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Large and small acorns contribute equally to early-stage oak seedlings: a multiple species study

Xianfeng Yi[1] · Jinxin Zhang[2] · Zhenyu Wang[1]

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Abstract Larger seeds generally produce larger seedlings either at intra- or at interspecific level; however, whether large seeds contribute more to seedlings than do small ones is largely unknown. We investigated fresh masses of acorns, seedling size, mobilization of cotyledonary reserves of nine red and white oak species (*Quercus rubra*, *Q. falcata*, *Q. palustris*, *Q. phellos*, *Q. coccinea*, *Q. variabilis*, *Q. mongolica*, *Q. aliena* and *Q. acutissima*) with contrasting acorn masses to investigate whether large seeds are better than small ones in supporting early-stage seedlings. Our study showed no significant effect of fresh acorn mass on seedling survival rates of the nine oak species at intra-specific level, though large acorns tended to produce large seedlings. Although acorn mass was positively correlated with seedling size (e.g., dry mass) both at intra- and at interspecific levels, large and small acorns allocated the same proportion of cotyledonary reserves into seedlings at intraspecific level. Moreover, variations in the proportion of mobilized cotyledonary reserves were not explained by fresh acorn mass at interspecific level. We also found that more soil-derived N was transferred into seedlings produced by small acorns than by large ones. Our results suggest that cotyledonary reserves in small and large seeds contribute equally to support their early-stage seedlings, but the role of large seeds may become more apparent later than the 50-day period of this experiment.

Keywords Oak · Acorn mass · Seedling size · Cotyledon reserve · Energy mobilization · Isotope labeling

Introduction

Seed size is one of the key seed traits that occupy an important position in the life history of a species (Seiwa and Kikuzawa 1996; Aparicio et al. 2002; Wu and Du 2008). Seed size also plays a crucial role in the ecology of reproduction and seedling establishment of plants around the world (Khurana and Singh 2004; Baraloto et al. 2005; Hanley et al. 2007). During the long-term evolutionary process, plants produce seeds in a wide range of sizes to ensure successful dispersal far away from their mother either by wind- or by animal-mediated seed dispersal (Michaels et al. 1988; Andresen and Levey 2004; Moles and Westoby 2004; Pollux et al. 2007). Much of the literature has shown that seed size varies within communities across 5–6 orders of magnitude (Leishman and Westoby 1994, Leishman 2001). For example, wind-dispersing orchids (*Orchidaceae*) bear tiny dust-like seeds (around 10^{-6} g), while double coconuts *Lodoicea seychellarum* produce huge seeds more than 10^{4} g each (Harper et al. 1970). Even within plant communities, seed size often spans half an order of magnitude (Michaels et al. 1988; Milberg et al. 1998; Bond et al. 1999; Yi and Yang 2011). It has been widely accepted that seeds with different sizes exhibit different chances to survive the hazardous environments in which they are involved during development,

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✉ Xianfeng Yi
yxfeng1975@126.com

[1] College of Life Sciences, Jiangxi Normal University, 330022 Nanchang, China

[2] Qingyuan Forest CERN, Chinese Academy of Sciences, 110016 Shenyang, China

dispersal and successful establishment as seedlings (Westoby et al. 1992, 1996; Leishman 2001; Zhang and Zhang 2008; Yi and Yang 2011).

An increasing body of literature has shown that environmental effects during development result in an impressively wide range of sizes (Michaels et al. 1988; Vaughton and Ramsey 1998). Therefore, it is commonly found that seed size variations often occur within species or at population level (Milberg et al. 1998; Baraloto et al. 2005; Moles and Westoby 2004).

Oaks are one of the most important forest trees in the world (Takahashi and Shimada 2008) and are characterized by large acorns containing a huge amount of nutritional reserves in their cotyledons (Short 1976; Servello and Kirkpatrick 1987). Not surprisingly, acorns of various oak species vary in their seed mass from 1.0 to 10.0 g (Aizen and Patterson 1990; Long and Jones 1996). Despite lack of long-term studies, size variation in acorns is usually found within (Koenig et al. 2009a; Ramos et al. 2013; Shimada et al. 2015) and among oak species (Aizen and Woodcock 1992), and even among years (Koenig et al. 2009b) and geographical ranges (Aizen and Patterson 1990), making oaks a well-studied system and particularly useful for examining the effects of seed size on seedling performance (Yi et al. 2015).

From the perspective of seeds, large size may be especially advantageous for early establishment and survival (Seiwa 2000; Lahoreau et al. 2006; Tilki 2010; Elwell et al. 2011). On one hand, seeds with large reserves result in bigger seedlings; on the other hand, seedlings from large-seeded species would have better access to light and/or to reliable water supply than seedlings from small-seeded species (Westoby et al. 1992, 1996). Although large seeds may perform better than small ones (Jakobsson and Eriksson 2000), the relationship between seed mass and seedling size both at intra- and at interspecific levels is needed to be clarified. Larger seeds generally produce larger seedlings with higher relative growth rates (Lehtilä and Ehrlén 2005; Du and Huang 2008; Akinyele and Adegeye 2011); however, it is not clear whether large seeds contribute more to seedlings than small ones.

In the present study, we investigated fresh masses of acorns, seedling size (termed as dry mass), mobilization of cotyledonary reserves and nutrient uptake characteristics of roots of nine red and white oak species (*Quercus rubra*, *Q. falcata*, *Q. palustris*, *Q. phellos*, *Q. coccinea*, *Q. variabilis*, *Q. mongolica*, *Q. aliena* and *Q. acutissima*) with contrasting fresh acorn masses (fresh mass ranges from 0.80 to 9.61 g), in order to answer the following questions: (1) Do large acorns result in higher seedling survival rates than small ones both at intra- and at interspecific levels? (2) Do large acorns show higher reserve mobilization capacities to seedlings than do small ones both at intra- and at interspecific levels? (3) Is seedling size positively correlated with fresh acorn mass both at intra- and at interspecific levels?

Materials and methods

Oak species

Acorns of red oaks *Quercus rubra*, *Q. falcata*, *Q. palustris*, *Q. phellos* and *Q. coccinea* were ordered from Sheffield's Seed Company (USA) in December 2013. Despite lack of information, it was highly impossible that these acorns were collected from single tree for each species. Acorns of four white oak species were collected from 8 to 12 trees for each species in China. *Q. mongolica* were collected from Xiaoxing'anling mountains, Heilongjiang Province (China) in October 2013. Acorns of white oaks *Q. variabilis* and *Q. aliena* were collected in Tianchishan mountains, Henan Province in October 2013. In November 2013, we collected acorns of white oak *Q. acutissima* in Xishuangbanna, Yunnan Province (China). Because the four white oak species remain nondormant for the winter, acorns of both red and white oaks were stored in ice box at 4 °C conditions prior to the experiments, which has been shown no significant effect on acorn germination and seedling development of white oak species (Yi and Liu 2014). No acorns of North American white oak species were used in this study because no company in China is willing to import them due to their early germination.

Seedling growth

In early March 2014, we selected 16 large and 16 small acorns of each oak species (Fig. S1). Acorns were individually numbered and weighted and then planted into plastic containers (Length × Width × Height: 6 cm × 6 cm × 10 cm) filling with 2 mm particle perlite. One acorn was buried 1 cm deep in each container. Each container received a total of 100 ml Hoagland culture solution throughout the experiments, while they were watered regularly with distilled water as necessary. Plant containers were kept indoor under 600–800 μmol m^{-2} s^{-1} radiation of fluorescent lamps in Jiangxi Normal University (Jiangxi, China). To determine the nutrition contribution of cotyledon reserves and culture solution into oak seedlings, each container was injected with 10 ml solution containing 1 mmol/L $K^{15}NO_3$, $^{15}NH_4Cl$, ^{15}N-urea and ^{15}N-glycine (enriched to 98 atom % of ^{15}N, Shanghai Laiang Biotech Co., Ltd., China) after sowing. Seedling survival rates of large and small acorns of each oak species were measured 50 days after germination when seedlings finished the first flush. Each seedling was harvested and cleaned under running water and oven-dried (70 °C for 48 h) for measurement of the dry masses of root, shoot and remnant cotyledons. The cotyledons, root and shoot of each seedling were weighed separately to the nearest ±0.01 g.

Mobilization of cotyledonary reserves

Twenty fresh acorns of each oak species were randomly selected and individually weighted. Then, they were oven-dried at 70 °C for 48 h for measurement of the dry masses of cotyledons. The regression formula between the fresh masses of acorns and the corresponding dry masses of cotyledons was determined for each oak species (Fig. S2), to estimate the initial dry mass of each fresh acorn we planted. We compared the estimated initial dry mass of each acorn to the dry mass of the corresponding remnant cotyledons of each seedling, to see how many cotyledonary reserves were mobilized into seedlings produced by large and small acorns for each oak species.

The amount of cotyledonary reserves mobilized into seedlings was determined by:

$$\begin{aligned} A(\mathrm{g}) = {} & \text{The estimated initial dry mass of cotyledons}(\mathrm{g}) \\ & - \text{Dry mass of the remnant cotyledons}(\mathrm{g}) \end{aligned}$$

The reserve mobilization capacity of each acorn into seedlings was determined by:

$$C\,(\%) = \frac{\text{The estimated dry mass of cotyledons (g)} - \text{Dry mass of the remnant cotyledons (g)}}{\text{The stimated dry mass of cotyledons (g)}} \times 100$$

Stable N isotope analyses

Dry shoots of seedlings produced by large and small acorns were separately ground for each oak species and analyzed for N stable isotope abundances at the Laboratory of Stable Isotope Spectrometer, Chinese Academy of Forestry Sciences (Beijing). The results are expressed in δ^{15}N relative to the standards in the conventional δ per mil notation as follows (see Yi and Wang 2015):

$$\delta^{15}N(‰) = \left[\left({}^{15}N/{}^{14}N\right)\text{sample}/\left({}^{15}N/{}^{14}N\right)\text{ standard} - 1\right] \times 1000$$

where ${}^{15}N/{}^{14}N$ are the isotopic ratios of sample and standard (atmospheric nitrogen). A mixing isotope model was used to determine the total N assimilated by roots (Yi and Liu 2014):

$$N\% = \left({}^{15}N_{\mathrm{S}} - {}^{15}N_{\mathrm{A}}\right)/\left({}^{15}N_{\mathrm{F}} - {}^{15}N_{\mathrm{A}}\right) \times 100$$

where N %, ${}^{15}N_{\mathrm{S}}$, ${}^{15}N_{\mathrm{A}}$ and ${}^{15}N_{\mathrm{F}}$ represent the total N assimilated by roots, the ${}^{15}N$ isotope abundance of shoots, acorns and ${}^{15}N$ fertilizer (98 atom %), respectively. The natural ${}^{15}N$ isotope abundance of the acorns was estimated at 0.36705 ± 0.00132 atom % for the nine oak species in this study.

Statistical analyses

We used Statistical Package for the Social Sciences (SPSS 16.0) for data analysis. Each seedling was considered a replicate for statistics. The difference in the fresh masses of large and small acorns was detected by using one-way ANOVA for each oak species. The correlation between survival rates of seedlings and fresh acorn masses was determined by using linear regression for each oak species. Two-way ANOVA was used to see the effects of acorn mass on seedling size at intraspecific (between large and small acorns) and interspecific levels (among different oak species). General linear model was used to determine whether there was difference in the amount of mobilized cotyledonary reserves into seedlings and in the reserve mobilization capacity (arc-sine transformed) between large and small acorns. The correlation between fresh masses and dry masses of acorns was determined by using linear regression. The same method was applied for detecting the relationship between initial acorn mass and seedling size, and between seedling size and the amount of mobilized cotyledonary reserves.

Results

Effect of acorn mass on seedling size

Despite great variations found in the fresh masses of large and small acorns of the nine oak species (Fig. S1, S3), linear regression showed no correlation between fresh acorn masses and seedling survival rates both at intra- and at interspecific levels ($R^2 = 0.075$, $P = 0.273$) (Fig. 1). However, acorn mass significantly affected seedling size for all oak species tested in our study (shoot: $F = 142.502$, df = 1, $P < 0.001$; root: $F = 206.474$, df = 1, $P < 0.001$; whole seedling: $F = 186.513$, df = 1, $P < 0.001$) (Fig. 2).

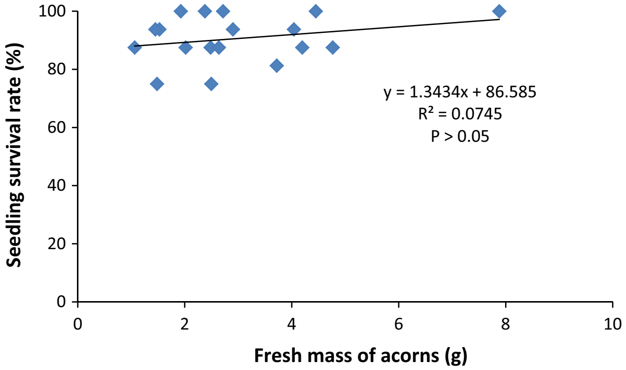

Fig. 1 Correlation between seedling survival rates and fresh masses of acorns at intra- and interspecific levels

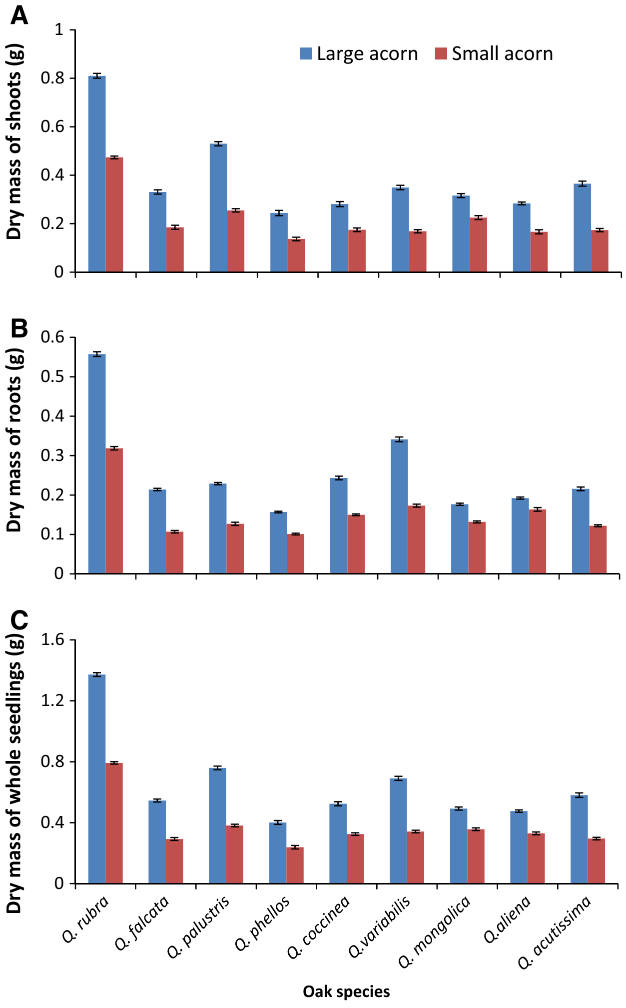

Fig. 2 Comparison of dry masses of shoots (**A**), roots (**B**) and whole seedlings (**C**) produced by large and small acorns of the nine oak species. Data are expressed as mean ± SE

Furthermore, we found significant effect of oak species on seedling size (shoot: $F = 23.798$, df = 8, $P < 0.001$; root: $F = 78.626$, df = 8, $P < 0.001$; whole seedling: $F = 56.840$, df = 8, $P < 0.001$), with oaks bearing large acorns producing bigger seedlings (Fig. 2). Linear regression showed that acorn mass was positively correlated with seedling mass both at intra- and at interspecific levels (all $P < 0.05$) (Fig. 3 and 4). We also found that large acorns were more likely to produce seedlings with low root/shoot ratio at interspecific level ($F = 7.310$, df = 1, $P = 0.007$) (Fig. S4).

Mobilization of cotyledonary reserves

We found that large acorns mobilized a larger amounts of cotyledonary reserves into seedlings than did small ones at intraspecific level ($F = 297.553$, df = 1, $P < 0.001$) (Fig. 5). The same pattern was also observed at interspecific level ($F = 57.610$, df = 8, $P < 0.001$) (Fig. 5). Moreover, the amounts of mobilized reserves were positively correlated with acorn mass both at intraspecific (*Q. rubra*: $R^2 = 0.916$, $P < 0.001$; *Q. falcata*: $R^2 = 0.757$, $P < 0.001$; *Q. palustris*: $R^2 = 0.602$, $P < 0.001$; *Q. phellos*: $R^2 = 0.366$, $P < 0.001$; *Q. coccinea*: $R^2 = 0.302$, $P = 0.005$; *Q. variabilis*: $R^2 = 0.870$, $P < 0.001$; *Q. mongolica*: $R^2 = 0.189$, $P = 0.015$; *Q. aliena*: $R^2 = 0.417$, $P < 0.001$; and *Q. acutissima*: $R^2 < 0.801$, $P = 0.001$; Fig. S5) and at interspecific levels ($R^2 = 0.830$, $P = 0.001$; Fig. S6). However, the mobilization capacity (proportion of reserves mobilized) of cotyledon reserves showed no significant difference between large and small acorns ($F = 2.072$, df = 1, $P = 0.151$) (Fig. 6). Although the reserve mobilization capacity of cotyledons differed within the nine oak species ($F = 5.915$, df = 8, $P < 0.001$), they were not correlated with fresh acorn masses at interspecific level ($R^2 = 0.0486$, $P = 0.651$; Fig. S7).

Allocation of soil-derived *N* into seedlings

Based on the isotope mass balance model, we found more soil-derived N in seedlings produced by small acorns at intraspecific level ($F = 47.016$, df = 1, $P < 0.001$), although soil-derived N only accounted for less than 3 % of the total N accumulated in seedlings produced by both large and small acorns (Fig. 7). We also found that nutrient uptake capacity of roots differed significantly within oak species regardless of acorn masses ($F = 1.022E3$, df = 8, $P < 0.001$) (Fig. 7).

Discussion

Acorn mass and survival rate

In our study, acorns of white and red oak species showed high germination and survival rates (>75 %), indicating

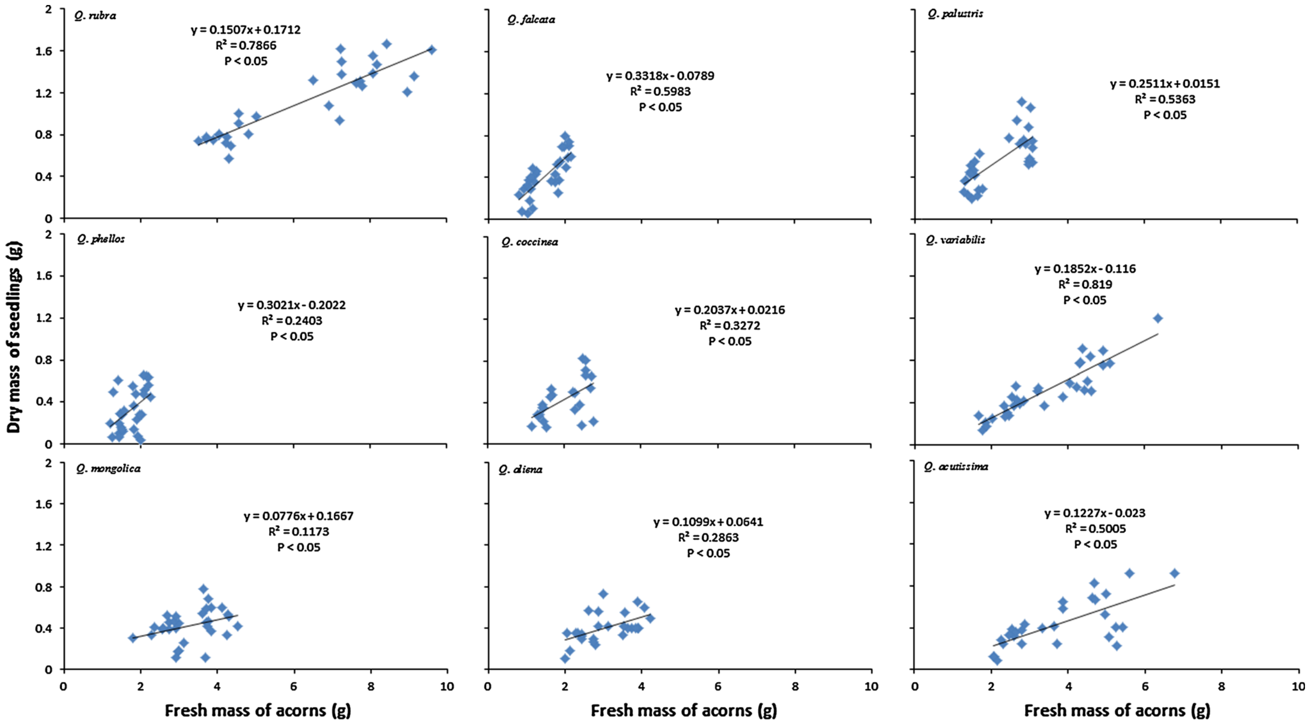

Fig. 3 Regression between fresh masses of acorns and dry masses of seedlings produced by large and small acorns of the nine oak species

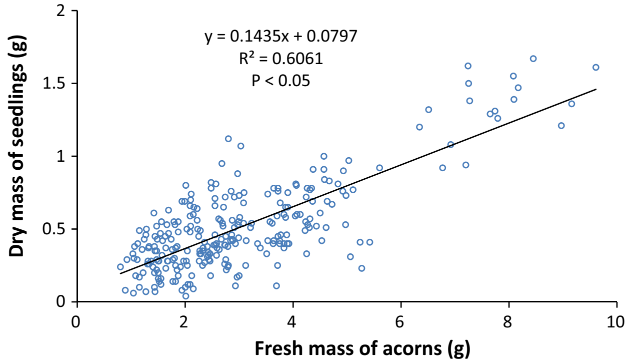

Fig. 4 Regression between fresh masses of acorns and dry masses of seedlings produced by the nine oak species

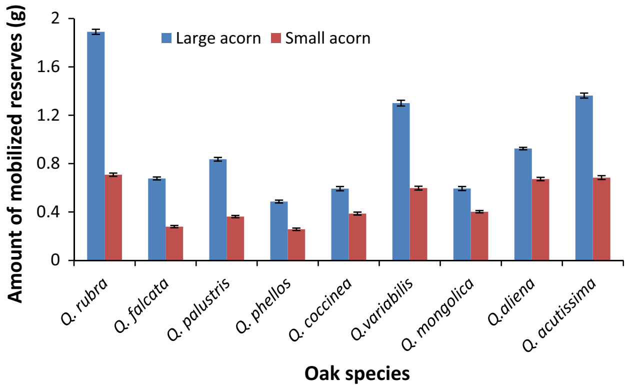

Fig. 5 Comparison of the amounts of mobilized cotyledonary reserves between large and small acorns of the nine oak species. Data are expressed as mean ± SE

that the way to store them shows no effect on acorn germination (Yi and Liu 2014). Seedling survival rates showed no significant difference between large and small acorns, indicating that seed mass is not a decisive factor determining acorn germination and survival in the first 50 days. This observation is consistent with the results of Andresen and Levey (2004) but different from those of Couvillon (2002) and Mandal et al. (2008). Previous studies have shown that acorns of several oak species germinate and successfully establish after being partially damaged (Hou et al. 2010; Yi and Yang 2010; Yang and Yi 2012; Perea et al. 2011). Acorns of another white oak, *Q. robur*, can germinate and establish even losing up to 2/3 of their cotyledon biomass (Giertych and Suszka 2011). These facts suggest that cotyledonary reserves in small acorns are still sufficient for supporting seedling survival of oak species, implying that bearing large acorns is not always better than producing small ones. However, we failed to measure the survival rates of large and small acorns under stressful conditions in our study. It can be anticipated that the contribution of large acorns to seedlings may become more apparent later, especially under environmental stresses (Hanley et al. 2007; Ramírez-Valiente et al. 2009; but see Yi and Wang 2015).

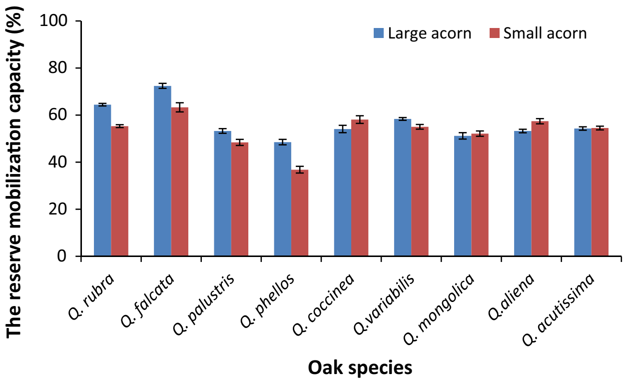

Fig. 6 Comparison of reserve mobilization capacities of cotyledons between large and small acorns of the nine oak species. Data are expressed as mean ± SE

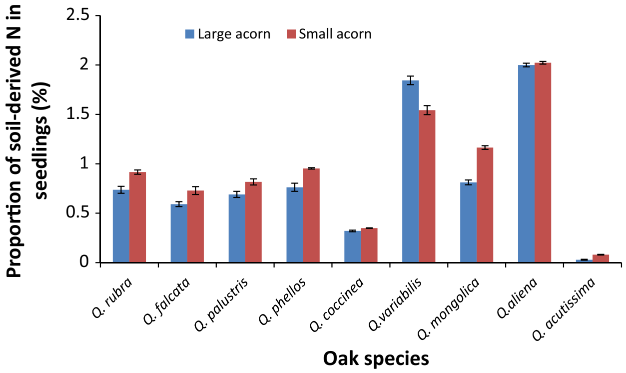

Fig. 7 Comparison of the proportion of soil-derived *N* in seedlings produced by large and small acorns of the nine oak species. Data are expressed as mean ± SE

Acorn mass and seedling size

Although acorn mass showed no effect on seedling survival rates, seedling size was significantly affected by acorn mass both at intra- and at interspecific levels. Large seeds are more likely to produce large seedlings at species level (Baraloto et al. 2005; Cicek and Tilki 2007), while Long and Jones (1996) found seed size is generally related to seedling size at interspecific level. Our results verify the positive effects of seed mass on seedling size both at intraspecific and at interspecific levels (Long and Jones 1996; Moles and Westoby 2004; Anis et al. 2014), possibly because most oak species have large hypogeal acorns and thus act as important store organs in supporting development and performance of 1-year seedlings (Baraloto and Forget 2007). We also found large acorns produced seedlings with small root/shoot ratio than did small acorns, indicating that more cotyledonary reserves in large acorns are transferred into shoots than in roots. Alternatively, shoots of seedlings produced by large acorns may exhibit higher assimilation capacity (e.g., photosynthesis) compared to those produced by small acorns. Positive correlation between acorn mass and seedling size both at intra- and at interspecific levels suggests that larger, better-provisioned seeds have a greater chance to produce large seedlings both at intra- and at interspecific levels.

Acorn mass and mobilization of cotyledonary reserves

Although the role of cotyledon metabolism in the seedling establishment has been well investigated (Ruffino et al. 2010), studies on the difference in cotyledon mobilization between large and small seeds are limited. Our results showed a positive relationship between the amounts of mobilized reserves in cotyledons and seedling sizes. Consistently, larger acorns mobilized more cotyledonary reserves to produce seedlings regardless of oak species, showing the advantage of large seeds over small ones in the evolutionary context. However, we found no difference in the reserve mobilization capacity of cotyledons at intraspecific level. Moreover, the reserve mobilization capacity was not correlated with acorn mass both at intra- and at interspecific levels. These observations suggest that large and small seeds show the same ability to mobilize their reserves into seedling. Seedlings produced by small acorns tended to absorb more nutrients from the soil in our study, indicating that seedlings of small-seeded species are more reliant on soil nutrients than large-seeded ones (Milberg et al. 1998). This is expected to compensate the disadvantage that small acorns allocate less cotyledonary reserves into their seedlings. However, we found no correlation between the amounts of soil-derived N and seedling sizes, suggesting that soil-derived nutrition plays a less important role in determining seedling size. These observations are well in agreement with previous studies that show that cotyledonary reserves, rather than soil-derived nutrition, are crucial for the development of 1-year seedlings (Yi and Liu 2014; Yi and Wang 2015).

Reserves in the remnant cotyledons

Although a great amount of cotyledonary reserves were mobilized by large acorns both at intra- and at interspecific levels, more than 30–40 % of dry mass reserves remain in cotyledons for both large and small acorns regardless of oak species. The role of the remaining reserves in the cotyledons attached onto 1-year seedlings is still controversial (Fox 1982; Yi et al. 2013). Previous studies show that up to 50 % (and possibly more) of the cotyledonary reserves is not essential for acorn germination and seedling survival (Hou et al. 2010; Giertych and Suszka 2011; Perea et al. 2011; Liu et al. 2012). However, the remnant cotyledons are found to play an essential role in supporting re-sprouting of 1-year seedlings of oaks (Sonesson 1994; Yi and Liu 2014). In the seed dispersal system, large seeds are preferred and consumed by rodents and birds (Xiao et al. 2004, 2005; Pons and Pausas 2007; Lai et al. 2014; Wang et al. 2014). Moreover, rodents and birds often show behavioral preferences to cache and disperse large seeds greater distances from the parent tree (Gómez 2003; Wang and Chen 2009; Xiao et al. 2005; Zhang et al. 2008; Steele et al. 2014). Coupling with the results of present study, we propose that the sufficient stores in large cotyledons are provisioned not only for producing large seedlings, but also for overcoming hazardous environments to support successful seedling establishment (Ramírez-Valiente et al. 2009; Yi and Liu 2014; Yi et al. 2015).

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