



# Acorn weight as determinant of germination in red and white oaks: evidences from a common-garden greenhouse experiment

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Received: 21 August 2017 / Accepted: 10 January 2018 / Published online: 31 January 2018  
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## Abstract

• **Key message** In Mexican oaks, germination increases with acorn fresh weight across oak species. Within species, these relationships are stronger in red oaks than in white oaks. In both oak groups, fresh weight of acorns increases with their dry biomass.

• **Context** Mexican oaks are phylogenetically grouped in red and white oaks. White oaks produce heavier acorns than red ones, but no studies have assessed whether this leads to different germination patterns.

• **Aims** This study was aimed to determine the influence of the fresh weight of acorns on their germination.

• **Methods** Acorns of red and white oaks were hydrated, weighed, and sowed under greenhouse conditions to assess whether their fresh weight was related with germination. We also assessed whether fresh weight of acorns was related with their dry biomass and/or water accumulation capability.

• **Results** Hydrated acorns of white oaks were heavier and germinated faster than those of red oaks. Germination percentages increased with acorn fresh weight across oak species. Within species, germination probability increased with acorn fresh weight, but these relationships were more marked in red oaks. Germination speed decreased with acorn fresh weight in red oaks, but these relationships were not found in white oaks. Fresh weight was positively related with acorn dry biomass in all oak species, but it was not related with water content.

• **Conclusion** Increasing acorn fresh weight enhances germination across oak species. Within species, however, this trait seems to have more influence in red than in white oaks.

**Keywords** *Lobatae* · Logistic regressions · Mexico · *Quercus* · Seed size

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**Handling Editor:** Gilbert Aussenac

## Contribution of the co-authors

Erik Sánchez and Lilia Silva developed the experiment, gathered the data, and co-wrote the article. Joel Flores, Felipe Barragán, and Jorge Flores contributed with the collection of acorns, analysis of data, and co-wrote the article. Ernesto Badano conceptualized the study, analyzed the data, and prepared the final version of the article.

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s13595-018-0693-y>) contains supplementary material, which is available to authorized users.

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## 1 Introduction

Seed weight is a fundamental life history trait of plants and ecologists have been largely interested in determining how it influences tree recruitment (Silvertown 1989; Leishman et al. 2000). In highly competitive habitats, such as forest under-stories, it was proposed that natural selection favors tree species with heavier seeds because this accelerates seedling development and enhances their competitive ability for light and soil resources (Foster 1986; Silvertown 1989; Westoby et al. 1992; Leishman and Westoby 1994; Bruun and Ten Brink 2008; Yi and Wang 2016). Conversely, lighter-seeded species are adapted to stressful habitats, such as forest clearings, where small seed sizes would confer them resistance to desiccation until favorable conditions for germination occur (Foster 1986; Silvertown 1989; Leishman et al. 2000). Within tree species, on the other hand, it was reported that heavier seeds give rise to seedlings that are more resistant to drought and herbivory, which increases their establishment chances (Bonfil 1998; Chacón et al. 1998; Chacón and Bustamante 2001; Gómez 2004; Huerta-Paniagua and Rodríguez-Trejo 2011). These interspecific and intraspecific effects of seed weight on the development and survival of early life-cycle stages of trees are well documented (Fenner and Thompson 2005), but the effects this trait on seed germination have received less attention. This could be due to the greater interest that plant ecologists have put in analyzing how seed weight relates with the fate of tree seedlings, as they are critical for forest regeneration, while their consequences on germination remained as experimental anecdotes (e.g., Bonfil 1998; Gómez 2004).

Germination starts with the development of the embryo after seed imbibition and this results in the emergence of the radicle (Fenner and Thompson 2005). Germination is proposed to increase with seed weight because heavier seeds are assumed to have larger cotyledonary reserves (Gómez 2004), but no previous study has analyzed whether this trait constitutes an adaptation that evolved from different environmental pressures. Tree species belonging to the same phylogenetic lineage (e.g., the same genus) could be useful to elucidate whether seed weight, besides affecting the fate of their seedlings, also influences germination. This is because closely related species usually produce seeds with similar morphoanatomical features but, if they differ in seed weight and variability in this trait affect their germination, this may be reflecting adaptation of species to germinate under different environmental conditions. Further, if seed weight varies within each tree species and this also relates to germination, these intraspecific relationships should be more similar among species that are phylogenetically closer to each other (e.g., species that diversified more recently from a common ancestor within the genus) than among phylogenetically distant species (e.g., species groups whose ancestors diverged much earlier within

the genus). This would occur if seeds of the ancestors that gave rise to different species groups within the genus were subjected to different selective pressures.

To assess these interspecific and intraspecific effects of seed weight on germination, we focused on oaks (*Quercus* spp., Fagaceae) because these trees produce acorns (nut-type fruits that contain a single seed) that largely differ in their weight, both across and within species (Long and Jones 1996; Bonfil 1998; Khan and Shankar 2001; Zavala-Chávez 2001; Landergott et al. 2012). Because of the elevated phylogenetic diversity of this plant group, oaks have been divided in several infrageneric categories. Nixon (1993) used morphological traits and DNA sequences to split this genus in two broad subgenera, including *Cyclobalanopsis* (only present in eastern Asia and northern Oceania) and *Quercus* (distributed across all continental masses of the northern hemisphere). Additionally, Nixon (1993) split the subgenus *Quercus* in three phylogenetic sections: (1) *Lobatae*, or red oaks, which are in America only (from USA to Colombia), (2) *Protobalanus*, or golden oaks, which are restricted to north-west Mexico and southwest USA (California Peninsula), and (3) *Quercus*, or white oaks, which spread across the entire northern hemisphere (North and Central America, Europe, Asia, and Northern Africa). Mexico is the most important diversification center of the subgenus *Quercus*, harboring more than 160 species (Valencia 2004). Further, red and white oaks widely overlap their distribution ranges across this country (Romero-Rangel et al. 2014), which provides exceptional opportunities to assess whether acorn biomass influences germination across and within species.

Acorns of white and red oaks are highly recalcitrant and germinate in short time after primary dispersion, which occurs during the rainy season (Zavala-Chávez and García-Moya 1996). On this issue, it was reported that acorns of Mexican oaks lose viability when their water contents decrease below 25–30%, but they need to be close to their maximum hydration capacity to germinate (Zavala-Chávez and García-Moya 1996; Zavala-Chávez 2008). Further, viable acorns of white oaks have been reported to be heavier than those of most red oaks (Zavala-Chávez and García-Moya 1996; Zavala-Chávez 2004; Rubio-Licona et al. 2011). Therefore, if acorn weight influences germination, white oaks can be expected to have higher germination rates (i.e., fraction of acorns that germinate across time within a cohort) and higher germination percentages (i.e., final fraction of germinated acorns of a cohort) than red oaks when their acorns are sowed under the same environmental conditions (e.g., a common-garden experiment). Nevertheless, as the fresh weight of viable acorns includes both water and nutrients, it would also be necessary to determine how variability in this trait relates with their dry biomass, which would be indicative of the amount of nutrients accumulated within acorns, and percent moisture content, which would be indicative of the amount of water that viable acorns

require to germinate. These relationships would provide insights about what of these variables (dry biomass or water content) is the main responsible of intraspecific differences in germination. Further, as maternal effects can also cause intraspecific differences in dry biomass and water content, germination probability (i.e., the chance of germinating) and germination speed (i.e., the time they require to germinate) are also feasible to increase with acorn fresh weight.

In this study, we analyzed the interspecific and intraspecific germination patterns of red and white oaks from Sierra Madre Oriental, Mexico. For this, we firstly assessed the fresh weight of viable acorns produced by different species of both phylogenetic sections and performed common-garden greenhouse experiment addressing the following questions: (i) does the fresh weight of viable acorns differ between red and white oaks, as well as among species of these two groups?; (ii) do differences in this trait lead to different germination rates and germination percentages in red and white oaks?; (iii) does intraspecific variability in acorn fresh weight affect germination probability and germination speed within oak species?; and (iv) are these relationships more similar among oak species from the same phylogenetic section that across species from different sections? After performing that experiment, we focused in determining whether the fresh weight of acorns related with their dry biomass and water content in order to determine what of these traits may be behind of the relationships between acorn weight and germination.

## 2 Materials and methods

### 2.1 Oak species and acorn collection

This study was performed with oak species from Sierra de Álvarez, a mountain range (2000–2500 m elevation) that comprises the westernmost section of Sierra Madre Oriental. Sierra de Álvarez is located 25 km to the east of the city of San Luis Potosí, central Mexico, and it harbors eight red oak species (section *Lobatae*) and nine white oak species (section *Quercus*) (García-Sánchez and Aguirre-Rivera 2011). Most these oaks have mast reproduction and produce acorns every 2–5 years, but these events are not always synchronized among species. For this reason, we focused on those species that produced acorns in 2015 and 2017, which included seven red oaks (*Quercus affinis* Scheidw., *Quercus castanea* Née, *Quercus crassifolia* Humb. & Bonpl., *Quercus eduardii* Trel., *Quercus jonesii* Trel., *Quercus mexicana* Humb. & Bonpl., and *Quercus viminea* Trel.) and three white oaks (*Quercus laeta* Liebm., *Quercus polymorpha* Schldl. & Cham., and *Quercus potosina* Trel.).

Acorns collected in 2015 were used to assess whether fresh weight influences their germination, while acorns collected in 2017 were used to assess whether fresh weight relates to their dry biomass and water content. In both years, collections were conducted immediately after acorns were released from parental trees. In 2015, this occurred between early August and middle September, while in 2017, this occurred between middle September and late October. Acorn collections included ten trees of each species and, beneath the canopy of each individual, we collected 100 mature acorns to capture as much variability in acorn weight as possible. Acorns belonging to each species were pooled in a single sample and carried to the laboratory to assess their viability with the float test (Gribko and Jones 1995). We did this because acorns collected in the field can quickly lose viability due desiccation or parasitism by insects or fungi (Ramos-Palacios et al. 2014). For this, acorn cupules were removed and nuts were placed in 20-L containers filled with water. After 2 h in water, sunken acorns were assumed as viable, while floating acorns were assumed as unviable (Gribko and Jones 1995; González-Salvatierra et al. 2013; Ramos-Palacios et al. 2014). With this noninvasive test, we retain more than 500 viable acorns of each species at each year. These viable acorns were stored in refrigerated chambers (5 °C) to prevent desiccation and retard their germination. As germination trials described below started in middle September 2015, acorns of those species collected in August of that year (*Q. affinis*, *Q. crassifolia*, *Q. eduardii*, *Q. jonesii*, *Q. laeta*, *Q. viminea*, and *Q. potosina*) were stored by a month, while acorns of species collected in September (*Q. castanea*, *Q. mexicana*, and *Q. polymorpha*) were stored by a few days. The relationships of the fresh weight of acorns vs. their dry biomass and water content were assessed in late October 2017 and, thus, these acorns were stored by less than a month.

### 2.2 Common-garden germination experiment

To assess the effects of acorn fresh weight on germination, we performed a common-garden experiment with the acorns collected in 2015. This experiment was conducted in a ventilated greenhouse located at the city of San Luis Potosí, Mexico. The roof of the greenhouse was covered with Raschel mesh (60% shade) to approximate temperature and light conditions to those of forest understories, where germination of most oak species occurs (Zavala-Chávez 2001). During the experiment, we used automatized sensors to measure these two environmental variables in the greenhouse and the understory of an oak forest near the city. The average temperature of the air in the greenhouse was 19.7 °C, while temperature in the forest was 18.3 °C (see Online Resource 1). Photon flux density during daytime (07:00 to 19:00 h) averaged 153  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the greenhouse and 134  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the forest (see

Online Resource 1). These values indicate that temperature and light conditions were similar between the greenhouse and the forest.

For the common-garden germination experiment, we randomly selected 100 viable acorns of each oak species during September 14, 2015 and placed them in water during 48 h. We soaked these acorns to approximate them to their maximum hydration capacity, as this is necessary to promote their germination (Zavala-Chávez and García-Moya 1996; Zavala-Chávez 2008). Soaking was also applied to standardize the germination capability across acorns because, otherwise, comparisons of germination responses across and within oak species could be influenced by differences in the moisture content that acorns had at the moment they were collected in the field. The fresh weight of these fully hydrated acorns was used as predictive variable in the analyses of their germination responses. For this, acorns were dried with paper towels after they were soaked and all of them were weighed in an analytical balance (resolution 0.1 mg, Sartorius, Germany) to determine their fresh weight. These acorns were sowed in individual plastic cups (50 mL) filled with a mixture of sterilized forest soil (80%) and perlite (20%). Because previous observations in the field indicate that recently released acorns can germinate on the soil surface, they were half-buried in the germination substrate (see Online Resource 1). We did not remove the pericarps of acorns because these structures prevent seed desiccation (Zavala-Chávez and García-Moya 1996). On all cases, acorns were assumed to have germinated when the radicle emerged from the pericarp (see Online Resource 1).

Germination cups were randomly distributed on an experimental table in the greenhouse (see Online Resource 1) and they were watered until saturating the substrate. We perforated the bottom of the cups to allow drainage of excess water and applied the same watering procedure every 2 days to maintain acorn moisture. Acorn germination was recorded daily between September 16 and November 15 (60 days). After finishing the experiment, we assessed whether ungerminated acorns were viable. For this, a small incision was performed on the pericarp of ungerminated acorns and they were incubated in solution 1% (mass/volume) of 2,3,5-triphenyltetrazolium chloride in dark, at 20–25 °C, during 24 h. If seed embryo is alive, the colorless tetrazolium salt reacts with the hydrogen released by active dehydrogenase enzymes and it is reduced to formazan, a red nondiffusible dye (Black et al. 2006). This test indicated that all ungerminated acorns lost their viability during the experiment.

### 2.3 Fresh weight, dry biomass, and moisture content of acorns

Acorns collected in 2017 were used to assess whether their fresh weight after soaking, dry biomass, and moisture content

differed between phylogenetic sections and among oak species, as well as to assess whether these variables were related between them. For this, we randomly selected 100 viable acorns of each oak species and soaked them as described above. After soaking, each acorn was weighed to determine their fresh weight (FW). They were later placed in individual paper envelopes and dried in a ventilated stove at 60 °C until their dry biomass (DB) remained constant. These data were later used to estimate the percent water content (PWC) of each acorn as  $PWC = (FW - DB)/FW \times 100$ .

### 2.4 Statistical analyses

If acorn fresh weight positively influences germination rates, the proportion of germinated acorns across time should be higher in oak species that produce heavier acorns, as compared to those that produce lighter ones. These effects were firstly tested at the level of oak phylogenetic section using the data of the greenhouse experiment conducted in 2015. For this, we assessed whether the fresh weight of soaked acorns differed between white and red oaks (section *Quercus* vs. section *Lobatae*) using a Student's *t* test, where each acorn was included as a replicate of the respective phylogenetic section. After that, we performed a failure time analysis to assess differences in germination rates between white and red oaks. In this test, acorns of red and white oaks had a value of 0 at the beginning of the experiment, which was turned into 1 on the date in which they germinated. Ungerminated acorns retained the zero value until the end of the experiment. This binary data (0–1) was used to calculate standardized germination rates with the Kaplan-Meier method (Kaplan and Meier 1958), which were compared between phylogenetic sections with Gehan-Wilcoxon tests (Kleinbaum and Klein 2012). We later assessed these effects at the species level. For this, one-way ANOVA and post hoc Tukey tests were used to compare the fresh weight of acorns (after soaking) among oak species, and failure time analyses similar to those described above were used to assess differences in germination rates. Additionally, the influence of acorn fresh weight on germination was assessed across oak species with a simple linear regression, where the final germination percentage of each species (fraction acorns germinated by the end of the experiment) was used as response variable and their average acorn fresh weight was used as predictive variable. If acorn fresh weight positively influences germination, this interspecific analysis should indicate a positive relationship between germination percentage and acorn weigh across oak species.

To assess intraspecific effects of acorn fresh weight on germination, we also used the data of the experiment conducted in 2015. We determined whether variability in this trait influences germination probability within each oak species using logistic regressions based on models of type  $Y = e^{(\alpha + \beta X)} / [1 + e^{(\alpha + \beta X)}]$ . In this model, *Y* is a binary response variable

(0–1; ungerminated and germinated acorns, respectively),  $X$  is the continuous predictive variable (acorn fresh weight),  $e$  is the Napier constant (2.718...), and the letters  $\alpha$  and  $\beta$  are the parameters that define the shape of regression function (Zar 2010). These regressions calculate the occurrence probability of an event as the values of the predictive variable increase, and their accuracy is provided by the number of cases (0–1) correctly classified by the model (Zar 2010). If acorn fresh weight influences germination, the logistic curve would indicate the critical weight that viable acorns must reach to germinate and, after this value, it would show how germination probability increases with acorn fresh weight. After these analyses, we focused on germinated acorns only and determined whether fresh weight influences germination speed (time elapsed between acorn sowing and germination) within each oak species using simple linear regressions. In these analyses, the response variable was the germination speed of each acorn (days after sowing) and the predictive variable was its fresh weight after soaking. If acorn fresh weight positively influences germination speed, the number of days elapsed between sowing and germination must decrease as fresh weight increases.

Fresh weight after soaking, dry biomass, and water of acorns collected in 2017 was compared between phylogenetic sections with Student's  $t$  test and among oak species with one-way ANOVA and post hoc Tukey tests. To assess whether fresh weights of soaked acorns related with DB or PWC within each oak species, we used simple linear regressions. All statistical analyses described in this section were conducted in R 3.3 (R Foundation 2016), and the datasets generated and analyzed during the current study are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.1100945>).

**Data availability** The datasets generated and analyzed during the current study are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.1100945>).

### 3 Results

#### 3.1 Interspecific effects of acorn fresh weight on germination

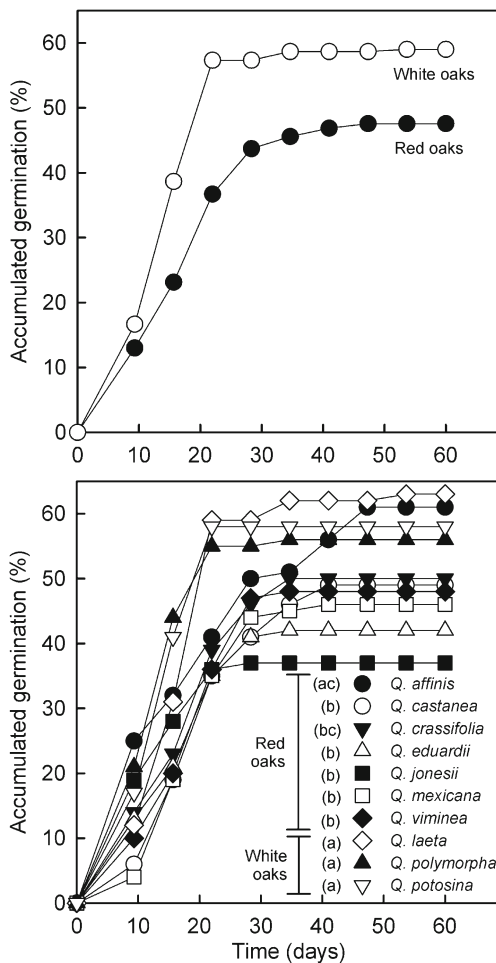
In 2015, fully hydrated acorns of white oaks were heavier than those of red oaks ( $2.16 \text{ g} \pm 0.039 \text{ S.E.}$  vs.  $0.961 \text{ g} \pm 0.024 \text{ S.E.}$ ,  $t = 26.725$ ,  $df = 998$ ,  $p < 0.001$ ). Differences in acorn fresh weight after soaking were also found among oak species ( $F_{(9, 990)} = 391.327$ ,  $p < 0.001$ ). Pairwise comparisons between species indicated that the fresh weight of acorns did not differ between the white oaks *Q. laeta* and *Q. potosina*, also indicating that these species had heavier acorns than all other ones (Table 1). They were followed by the acorns of the red oak *Q. affinis* and the white oak *Q. polymorpha*, which were heavier than those of the remaining species (Table 1). The red oaks *Q. eduardii*, *Q. jonesii*, *Q. mexicana*, and *Q. viminea* had lighter acorns than the other species, while *Q. castanea* and *Q. crassifolia* had intermediate acorn fresh weights (Table 1).

Acorns of white oaks had higher germination rates than those of red oaks (Gehan-Wilcoxon statistic = 4.676,  $df = 1$ ,  $p < 0.001$ ; Fig. 1). Differences in germination rates were also found among species (Gehan-Wilcoxon statistic = 31.743,  $df = 9$ ,  $p < 0.001$ ). Pairwise comparisons of germination rates indicated that the acorns of the three white oaks included in the experiment (*Q. laeta*, *Q. polymorpha*, and *Q. potosina*)

**Table 1** Average fresh weight ( $\pm$ S.E.) of acorn of red and white oaks included in the common-garden experiment conducted in 2015

| Phylogenetic section          | Oak species           | Fresh acorn weight after soaking (g)   | Logistic regression results            | Linear regression results                     |
|-------------------------------|-----------------------|--|--|---|
| Red oaks ( <i>Lobatae</i> )   | <i>Q. affinis</i>     | 2.07 ( $\pm 0.043$ S.E.) <sup>a</sup>  | $\chi^2 = 71.070$ , $p < 0.001$ (89%)  | $F_{(1, 59)} = 100.171$ , $p < 0.001$ (0.629) |
|                               | <i>Q. castanea</i>    | 1.55 ( $\pm 0.027$ S.E.) <sup>b</sup>  | $\chi^2 = 78.357$ , $p < 0.001$ (88%)  | $F_{(1, 47)} = 88.935$ , $p < 0.001$ (0.654)  |
|                               | <i>Q. crassifolia</i> | 1.06 ( $\pm 0.030$ S.E.) <sup>c</sup>  | $\chi^2 = 93.850$ , $p < 0.001$ (91%)  | $F_{(1, 48)} = 131.102$ , $p < 0.001$ (0.732) |
|                               | <i>Q. eduardii</i>    | 0.493 ( $\pm 0.013$ S.E.) <sup>d</sup> | $\chi^2 = 85.117$ , $p < 0.001$ (88%)  | $F_{(1, 40)} = 144.077$ , $p < 0.001$ (0.783) |
|                               | <i>Q. jonesii</i>     | 0.436 ( $\pm 0.011$ S.E.) <sup>d</sup> | $\chi^2 = 100.310$ , $p < 0.001$ (92%) | $F_{(1, 35)} = 72.239$ , $p < 0.001$ (0.674)  |
|                               | <i>Q. mexicana</i>    | 0.643 ( $\pm 0.016$ S.E.) <sup>c</sup> | $\chi^2 = 96.728$ , $p < 0.001$ (91%)  | $F_{(1, 44)} = 42.907$ , $p < 0.001$ (0.494)  |
|                               | <i>Q. viminea</i>     | 0.467 ( $\pm 0.009$ S.E.) <sup>d</sup> | $\chi^2 = 73.605$ , $p < 0.001$ (85%)  | $F_{(1, 46)} = 69.558$ , $p < 0.001$ (0.602)  |
| White oaks ( <i>Quercus</i> ) | <i>Q. laeta</i>       | 2.43 ( $\pm 0.047$ S.E.) <sup>f</sup>  | $\chi^2 = 27.651$ , $p < 0.001$ (66%)  | $F_{(1, 61)} = 0.245$ , $p = 0.622$ (0.004)   |
|                               | <i>Q. polymorpha</i>  | 1.78 ( $\pm 0.049$ S.E.) <sup>e</sup>  | $\chi^2 = 20.047$ , $p < 0.001$ (67%)  | $F_{(1, 54)} = 1.780$ , $p = 0.187$ (0.031)   |
|                               | <i>Q. potosina</i>    | 2.26 ( $\pm 0.086$ S.E.) <sup>f</sup>  | $\chi^2 = 21.135$ , $p < 0.001$ (64%)  | $F_{(1, 56)} = 0.263$ , $p = 0.609$ (0.005)   |

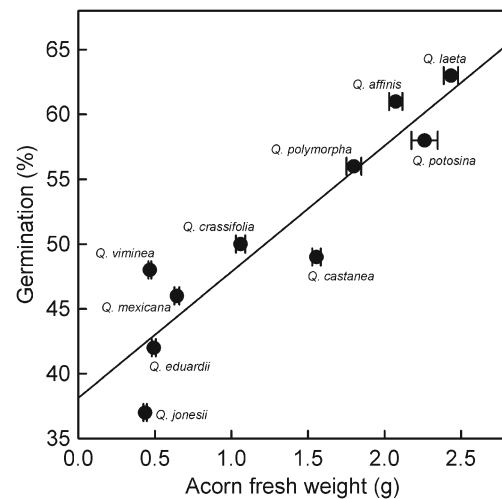
Different superscript letters on the side of averages indicate significant differences between oak species (Tukey test critical  $\alpha = 0.05$ ). The table also shows the results of the logistic regressions ( $\chi^2$  value and  $p$  value; the percent of cases correctly classified by the model is shown in brackets) addressed to determine how germination probability relates with fresh acorn weight within each species (critical  $\alpha$  for significant effects = 0.05), as well as the results of the simple linear regressions ( $F$  value with degrees of freedom and  $p$  value; the  $r^2$  value is shown in brackets) conducted to assess the relationships between fresh acorn weight and germination speed (critical  $\alpha$  for significant effects = 0.05)



**Fig. 1** Acorn germination rates estimated with the Kaplan-Meier method. The upper panel shows the germination rates of red oaks (phylogenetic section *Lobatae*) and white oaks (phylogenetic section *Quercus*) irrespective of the species. The lower panel shows the germination rates of each oak species included in the common-garden experiment. Different letters on the side of each oak name indicate significant differences in germination rates between species (Gehan-Wilcoxon critical  $\alpha$  for pairwise comparisons = 0.05)

germinated faster than those of most red oaks (Fig. 1). The only exception was the red oak *Q. affinis*, whose germination rates were similar to those of white oaks (Fig. 1). No difference in germination rates was found among the other red oak species (Fig. 1).

Germination percentages across oak species were positively related with increases in the average weight of fully hydrated acorns ( $F_{(1, 8)} = 539.288, p < 0.001, r^2 = 0.850$ ). In this relationship, those oaks with acorn fresh weights above 1.7 g (*Q. laeta*, *Q. polymorpha*, *Q. potosina*, and *Q. affinis*) had the highest germination percentage, while oaks with acorn fresh weight below 0.7 g (*Q. eduardii*, *Q. jonesii*, *Q. mexicana*, and *Q. viminea*) had the lowest germination percentage (Fig. 2). Oak species with intermediate acorn fresh weights (*Q. crassifolia* and *Q. castanea*) were in the middle section of this relationship (Fig. 2).



**Fig. 2** Linear relationship between germination percentage and average acorn fresh weight ( $g \pm S.E.$ ) across the ten oak species included in the common-garden experiment

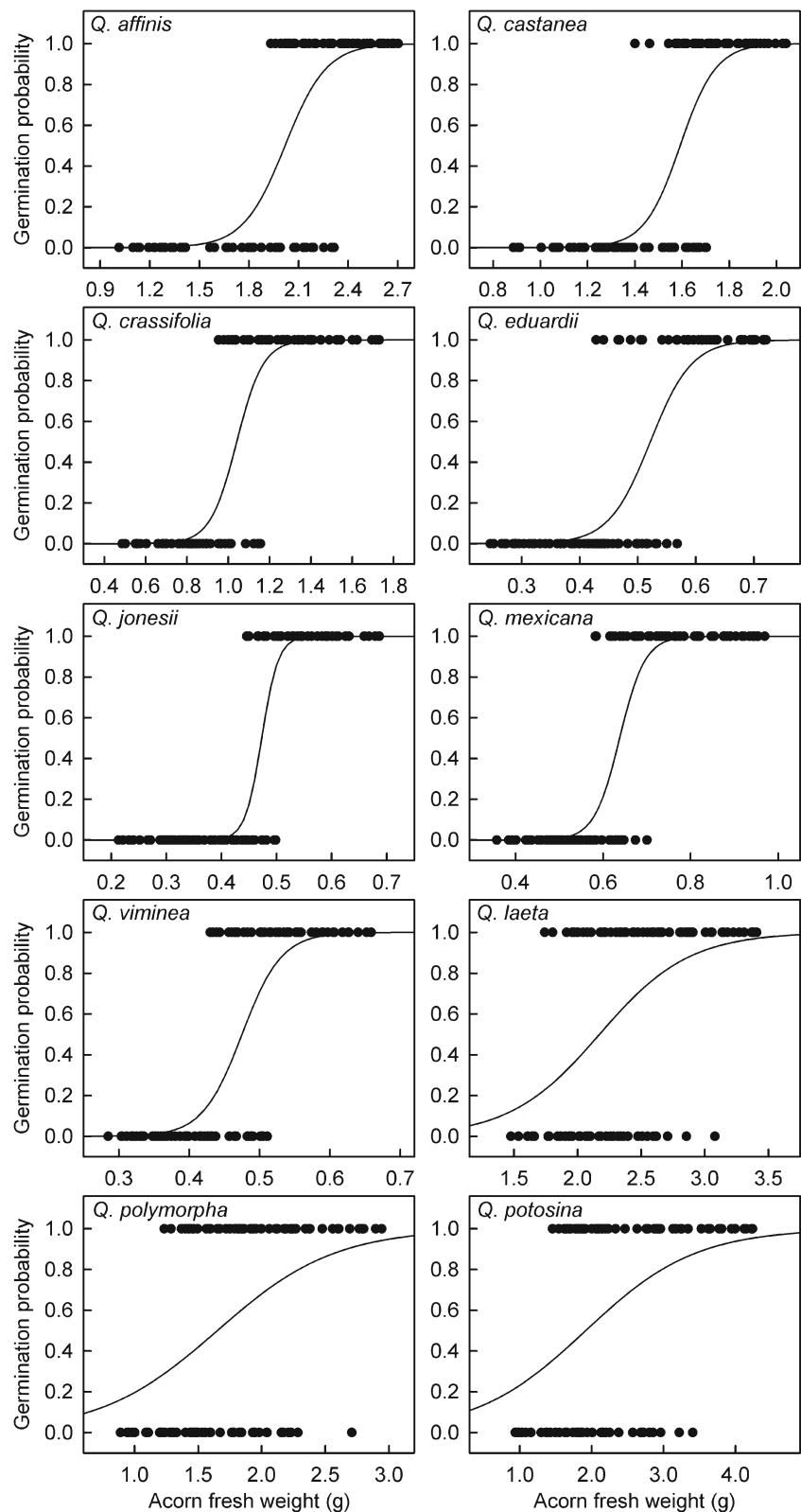
### 3.2 Intraspecific effects of acorn fresh weight on germination

In all oak species, logistic regressions indicated that germination probability increased with the fresh weight of fully hydrated acorns (Table 1). However, these relationships fitted better in red oaks than in white ones (Fig. 3). These results are supported by the proportion of cases correctly classified by logistic models, which surpassed 85% for red oaks and were below 70% for white oaks (Table 1). On the other hand, germination speed decreased with acorn fresh weight in all red oaks, but these variables were not related in any white oak (Table 1 and Fig. 4).

### 3.3 Fresh weight, dry biomass, and moisture content of acorns

Fresh weights (after soaking) of acorns collected in 2017 concurred with those obtained in 2015, as these values were higher in white oaks than in red oaks ( $2.02 g \pm 0.036 S.E.$  vs.  $0.964 g \pm 0.021 S.E., t = 26.763, df = 998, p < 0.001$ ). Further, acorns of white oaks collected in 2017 had higher dry biomasses and higher water contents than those of red oaks (dry biomass =  $0.821 g \pm 0.015 S.E.$  vs.  $0.584 g \pm 0.014 S.E., t = 9.545, df = 998, p < 0.001$ ; water contents =  $59.3\% \pm 0.402 S.E.$  vs.  $40.8\% \pm 0.264 S.E., t = 28.999, df = 998, p < 0.001$ ). All these acorn variables also differed among oak species (fresh weight:  $F_{(9, 990)} = 312.552, p < 0.001$ ; dry biomass:  $F_{(9, 990)} = 320.772, p < 0.001$ ; water content:  $F_{(9, 990)} = 965.273, p < 0.001$ ). The white oak *Q. potosina* had the highest acorn fresh weight after soaking (Table 2), followed by the white oaks *Q. polymorpha* and *Q. laeta* and the red oak *Q. affinis* (Table 2). Acorn fresh weights of the other red oaks

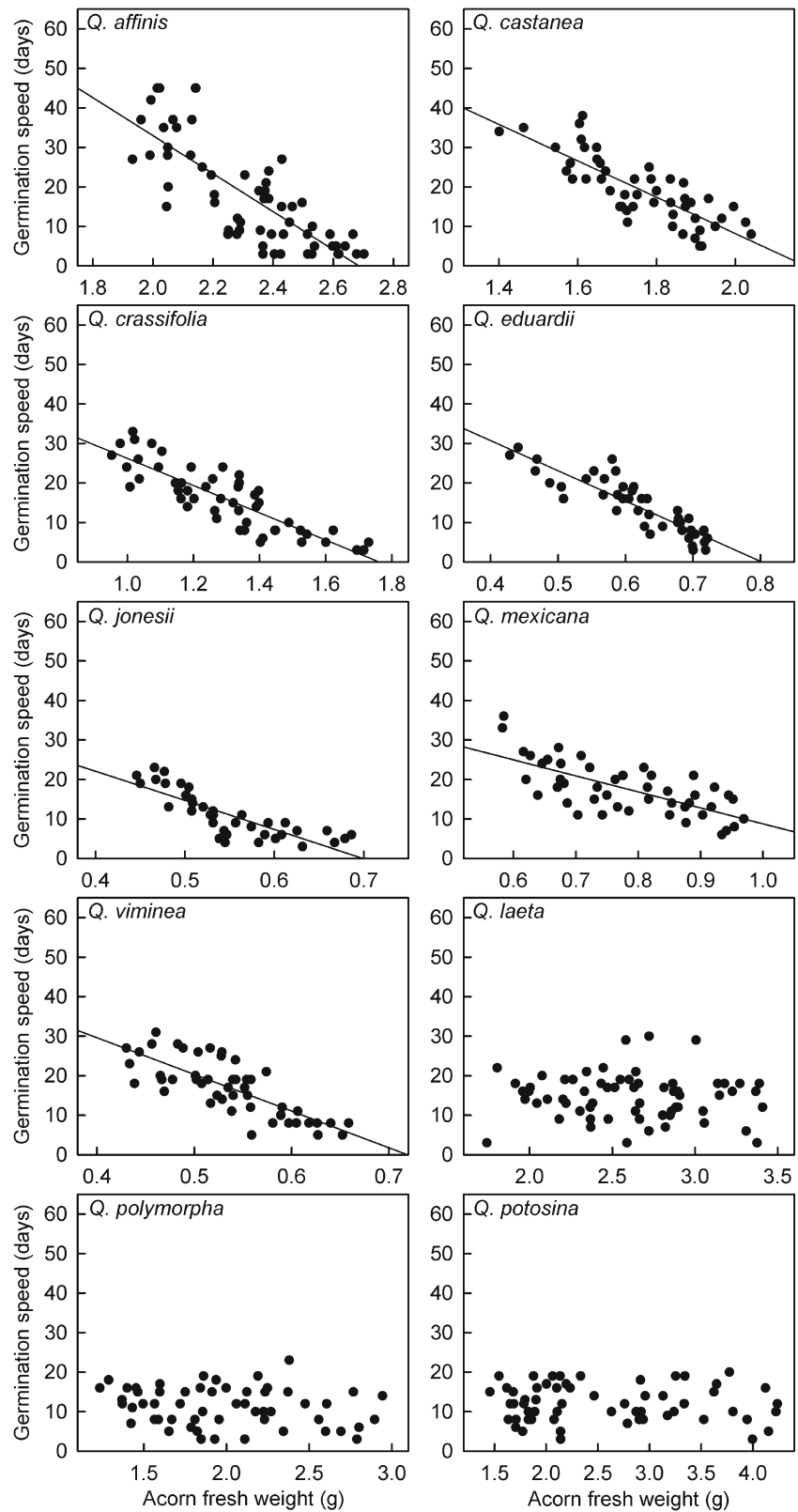
**Fig. 3** Results of logistic regressions addressed to assess relationships between germination probability and acorn fresh weight within each oak species included in the common-garden experiment. Note that the range of values of the predictive variable (acorn fresh weight) varies across oak species. Red oaks are *Q. affinis*, *Q. castanea*, *Q. crassifolia*, *Q. eduardii*, *Q. jonesii*, *Q. mexicana*, and *Q. viminea*, and white oaks are *Q. laeta*, *Q. polymorpha*, and *Q. potosina*



(*Q. castanea*, *Q. crassifolia*, *Q. eduardii*, *Q. mexicana*, and *Q. viminea*) were lower than those recorded for the former species (Table 2). The highest acorn dry biomass,

however, was recorded for *Q. affinis*, followed by the three white oaks and, later, by the remaining red oak species (Table 2). The acorns of the three white oak species

**Fig. 4** Results of linear regressions addressed to assess relationships between germination speed and acorn fresh weight within each oak species included in the common-garden experiment. These analyses included germinated acorns only. Note that the range of values of the predictive variable (acorn fresh weight) varies across oak species. Red oaks are *Q. affinis*, *Q. castanea*, *Q. crassifolia*, *Q. eduardii*, *Q. jonesii*, *Q. mexicana*, and *Q. viminea*, and white oaks are *Q. laeta*, *Q. polymorpha*, and *Q. potosina*. No regression lines are provided for white oaks because no significant effects of acorn weight on germination speed were found



had higher water contents than those of red oaks (Table 2). Further, within all oak species, the fresh weight of acorns after soaking increased with their dry biomass

(Table 2, Fig. 5), but no relationship was found between fresh weight and water content of acorns (see Online Resource 1).



**Table 2** Average fresh weight, dry biomass and percent water content ( $\pm$  S.E.) of acorns of the red and white oaks collected in 2017

| Phylogenetic section          | Oak species           | Fresh acorn weight after soaking (g)   | Acorn dry biomass (g)                   | Acorn percent water content (%)       | Linear regression results                     |
|-------------------------------|-----------------------|--|---|---------------------------------------|---|
| Red oaks ( <i>Lobatae</i> )   | <i>Q. affinis</i>     | 1.92 ( $\pm$ 0.044 S.E.) <sup>a</sup>  | 1.36 ( $\pm$ 0.031 S.E.) <sup>a</sup>   | 29.4 ( $\pm$ 0.365 S.E.) <sup>a</sup> | $F_{(1, 98)} = 2323.738, p < 0.001$ (0.959)   |
|                               | <i>Q. castanea</i>    | 1.36 ( $\pm$ 0.024 S.E.) <sup>b</sup>  | 0.842 ( $\pm$ 0.015 S.E.) <sup>b</sup>  | 37.9 ( $\pm$ 0.341 S.E.) <sup>b</sup> | $F_{(1, 98)} = 901.790, p < 0.001$ (0.902)    |
|                               | <i>Q. crassifolia</i> | 1.06 ( $\pm$ 0.029 S.E.) <sup>c</sup>  | 0.514 ( $\pm$ 0.015 S.E.) <sup>c</sup>  | 51.7 ( $\pm$ 0.379 S.E.) <sup>c</sup> | $F_{(1, 98)} = 1349.742, p < 0.001$ (0.932)   |
|                               | <i>Q. eduardii</i>    | 0.516 ( $\pm$ 0.012 S.E.) <sup>d</sup> | 0.386 ( $\pm$ 0.009 S.E.) <sup>d</sup>  | 25.3 ( $\pm$ 0.152 S.E.) <sup>d</sup> | $F_{(1, 98)} = 12,068.524, p < 0.001$ (0.992) |
|                               | <i>Q. jonesii</i>     | 0.546 ( $\pm$ 0.012 S.E.) <sup>d</sup> | 0.287 ( $\pm$ 0.007 S.E.) <sup>e</sup>  | 47.4 ( $\pm$ 0.547 S.E.) <sup>c</sup> | $F_{(1, 98)} = 504.373, p < 0.001$ (0.837)    |
|                               | <i>Q. mexicana</i>    | 0.779 ( $\pm$ 0.022 S.E.) <sup>e</sup> | 0.371 ( $\pm$ 0.011 S.E.) <sup>d</sup>  | 52.6 ( $\pm$ 0.513 S.E.) <sup>c</sup> | $F_{(1, 98)} = 695.915, p < 0.001$ (0.877)    |
|                               | <i>Q. viminea</i>     | 0.563 ( $\pm$ 0.009 S.E.) <sup>d</sup> | 0.329 ( $\pm$ 0.006 S.E.) <sup>de</sup> | 41.6 ( $\pm$ 0.368 S.E.) <sup>f</sup> | $F_{(1, 98)} = 726.034, p < 0.001$ (0.881)    |
| White oaks ( <i>Quercus</i> ) | <i>Q. laeta</i>       | 1.77 ( $\pm$ 0.025 S.E.) <sup>a</sup>  | 0.755 ( $\pm$ 0.011 S.E.) <sup>f</sup>  | 57.3 ( $\pm$ 0.329 S.E.) <sup>g</sup> | $F_{(1, 98)} = 291.639, p < 0.001$ (0.748)    |
|                               | <i>Q. polymorpha</i>  | 1.98 ( $\pm$ 0.053 S.E.) <sup>a</sup>  | 0.755 ( $\pm$ 0.024 S.E.) <sup>f</sup>  | 62.1 ( $\pm$ 0.476 S.E.) <sup>h</sup> | $F_{(1, 98)} = 558.691, p < 0.001$ (0.851)    |
|                               | <i>Q. potosina</i>    | 2.31 ( $\pm$ 0.084 S.E.) <sup>f</sup>  | 0.951 ( $\pm$ 0.035 S.E.) <sup>g</sup>  | 58.6 ( $\pm$ 0.419 S.E.) <sup>g</sup> | $F_{(1, 98)} = 1460.344, p < 0.001$ (0.937)   |

Different superscript letters on the side of averages indicate significant differences between oak species (Tukey test critical  $\alpha = 0.05$ ). The table also shows the results of the simple linear regressions ( $F$  value with degrees of freedom and  $p$  value; the  $r^2$  value is shown in brackets) conducted to assess whether the fresh weight of acorns was related with their dry biomass (critical  $\alpha$  for significant effects = 0.05)

## 4 Discussion

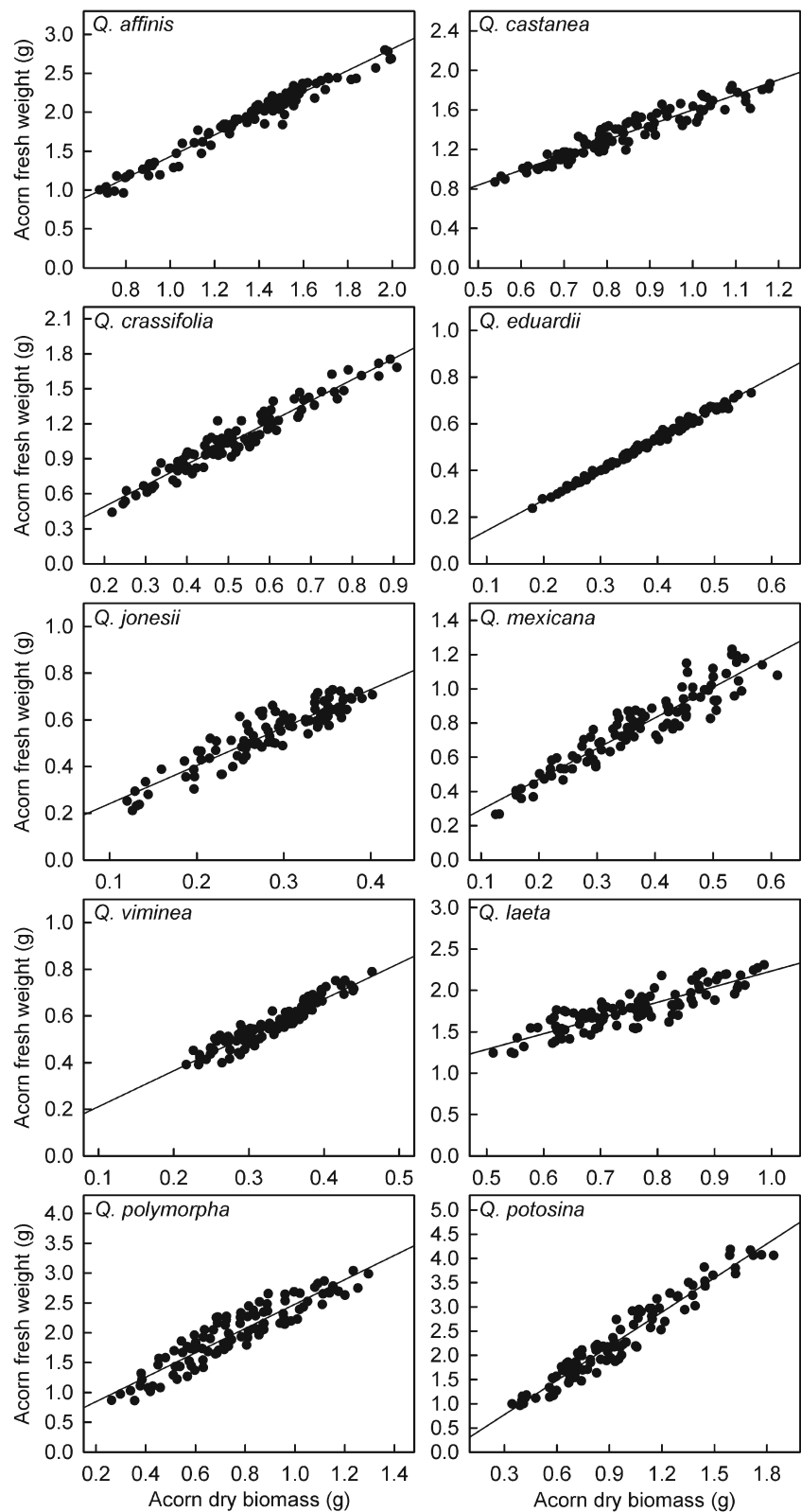
Our results indicate that increasing acorn fresh weight improves germination in the ten oak species included in the common-garden experiment and, as fresh weights of acorns after soaking were positively related with their dry biomasses, it is feasible to propose that these effects are due to differences in the amount of nutritional reserves accumulated in the acorns. The germination patterns assessed with different response variables (i.e., germination rates and germination percentage for interspecific effects and germination probability and germination speed for intraspecific effects) were consistent among and within species, suggesting that acorn weight is an important life history trait that influences germination in oaks.

White oaks (phylogenetic section *Quercus*) had heavier acorns than red oaks (phylogenetic section *Lobatae*), and our results indicate that this may be linked with the higher germination rates observed for white oaks. Variability in propagule weight across plant groups has been associated with the output of differential selective pressures that adapted them to germinate in different environments (Foster 1986; Silvertown 1989; Westoby et al. 1992; Leishman and Westoby 1994; Geritz et al. 1999; Burslem and Miller 2001; Bruun and Ten Brink 2008; Venable and Rees 2009). The differential germination responses that white and red oaks exhibited under the same environmental conditions may be reflecting this kind of adaptation. Otherwise, if acorn weight is irrelevant for germination, all species should have displayed similar germination rates irrespectively of the phylogenetic section they belong to. As the common-garden experiment attempted to emulate the shaded conditions of the forest understory, it can be proposed that white oaks are better adapted than red oaks to germinate

in this kind of habitats. This earlier germination of white oaks could allow them to quickly occupy sites available for seedling establishment beneath the forest canopy, which in turn may confer them some advantages over red oaks at the recruitment stage. Nevertheless, it is important to highlight that detailed field experiments are still required to test the validity of this proposal.

Besides these differences in germination rates between red and white oaks, germination percentages increased with acorn fresh weight across oak species. This suggests that variability in this trait, which seems to be related with the dry biomass of acorns, also influences germination across red and white oak species. Several authors have proposed that heavier-seeded tree species belong to late-successional forest stages and, because they germinate beneath the forest canopy, their seeds would require large reserves to support the development of seedlings (Foster 1986; Silvertown 1989; Venable and Brown 1988; Leishman et al. 2000; Yi and Wang 2016). Conversely, lighter-seeded species have been associated with disturbed sites where germination mainly depends on stochastic environmental factors and, thus, producing large and heavy seeds would not represent any advantage because all seeds have the same chance of germinating (Gross 1984; Jurado and Westoby 1992; Long and Jones 1996; Khurana and Singh 2001). As our experiment emulated understory conditions and germination percentages increased with acorn fresh weight, it can be proposed that oak species with heavier acorns would belong to late forest stages, while oaks with lighter acorns would belong to early forest stages. However, comprehensive field experiments are required to elucidate whether oak species that produce differentially weighed acorns actually correspond with different successional stages of forests.

**Fig. 5** Results of linear regressions addressed to assess relationships between the fresh weight of acorns and their dry biomass for each oak species included in the common-garden experiment. Note that the range of values of both, the response variable (acorn fresh weight), and the predictive variable (acorn dry biomass) vary across oak species. Red oaks are *Q. affinis*, *Q. castanea*, *Q. crassifolia*, *Q. eduardii*, *Q. jonesii*, *Q. mexicana*, and *Q. viminea*, and white oaks are *Q. laeta*, *Q. polymorpha*, and *Q. potosina*



At the intraspecific level, increasing acorn fresh weight led to higher germination probabilities in all oak species. These effects may be due to differential maternal effects among parental trees, or even among different branches of the same tree,

where the amount of reserves that propagules receive depends on the physiological status of these individuals and/or branches (Roach and Wulff 1987; Gómez 2004). In this way, heavier acorns may have larger reserves of proteins and

carbohydrates in their cotyledons, which could provide readily available energy to stimulate the elongation of the embryonic axis after imbibition (Tripathi and Khan 1990; Khan and Shankar 2001; Purohit et al. 2003; Gómez 2004; Quero et al. 2007; Lopes-Souza and Fagundes 2014). Alternatively, these effects could be due to differential loads of germination phytohormones among acorns of different weight, such as gibberellins and cytokinins (Farnsworth 2000).

When the intraspecific analyses focused on germinated acorns only, all red oak species displayed higher germination speeds as acorn fresh weight increased, but these relationships were not found in any white oak. Several studies have previously reported higher germination speeds with increasing seed weight, and these relationships have been mainly attributed to maternal effects as those described in the former paragraph (Khan and Shankar 2001; Purohit et al. 2003; Gómez 2004; Lopes-Souza and Fagundes 2014). However, as far as we are aware, this is the first study reporting these relationships between germination speed and acorn weight in red oaks, which complement the strong positive effects of acorn weight on germination probability that we found for these species. These results then suggest that acorn weight is a critical trait involved in the germination of oaks belonging to the phylogenetic section *Lobatae*. On the other hand, the weaker relationships between germination probability and acorn weight in species of the phylogenetic section *Quercus*, as well as the lack of effect of this trait on germination speed, suggest that germination of white oaks do not fully depend on acorn weight. These differential germination responses between red and white oaks could be related to the marked discrepancies in acorn weight that we observed among species of these two phylogenetic sections, where even the smaller acorns of white oaks were heavier than the largest acorns of most red oak. Thus, while acorn weight seems to be a strong determinant of germination in red oak species, the influence of this trait on germination of white oak species would be negligible.

## 5 Conclusions

The fresh weight of viable acorns is positively related to their dry biomass, while this trait is not affected by the water content of acorns. These results suggest that interspecific variability in fresh and dry weight of acorns influences germination rates and germination percentages across the oak species included in this study, where increasing acorn weight has positive effects on these two germination variables. The intraspecific variability in these traits, however, seems to have more influence on the germination of red oaks (phylogenetic section *Lobatae*) than on germination of white oaks (phylogenetic section *Quercus*). Therefore, it is feasible to propose that germination across white oak species is not as strongly determined by acorn weight as it is in red oaks.

**Acknowledgements** We thank the support of JP Rodas-Ortiz during the collection of acorns and the measurements performed in the laboratory. We also thank the valuable comments of the editors of the journal, which strongly contributed to improve the earlier versions of the manuscript. Erik J. Sánchez-Montes de Oca thanks the doctoral fellowship of Consejo Nacional de Ciencia y Tecnología de Mexico (no. 150830) and Lilia E. Silva-Alvarado thanks the fellowship provided by project SEP-CONACYT CB-2013/221623.

**Funding** This work was supported by project SEP-CONACYT CB-2013/221623 to EIB.

## Compliance with ethical standards

**Conflict of interest** The authors state there are no conflicts of interests of any nature.

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