa et al., 2002). Nevertheless, while absolute darkness is required for triggering the germination of some seeds (negative photoblastic species), other seeds require full exposure to light in order to germinate (positive photoblastic species) (Baskin and Baskin, 1998; Flores et al., 2011). Furthermore, between these two extreme light responses, there is a wide range of germination response to different light intensities (Pons, 2000).

For example, light availability had a negative effect on the germination of *Quercus suber* and *Q. canariensis*, but a small positive effect on *Q. pyrenaica* (Urbieta et al., 2008). Therefore, since the influence of sunlight radiation decreases with increasing soil depth, germination responses are expected to change depending on the seed burial depth and the specific light requirements of each species (Fenner and Thompson, 2005). Findings reported for oaks from Asia, Europe and the USA show lower germination when acorns are exposed to direct sunlight at the soil surface (Shaw, 1968; Borchert et al., 1989; Kollmann and Schill, 1996; Nilsson et al., 1996; Khan and Shankar, 2001; García et al., 2002; Li and Ma, 2003; Xiao et al., 2004; Gómez et al., 2004; Guo et al., 2009).

Oaks (genus *Quercus* L., Fagaceae) are perhaps the most important group of trees in northern hemisphere forests. This is because of their high commercial value for timber, as well as their significance in supporting wildlife (McWilliams et al., 2002). Acorn germination is one of the main determinants of the natural regeneration of oak forests (Day, 2002), but little is known about the influence of different burial depths on the germination of American oak seeds. As far as we know, the few studies performed on this issue were conducted in China, showing that acorn germination decreases as burial depth increased (Guo et al., 2001; 2009). Studies on oak and acorn ecology are particularly important for Mexico, because this country is the center of diversification of the genus *Quercus* in the Western hemisphere (Nixon, 1993). Mexico contains the largest oak diversity (161 of the estimated 400 species), and the highest number of endemic species (109 species) in the world (Valencia-A., 2004). Oak forests and mixed pine-oak forests cover 15-18% of the Mexican land surface and strongly contribute to the high diversity of this country (Mittermeier and Goetsch-Mittermeier, 1997). However, almost all of them show clear signs of environmental degradation because they are located at sites that are particularly well suited for human settlement, farming and ranching (Bonfil and Soberón, 1999). Therefore, these forests require to be urgently restored because of the high economic, social and

cultural values that they have for Mexico (Luna-José et al., 2003).

Despite the current interest of governmental and non-governmental agencies in restoring Mexican oak forests, little is known about the factors that affect their regeneration (López-Barrera and González-Espinosa, 2001; Zavala-Chávez, 2004; Martínez-Pérez et al., 2006). It is therefore important to understand the requirements for oak germination and establishment; studies about the oak requirements to germinate and establish are critical. This study focuses on determining the impact of burial depth on acorn germination and seedling emergence for eight representative Mexican oak species.

MATERIALS AND METHODS

Species

The studied species were *Q. affinis* Scheidw., *Q. castanea* Née, *Q. coccolobifolia* Trel., *Q. laeta* Liebm., *Q. mexicana* Bonpl., *Q. polymorpha* Schltld. et Cham., *Q. tinkhamii* C.H. Mull., and *Q. viminea* Trel. (Nomenclature of species and authorities following the TROPICOS® database of the Missouri Botanical Garden; available at <http://www.tropicos.org>). We chose these eight species for a number of reasons. First, they are widely distributed throughout the Mexican forests (Llorente-Bousquets and Ocegueda, 2008). Second, more than half are endemic (Llorente-Bousquets and Ocegueda, 2008). Third, they include representatives of the two main *Quercus* subgenera of Mexico, *Lepidobalanus* (white oaks) and *Erythrobalanus* (red oaks), which are thought to differ in several seed traits, such as the time required for fruit maturation, chemical composition of their stored food reserves, and degree of dormancy (Zavala-Chávez and García, 1996; Bonner, 2008). Moreover, while white oaks seem to be more abundant than red oaks in northern Mexico, the converse situation occurs in southern Mexico (Zavala-Chavez, 1998). Finally, a recent study indicated that these oak species recruit at different forest successional stages (Castillo-Lara et al., 2008). Details on infrageneric taxonomy, distribution range

Table 1. Oak species that were considered in this study. The table indicates the subgenus of each species, as well as the distribution range and successional stages to which each oak species belongs. The last column indicates the time that seeds were stored at 5°C after harvesting

Species	Subgenus	Distribution range	Successional stage	Seed storing time (months)
<i>Quercus affinis</i>	<i>Erythrobalanus</i>	Endemic for Mexico	Late	1
<i>Quercus castanea</i>	<i>Erythrobalanus</i>	Mexico and USA	Intermediate	0
<i>Quercus coccolobifolia</i>	<i>Erythrobalanus</i>	Endemic for Mexico	Pioneer	2
<i>Quercus laeta</i>	<i>Lepidobalanus</i>	Endemic for Mexico	Pioneer	1
<i>Quercus mexicana</i>	<i>Erythrobalanus</i>	Endemic for Mexico	Intermediate	0
<i>Quercus polymorpha</i>	<i>Lepidobalanus</i>	Mexico and USA	Intermediate	1
<i>Quercus tinkhamii</i>	<i>Lepidobalanus</i>	Endemic for Mexico	Pioneer	1
<i>Quercus viminea</i>	<i>Erythrobalanus</i>	Mexico and USA	Intermediate	2

Table 2. Acorn quality characteristics from eight *Quercus* species from San Luis Potosí, México.

Species	Seed viability (%)	Seed mass (mg)
<i>Q. affinis</i>	98.8	1784.797
<i>Q. castanea</i>	100	743.009
<i>Q. coccolobifolia</i>	97.6	230.727
<i>Q. laeta</i>	100	1015.990
<i>Q. mexicana</i>	99	1032.990
<i>Q. polymorpha</i>	100	1381.189
<i>Q. tinkhamii</i>	90	603.062
<i>Q. viminea</i>	97.5	174.986

and successional stages to which each oak species belongs are given in Table 1.

Collecting site

We collected acorns of all these species at Sierra de Álvarez (21°42'32"–22°23' 21" N; 100°05'24"–100°49'30" W), a priority conservation area for Mexico located in the State of San Luis Potosí (Arriaga et al., 2000). This mountain range covers 2265 km². Climate and vegetation both vary strongly with elevation. The prevailing climate below 2000 m.a.s.l. is semi-temperate and semi-arid, and the vegetation is mainly composed of xerophytic plants. The climate at upper elevations is temperate-humid, where oak forests are the dominant vegetation type (Rzedowski, 1965). Annual precipitation averages 352 mm at 1970 m.a.s.l., but it increases with eleva-

tion and exceeds 800 mm above 2200 m.a.s.l. (Arriaga et al., 2000).

In late spring 2009, 20-30 adult oaks of each species were selected across this site when mature acorns were directly collected from them. Acorns from trees belonging to the same species were mixed and stored in polyethylene bags to avoid desiccation. Approximately 800-1000 acorns were collected for each oak species. Bags with seeds were stored at 5°C to inhibit germination (Zavala-Chávez, 2004). Acorns of some species were ready for harvesting in July, but others were not ready until October; thus, the storing time varied between zero (late species) and two months (early species), depending on the species (Table 1). Nevertheless, prior to the germination trial (see below), the acorns of late species were stored at 5°C for two weeks to standardize the effect of cold.

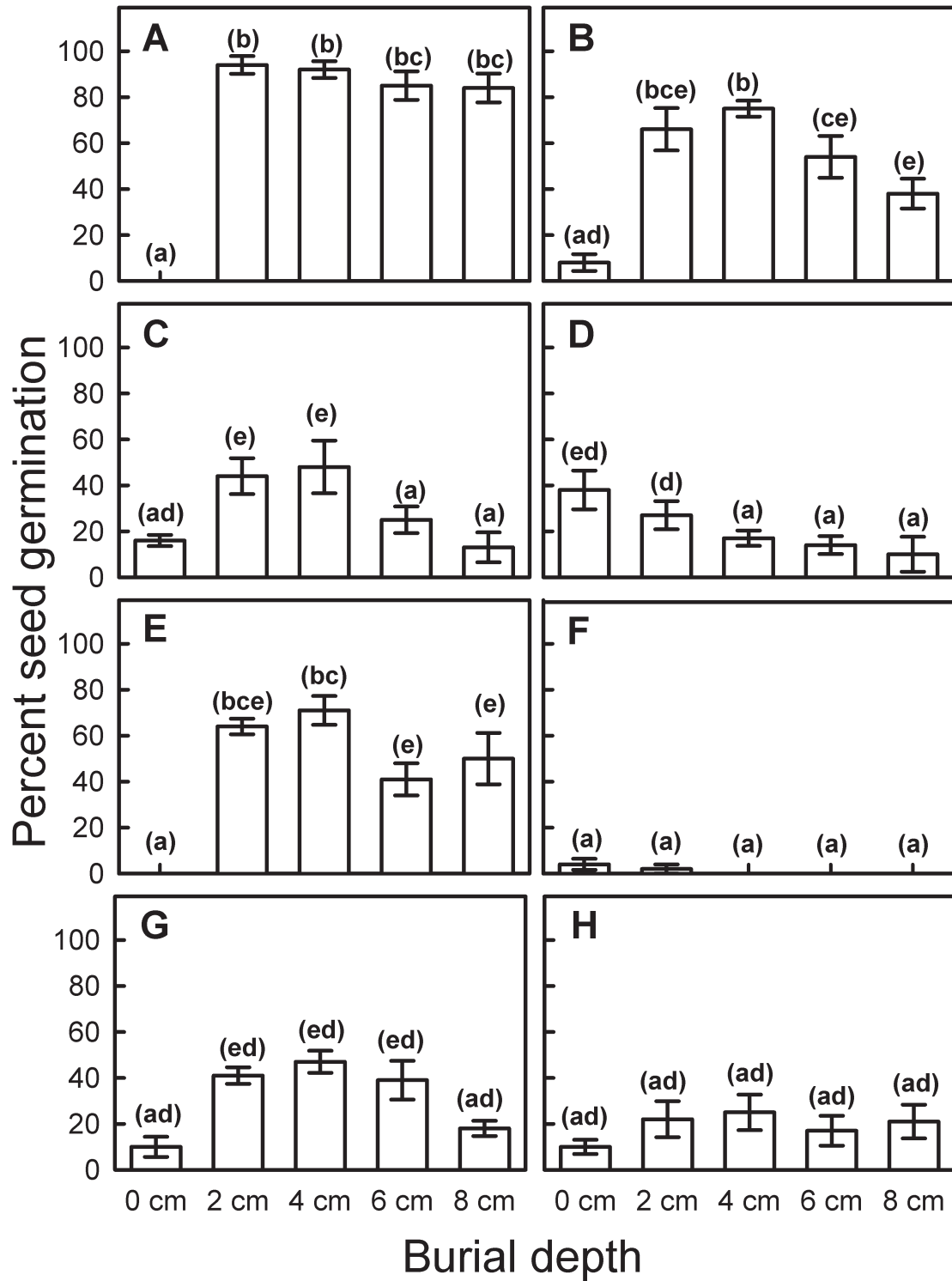


Fig. 1. Effect of burial depth on acorn germination (values are means \pm S.E.) of (a) *Q. affinis*, (b) *Q. castanea*, (c) *Q. coccolobifolia*, (d) *Q. laeta*, (e) *Q. mexicana*, (f) *Q. polymorpha*, (g) *Q. tinkhamii*, and (h) *Q. viminea*. Different letters on the bars indicate statistical differences between treatments (Tukey test critical $\alpha = 0.05$).

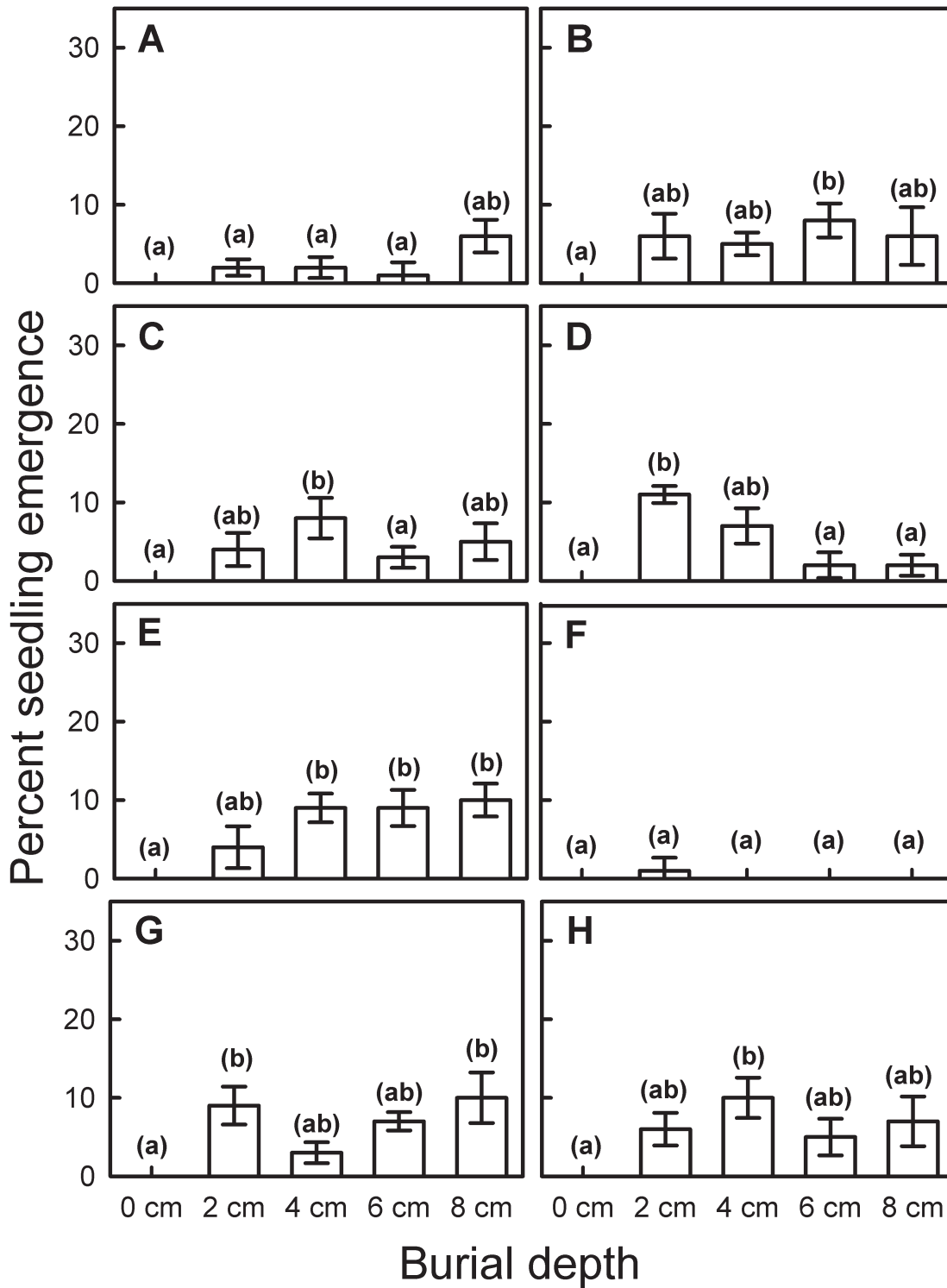


Fig. 2. Effect of burial depth on seedling emergence (values are means \pm S.E.) of: (a) *Q. affinis*, (b) *Q. castanea*, (c) *Q. coccolobifolia*, (d) *Q. laeta*, (e) *Q. mexicana*, (f) *Q. polymorpha*, (g) *Q. tinkhamii*, and (h) *Q. viminea*. Different letters on the bars indicate statistical differences between treatments (Tukey test critical $\alpha = 0.05$).

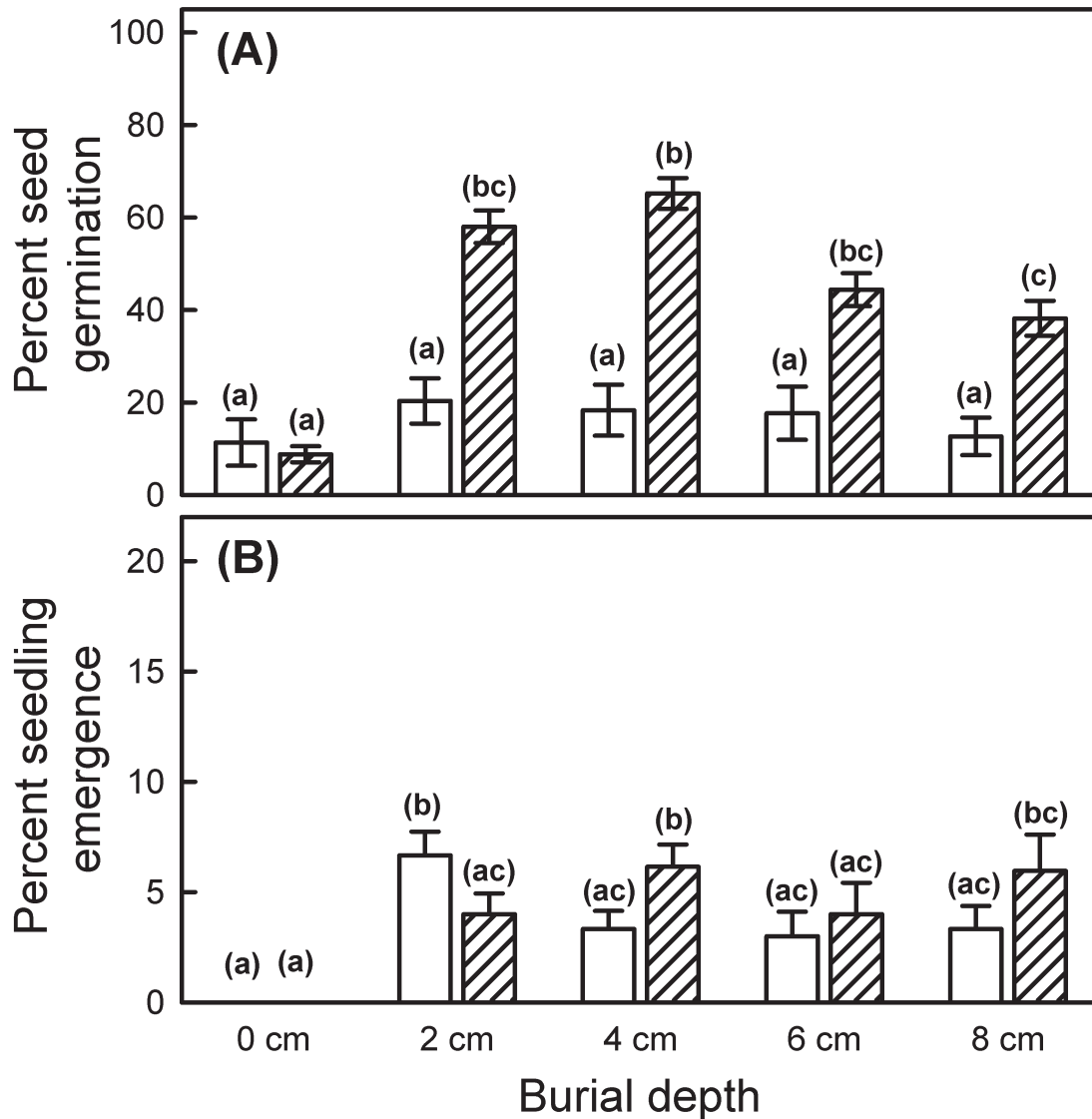


Fig. 3. Effect of burial depth on acorn germination (A) and seedling emergence (b) for oaks of the subgenus *Lepidobalanus* (white oaks = empty bars) and the subgenus *Erythrobalanus* (red oaks = dashed bars). Values are means \pm S.E.; different letters indicate statistical differences between treatments (Tukey test critical $\alpha = 0.05$).

Seed mass

Seed mass is strongly related to seedling emergence and allometric relationships have been developed to explain this phenomenon (Bond et al., 1999). At the same time, seed mass is also strongly related to the sensitivity of the seeds to light irradiance (Flores

et al., 2011), explaining differences in germination between buried and unburied seeds (Milberg et al., 2000; Pearson et al., 2002). Thus, in order to evaluate dry seed mass, 10 seeds per species were placed at 70°C for 48 h, after which the seeds were individually weighed and classified into small (<2 mg) or large (>10 mg) seeds, following Bond et al. (1999).

Acorn germination and seedling emergence experiment

The germination trial began on October 24th 2009. To assess whether burial depth affects germination, we considered five sowing depths (0, 2, 4, 6 and 8 cm). The combination of burial depths and oak species resulted in 40 treatments (5 burial depths x 8 species = 40 treatments). We had 20 replicates (pots) per treatment, with 1 acorn per pot. These pots were later watered to field capacity every two days to avoid the confounding effects of drought on seed germination. This experiment was realized at the greenhouse of the Instituto Potosino de Investigación Científica y Tecnológica (San Luis Potosí, México), which is protected against seed removers. Thus, acorns in the experiment could not be removed, especially where acorns were not buried.

Just before beginning this experiment, the floatability method, suggested by Zavala-Chávez and García (1996), was used to assess acorn viability. In acorns, the results of this method were compared against that from the tetrazolium test by Ponce de León-García (2005), which did not find significant differences between them. The acorns were placed in a 100-liter container that was later filled with water; floating acorns were assumed to be inviable due to insect predation or seed malformations, while sunken acorns were assumed to be viable. Inviability acorns were discarded for the germination experiments.

Since acorns may take several weeks or even months to germinate (Zavala-Chávez, 2004; Martínez-Pérez et al., 2006), the experiment remained at the greenhouse for 112 days. At the end of the experiment, we counted the number seedlings that emerged in each pot. Subsequently, the content of each pot was sieved with a 5 mm mesh to recover the buried acorns. Recovered acorns were carefully inspected in order to assess whether a radicle, but not the aerial shoot, had emerged during the experiment. Therefore, we had two response variables for each treatment: (1) the seedling emergence percentage, computed as the proportion of acorns that developed the aerial shoot in each pot; and (2) the

germination percentage, estimated as the number of emerged seedlings plus the number of seeds that developed the radicle but not the aerial shoot, in each pot.

Statistical analysis

These two variables were compared among the treatments (depths x species) with a factorial ANOVA. After that, given that the two oak subgenera considered in this study (*Lepidobalanus* and *Erythrobalanus*) are suspected to differ in their acorn biology (Bonner, 2008), we used the same statistical analysis to compare acorn germination and seedling emergence among the treatments resulting from the combinations of burial depths and subgenera. In both cases, if ANOVAs indicated differences among treatments, the *post-hoc* Tukey test was used to assess differences between pairs of treatments. All statistical analyses were conducted with the software R 2.11 (R Development Core Team 2010).

RESULTS

Seed mass

The seed weight of the studied species ranged from c. 175 mg for *Q. viminea* to c. 1785 mg for *Q. affinis* (Table 2). All species were considered as having large seeds, following Bond et al. (1999), which suggested that seeds higher than 10 mg are large seeds.

Seed viability

Acorn viability was high for all species; *Q. tinkhamii* had 90% viability and the other species had higher seed viability (at least 97.5%; Table 2).

Seed germination

Acorn germination (%) significantly differed among burial depths ($F_{(4,160)} = 8555.000$; $p < 0.001$) and oak species ($F_{(7,160)} = 11266.696$; $p < 0.001$), and significant effects were also indicated for the interaction between these two factors ($F_{(28,160)} = 1435.357$; $p < 0.001$). The germination percentage of unburied acorns (i.e., at 0

cm depth) was extremely low, or even null, in most oak species. On the other hand, although burial promoted germination in most oak species, this variable was strongly influenced by burial depth (Fig. 1). The buried acorns of *Q. affinis* showed higher germination percentages than those of the other oak species, and germination in this species was not affected by burial depth (Fig. 1). Conversely, *Q. castanea*, *Q. coccolobifolia* and *Q. mexicana* showed a trend for higher germination % at both 2 and 4 cm burial depth (Fig. 1).

Although germination of *Q. laeta* also decreased with burial depth, this was the only species that showed higher germination percentages at the surface of the pots (Fig. 1). Acorn germination did not differ among burial depths in *Q. polymorpha*, *Q. tinkhamii* and *Q. viminea*, but these species showed lower germination percentages than the other oak species (Fig. 1).

Seedling emergence

Seedling emergence (%) also differed among burial depths ($F_{(4,160)} = 4.460$; $p = 0.002$) and species ($F_{(7,160)} = 2.210$; $p = 0.036$), but in this case the effects of the interaction between these two factors was marginally significant ($F_{(28,160)} = 1.517$; $p = 0.058$). Burial depth differentially affected the seedling emergence of the different oak species. Here, *Q. affinis* and *Q. polymorpha* did not show differences in seedling emergence among burial depths and, in most of the cases, these values were lower than those observed for the other oak species. Seedling emergence was lower at the surface than when buried at 2, 4, 6 and 8 cm depth for *Q. castanea*, *Q. mexicana*, *Q. tinkhamii*, and *Q. viminea*. Increasing burial depth decreased seedling emergence in *Q. laeta* (Fig. 2). Finally, *Q. coccolobifolia* displayed higher values of seedling emergence at 2, 4 and 8 cm depth (Fig. 2).

The analysis conducted at the infrageneric level indicated that acorn germination, besides being affected by burial depth ($F_{(4,190)} = 9.981$; $p < 0.001$), also varies between subgenera ($F_{(1,190)} = 49.374$; $p < 0.001$), and highly significant effects were indicated

for the interaction between these two factors ($F_{(4,190)} = 3874.799$; $p < 0.001$). Germination of unburied acorns (*i.e.*, 0 cm depth) did not differ between subgenera, but red oaks (*Erythrobalanus*) showed higher germination responses than white oaks (*Lepidobalanus*) at all the other burial depths (Fig. 3A).

Seedling emergence was influenced by burial depth ($F_{(4,190)} = 3.963$; $p = 0.004$), but no effect was detected for the subgenus ($F_{(1,190)} = 1.419$; $p = 0.234$). Nevertheless, marginally significant effects were indicated for the interaction of these factors ($F_{(4,190)} = 2.382$; $p = 0.052$). At 2 cm depth, seedling emergence was slightly higher for white oaks than for red oaks, but the converse pattern was observed at 4 and 8 cm depth (Fig. 3B).

DISCUSSION

Despite the interest in restoring oak forests, their regeneration ecology is very little known in Mexico (Bonfil and Soberón, 1999; López-Barrera and González-Espinosa, 2001; Zavala-Chávez, 2004; Martínez-Pérez et al., 2006) and in the entire world (Shaw, 1968; Barnett, 1977; Borchert et al., 1989; Nilsson et al., 1996; Fuchs et al., 2000; Plieninger et al., 2010; Feng and Xiao 2011). Although field experiments may differ from our glasshouse experiment due other factors, e.g. predators and water availability, which might favor deeper burial depths, this study is very important because as far as we know, it is the first to assess the effects of acorn burial on Mexican oaks and, therefore, the results could become important for forestry practices addressing the restoration of degraded areas of this country.

Seed burial depth in the soil profile is one of the most obvious factors influencing regeneration success (Fuchs et al., 2000; Traba et al., 2004). Our results suggest that burial depth differentially affected acorn germination and seedling emergence across the Mexican oak species studied. With the exception of *Q. laeta*, acorn germination seems to be reduced on the soil surface. This concurs with the findings reported for oaks from Asia, Europe and USA, which showed lower germination when acorns

were exposed to direct sunlight at the soil surface, in field conditions (Borchert et al., 1989; Kollmann and Schill, 1996; Nilsson et al., 1996; García et al., 2002; Li and Ma, 2003; Gómez et al., 2004; Xiao et al., 2004), as well as in greenhouse (Khan and Shankar, 2001; Guo et al., 2009) and laboratory conditions (García et al., 2002). In Mexico, this inhibition of germination on the soil surface was also reported for acorns of *Q. rugosa* Née from the tropical mountains of southern Mexico (López-Barrera and González-Espinosa, 2001). The lower germination we observed on acorns placed on the soil surface could be partially caused by reductions in seed viability due to the great water loss to which they are subjected compared to buried acorns. On the other hand, it is also feasible that most of the oak species included in this study have negative photoblastic seeds and their germination is therefore inhibited by direct sunlight (Barnett, 1977). Irrespective of the mechanisms that caused these germination patterns, it is important to note that none of the acorns that germinated on the soil surface developed the aerial shoot. This suggests that the recruitment of these Mexican oaks in natural populations may depend on acorn burial.

Putting aside the impact of acorn sowing on the soil surface, the different oak species displayed different patterns of germination and seedling emergence when acorns were buried, although these patterns were not related to the successional stage. The germination of two intermediate, *Q. castanea* and *Q. mexicana*, as well as three pioneer species, *Q. coccolobifolia*, *Q. laeta*, and *Q. tinkhamii*, decreased as burial depth increased. These germination patterns coincide with those reported by Guo et al. (2001; 2009) for Chinese oak species, which showed that acorn germination diminishes as burying depth increases. On the other hand, germination of a late species, *Q. affinis*, and two intermediate species, *Q. polymorpha* and *Q. viminea*, was similar across the depth treatments. Seedling emergence also strongly varied among oak species and burial depths. For instance, seedling emergence in *Q. affinis* (a late species) and *Q. polymorpha* (an intermediate) was similar among the burial depths and soil surface; it was higher in all burial depths than at the surface for *Q. castanea*,

Q. mexicana, and *Q. viminea* (three intermediates), as well as *Q. tinkhamii* (a pioneer); it was lower at increasing burial depth for *Q. laeta* (a pioneer) and it was higher at 2, 4 and 8 cm depth, but not at 6 cm, for *Q. coccolobifolia* (a pioneer).

Patterns of germination and seedling emergence were not related to seed mass, because all studied species had big seeds. These findings are contrary to Bond et al. (1999) who predicted that species with large seeds would be able to emerge from deeper soil than those with small seeds. Thus, differences in germination and seedling emergence among oak species could be related, at least in part, to differences in their life histories and recruitment strategies, but not to the successional stage or the seed mass. Instead, within each species, the effects of burial depth could be linked to changes in micro-environmental conditions that co-vary with depth. However, fully controlled experiments, with detailed measures of micro-environmental conditions at different depths (e.g., soil water content and soil temperature), should be conducted in order to determine the exact mechanisms that regulate recruitment for each oak species.

At the infrageneric level, no differences in germination were observed between red and white oaks when acorns were placed on the soil surface. Nevertheless, red oaks showed higher acorn germination than white oaks at all the other burial depths. This suggests that darkness in acorn burial promotes seed dormancy in white oaks, a phenomenon known as "skotodormancy" (Flores et al., 2006), while it breaks dormancy in red oaks. On the other hand, although shallow burial at 2 cm depth seems to promote seedling emergence in white oaks, red oaks showed higher seedling emergences at higher burial depths.

CONCLUSIONS

Buried acorns displayed higher seed germination and seedling emergence than unburied ones, but burial depth also influenced these variables. The effect of burial depth idiosyncratically varied among species, so that no general pattern can be identified

for these processes. However, our results suggest that acorn burial is critical for oak recruitment. Optimum burial depth for seedling emergence of each species is 2, 4, 6 and 8 cm depth for *Q. castanea*, *Q. mexicana*, *Q. tinkhamii*, and *Q. viminea*; 2 and 4 cm for *Q. laeta*; and 2, 4 and 8 cm for *Q. coccolobifolia*. Acorns of *Q. affinis* and *Q. polymorpha* had low seedling emergence in all treatments, which suggest that these species have dormant viable seeds. Despite the fact that field experiments may differ from our glasshouse experiment, this study is very important because, as far as we are aware, this is the first one assessing the effects of acorn burial on Mexican oaks and, therefore, conservation management could increase oak regeneration by acorn burial.

Acknowledgments - J. Flores-Cano thanks the postdoctoral grant given by CONACYT. This study was founded by Fondos Sectoriales CONACYT-SEMARNAT 2006-C01-23818 to J. Flores and Fondo Mixto de Fomento a la Investigación Científica y Tecnológica CONACYT-Gobierno del Estado de Puebla 10857 to E. I. Badano.

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