

The Effect of Seed Size Variation in *Quercus pacifica* on Seedling Establishment and Growth¹

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Abstract

Quercus pacifica, the island scrub-oak, is the dominant species in oak chaparral on the three largest California Channel Islands. While the population on Santa Cruz Island has experienced a strong recovery, the populations on Santa Rosa and Santa Catalina islands are of conservation concern, and managers are actively restoring oak habitat by planting acorns. Previous work shows that acorn size, a factor that is known to affect planting success, varies significantly across the range of the species. To determine whether acorn size in *Q. pacifica* affects early seedling growth, I planted over 600 acorns from Santa Cruz Island in a greenhouse. Our results show that larger acorns are more likely to germinate, and that acorn mass had strong effects on root mass, shoot mass, seedling height and leaf surface area. Assuming that acorn size may have a similar effect on Santa Rosa and Santa Catalina, I suggest that managers plant larger acorns to maximize the effect of restoration efforts.

Key words: acorns, Channel Islands National Park, *Quercus pacifica*, restoration, seed size, seedling establishment

Introduction

In restoration ecology, understanding the reproductive limitations of target species is essential for the formulation of effective management strategies. When restoring oaks by seeding, for example, variation in seed size can determine the proportion of seeds that successfully establish seedlings, and affect biomass production below and above ground (Navarro and others 2006, Quero and others 2007). Alternatively, seed dispersers providing ecosystem services often show seed size preferences (Wenny and others 2011), and preferentially disperse smaller seeds that show reduced survival (for example, Gómez, 2004). Therefore, managers must be able to identify plant traits that affect the success of restoration efforts, and to consider within-species variation of those traits before deploying seeds (Pywell and others 2003). Here, I investigate the functional consequences of variation in seed size in an oak species of conservation concern.

Quercus pacifica, a keystone species of California Channel Islands' oak chaparral, has been the focus of extensive conservation efforts (Knapp 2010a). On Santa Catalina Island, the oak has experienced 35 percent dieback within the last 60 years (Knapp 2010b). On the other large islands in its range, Santa Cruz and Santa Rosa, *Q. pacifica* populations were long reduced by ranching activity and herbivory by feral non-native livestock (Lombardo and Faulkner 1999, Morrison 2011). The removal of sheep (*Ovis aries*) and pigs (*Sus scrofa*) over the last 25 years has led to a strong rebound of the Santa Cruz Island population, and raised hopes that the recent removal of non-native vertebrates from a second island would result in similar recovery (Morrison 2011). Only Santa Cruz Island has a mutualist, avian disperser of acorns,

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the island scrub-jay (*Aphelocoma insularis*). The recovery of the Santa Rosa and Santa Catalina populations will thus initially rely on active seed planting by managers (Stratton 2009). The current study aims to inform management efforts on these islands, but the inference is limited as I only used acorns from Santa Cruz Island.

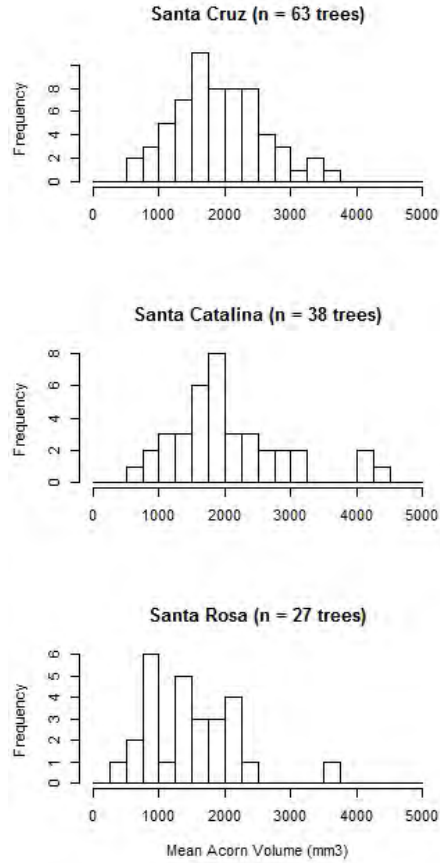


Figure 10—Variation of acorn volume in three island populations of *Quercus pacifica*. Histograms depicting the frequency of mean acorn volume per tree. Original data in Pesendorfer and others 2014.

Acorn size is thought to be important for seedling establishment and growth in oaks. In greenhouse grown Holm oak (*Q. ilex*) seedlings, acorn size determined total biomass, and biomass of different parts of the seedlings, but the partitioning among those parts was mostly determined by the parent tree (Leiva and Fernández-Alés 1998, Navarro and others 2006). The effect of acorn size on seedling growth is often strongest in sub-optimal conditions. For example, in low-light areas larger acorns are more competitive than in full-light (Quero and others 2007). The root/shoot ratio, an important predictor of drought tolerance, does not seem to be affected by acorn size, and is likely determined by genetic variation in populations (Leiva and Fernández-Alés 1998). To determine if this relationship holds for *Q. pacifica*, I conducted a greenhouse experiment under optimal growth conditions. I predicted that total

seedling mass, as well as below- and above-ground growth would correlate positively with acorn size.

Methods

In October 2009, I collected 619 *Q. pacifica* acorns from 77 trees on the annual Santa Cruz Island oak survey (Pesendorfer and others 2014). The acorns were assessed for visual damage from insect activity (for example, oviposition and exit holes), weighed, and length and width at widest point recorded using digital calipers. Until planting, I stored the acorns in a refrigerator at 4 °C, a common technique to keep acorns viable (Navarro and others 2006).

In December 2009, I planted the acorns in a mixture of pyrolite growth mix and sand, homogeneously distributed among 20 propagation trays with 32 round cells of 6 cm diameter and 5 cm depth. The trays were watered daily and maintained on a 14-10 light-dark cycle for the whole study period. After 25 weeks, the seedlings were harvested, dried at 60 °C for 48 hours, and processed. I measured the mass of dry above- and below-ground growth to the nearest 0.1 g using a digital scale (Mettler Toledo MS105), seedling height, number of leaves, and leaf surface area (LiCor LI 3000-A).

I used a set of linear mixed models to test the relationship between acorn mass, seedling emergence and growth parameters. I did not model the interaction between tree identity and acorn mass. All models contained the fixed effect “acorn mass” and the random effect “tree” to account for the repeated sampling (in other words, multiple acorns) on the same individual. To determine the effect of acorn mass on germination, a binary variable, I constructed a general linear mixed model with a binomial error distribution, again using “tree” as a random effect. All analyses were performed in R version 3.01 (R Development Core Team 2013). I used the package “lme4” (Bates and others 2013) for model construction and significance testing of LMMs, and I report the model coefficient B , as well associated t -values, degrees of freedom and P -values. For the GLMM, I used Wald Type II tests in the package “car” (Fox and Weisberg 2011) that estimate χ^2 values and associated P -values.

Results

Mass was an important predictor of acorn germination (figs. 2, 3). The mean mass of the 619 viable acorns was $1.49 \text{ g} \pm 0.05 \text{ g}$ (\pm s.e.) and mean acorn mass per tree ranged from 0.23 g to 10.32 g. After 25 weeks, 188 acorns (30.4 percent) germinated, while 431 (69.6 percent) did not show any signs of growth. Acorns that germinated were significantly heavier than non-germinating acorns (fig. 2; GLMM, $\chi^2 = 56.13$, $df = 1$, $P < 0.001$). Acorns that germinated weighed an average of $2.14 \text{ g} \pm 0.09 \text{ g}$ (\pm s.e.), while unsuccessful acorns weighed $1.21 \text{ g} \pm 0.06 \text{ g}$. The smallest acorn to germinate weighed 0.33 g, which was heavier than the bottom 7 percent of all planted acorns. Of the 188 acorns that germinated, 40 (21.3 percent) produced only a root, but no seedling. Therefore, only 148 of 619 (23 percent) of all collected acorns produced a seedling.

For the acorns that germinated, mass correlated with the growth of seedling parts, but not the root/shoot ratio. Acorn mass explained more variation in root mass, than in shoot mass or leaf surface area (fig. 3 A-D). In contrast, the root/shoot ratio did not correlate with acorn mass (LMM; $B = 0.044$, $t = 0.727$, $P = 0.467$).

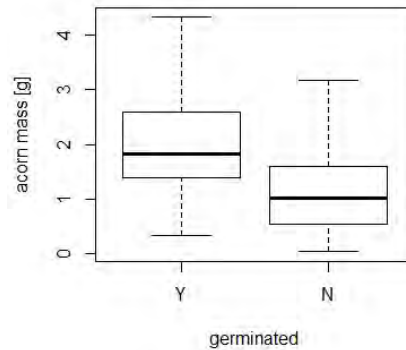


Figure 2—The effect of acorn mass on germination. Bold line indicates median, boxes span interquartile range (IQR) and whiskers extend to 1.5 x IQR.

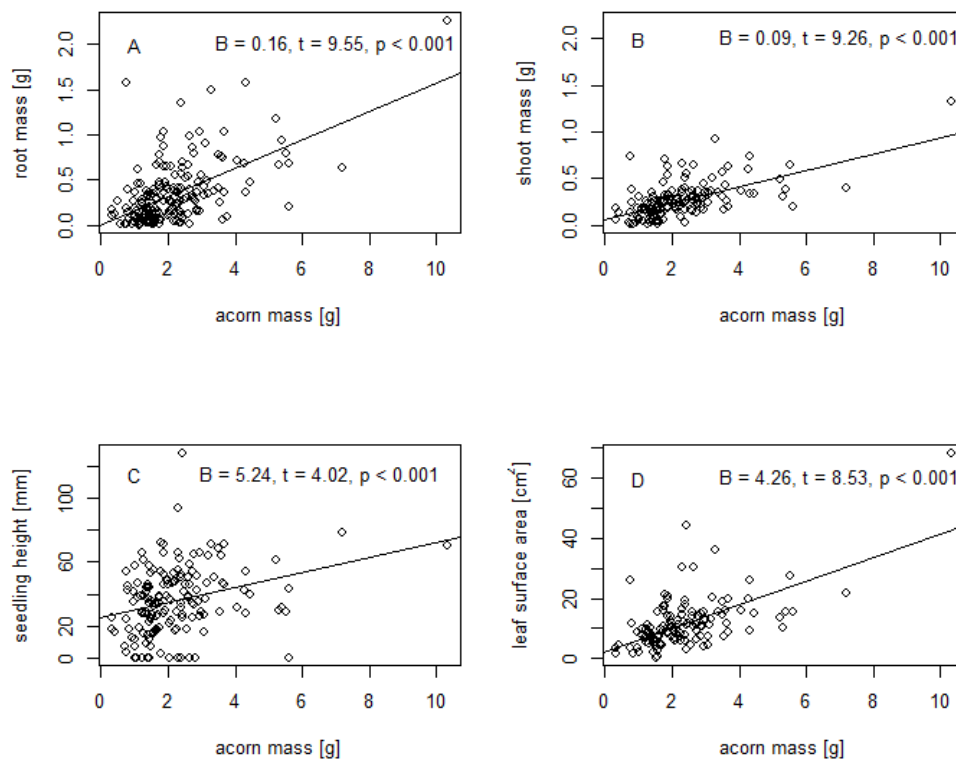


Figure 3—The effect of acorn mass on seedling growth. Acorn mass was significantly correlated with (A) root mass ($n = 188$), (B) shoot mass, (C) height and (D) leaf surface area of seedlings (all $n = 148$). For each dependent variable, model coefficient, t-statistic and associate P-value are reported for linear mixed models with individual tree as random effect and acorn mass as fixed effect.

Discussion

The data from this greenhouse experiment suggest an important role of acorn size in germination and early seedling growth of *Q. pacifica*. Under optimal conditions, larger acorns were more likely to germinate, and acorn size was also positively correlated with seedling growth above and below ground. However, the root/shoot ratio of the seedlings was not associated with acorn size, despite considerable variation, suggesting that seed size does not affect the allocation of growth to different plant organs.

Our results largely echo the findings from other studies on the role of seed size in the early development of Mediterranean oaks. Gómez (2004) found in a field study that the mass of Holm oak acorns in Spain was positively correlated with germination rate, seedling height growth and survival over the first 2 years. Similarly, larger blue oak (*Q. douglasii*) and valley oak (*Q. lobata*) acorns had greater emergence rates, survival throughout the first year and increased seedling height (Tecklin and McCreary 1991, Sage and others 2011). The role of acorn size may, however, be diminished under field conditions. When planting *Q. ilex* acorns in the greenhouse and in the field, Navarro and others (2006) found that after 32 months of development, acorn size only explained variation of seedling growth in the greenhouse, but not under natural conditions. The positive effect of seed mass may thus be limited to early phases of seedling development. Nonetheless, I suggest that managers preferentially select large acorns when restoring oak habitat on the Channel Islands, as the combined effect of increased germinability and early growth could still provide a crucial advantage for seedlings.

In addition to selecting seed size, several other management actions may affect the success of seedlings growing from planted *Q. pacifica* acorns. Restoration efforts on Santa Catalina Island suggest that microhabitat variation, post-dispersal seed predation and seedling herbivory play an important role in seedling survival (Stratton 2009). Experiments using exclosures and tree tubes show that *Q. pacifica* seedlings perform best in tree tubes, at least where large herbivores still decimate a large proportion of young oaks (Stratton 2009). In addition to preventing herbivory, tree tubes may also provide seedlings with more water from fog precipitation, a factor that was not assessed previously. In future research, I aim to examine how tree tubes, as well as microhabitat variation and habitat-specific seed placement affect recruitment success of planted acorns.

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References

- Bates, Douglas; Maechler, Martin; Bolker, Ben. 2013. **lme4: Linear mixed-effects models using S4 classes**. R package version 0.999999-2.
- Fox, John; Weisberg, Sanford. 2011. **An R companion to applied regression**. Thousand Oaks, CA: Sage.
- Gómez, José M. 2004. **Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex***. *Evolution* 58(1): 71–80.
- Knapp, Denise A. 2010a. **Oak ecosystem restoration on Santa Catalina Island, California:**

- a synthesis of resources and threats.** In: Knapp, D.A., ed. Oak ecosystem restoration on Santa Catalina Island, California. Proceedings of an on-island workshop. Avalon, CA: Catalina Island Conservancy: 135–215.
- Knapp, Denise A. 2010b. **Changes in oak distribution and density by decade on Santa Catalina Island, 1943-2005.** In: Knapp, D.A., ed. 2010. Oak ecosystem restoration on Santa Catalina Island, California. Proceedings of an on-island workshop. Avalon, CA: Catalina Island Conservancy: 47–53.
- Leiva, Maria J; Fernández-Alés, Rocío. 1998. **Variability in seedling water status during drought within a *Quercus ilex* subsp. *ballota* population, and its relation to seedling morphology.** Forest Ecology and Management 111(2): 147–156.
- Lombardo, Carmen A.; Faulkner, Kate R. 1999. **The eradication of pigs (*Sus scrofa*) from Santa Rosa Island, Channel Islands National Park, California.** In: Browne, David R., ed. Proceedings of the fifth California Islands symposium. Camarillo, CA: Minerals Management Service, Pacific OCS Region: 300–306.
- Morrison, Scott A. 2011. **Trophic considerations in eradicating multiple species.** In: Veitch, C.R.; Clout, M.N.; Towns, D.R., eds. Island invasives: eradication and management. Proceedings of the International Conference on Island Invasives. Gland, Switzerland: IUCN and Auckland, New Zealand: 208–212.
- Navarro, Francisco B.; Jiménez, María N; Ripoll, María Á; Fernández-Ondoño, Emilia; Gallego, Eduardo; De Simón, Estanislao. 2006. **Direct sowing of holm oak acorns: effects of acorn size and soil treatment.** Annals of Forest Science 63(8): 961–967.
- Pesendorfer, Mario B.; Langin, Kathryn, M., Cohen, Brian; Principe, Zachary; Morrison, Scott A.; Sillett, T.S. 2014. **Stand structure and acorn production of the island scrub oak (*Quercus pacifica*).** Western North American Naturalist 7: 246–259.
- Pywell, Richard F.; Bullock, James M.; Roy, David B.; Warman, L.I.Z.; Walker, Kevin J.; Rothery, Peter. 2003. **Plant traits as predictors of performance in ecological restoration.** Journal of Applied Ecology 40(1): 65–77.
- Quero, José L.; Villar, Rafael; Marañón, Teodoro; Zamora, Regino; Poorter, Lourens. 2007. **Seed-mass effects in four Mediterranean *Quercus* species (Fagaceae) growing in contrasting light environments.** American Journal of Botany 94(11): 1795–1803.
- R Development Core Team. 2013. **R: a language and environment for statistical computing.** R Foundation for Statistical Computing, Vienna, Austria.
- Sage, Richard D.; Koenig, Walter D.; McLaughlin, Blair C. 2011. **Fitness consequences of seed size in valley oak *Quercus lobata* Née (Fagaceae).** Annals of Forest Science 68(3): 4774–84.
- Stratton, Lisa. 2009. **Restoration strategies for overcoming limitations to scrub oak regeneration on Catalina Island.** In: Damiani, C.C.; Garcelon, David K., eds. Proceedings of the 7th California Islands symposium. Arcata, CA: Institute for Wildlife Studies: 185–200.
- Tecklin, Jerry; McCreary, Douglas D. 1991. **Acorn size as a factor in early seedling growth of blue oaks.** In: Standiford, R.B., tech. coord. Proceedings of the symposium on oak woodlands and hardwood rangeland management. Gen. Tech. Rep. PSW-126. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 48–53.
- Wenny, Daniel G.; Devault, Travis L.; Johnson, Matthew D.; Kelly, Dave; Sekercioglu, Cagan H.; Tomback, Diana F.; Whelan, Christopher J. 2011. **The need to quantify ecosystem services provided by birds.** The Auk 128 (1): 1–14.