Climatic determinants of acorn size and germination percentage of *Quercus rugosa* (Fagaceae) along a latitudinal gradient in Mexico

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Botanical Sciences
95 (1): 37-45, 2017

DOI: 10.17129/botsci.640

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Abstract

Background. Abiotic constraints, historical effects of the last glaciation, and differential dispersal, have been proposed as potential explanations to account for the latitudinal decrease in acorn size of wide-ranging oak species distributed in the U.S. and Canada.

Hypothesis. We specifically tested the abiotic constraints hypothesis on oak acorn size in a geographical area without the counfounding influence of glaciation and related dispersal history.

Data description. Acorns from seven populations of the white oak *Quercus rugosa* were collected, encompassing the distribution of the species in Mexico.

Study site and years of study. Mexico, 2009-2010.

Results. Acorn length, width, mass and volume differed significantly among populations and indicated a marked clinal latitudinal reduction in acorn size. A multiple regression model revealed that this reduction in size (measured as acorn volume) can be explained by two important bioclimatic variables (growing season precipitation and growing season degree-days above 5 °C), while spatial variables (latitude and longitude) are not significant. Furthermore, germination percentage was significantly correlated to acorn mass and volume.

Conclusions. The main determinants of the latitudinal decline in acorn size are climate factors constraining seed development. This decline is maladaptive for seedling establishment, with important implications for the delination of northern limits of species ranges.

Key words: acorn size, climate factors, geographical variation, latitudinal distribution, *Quercus*.

Determinantes climáticos del tamaño de las bellotas y el porcentaje de germinación de *Quercus rugosa* (Fagaceae) a lo largo de un gradiente latitudinal en México

Resumen

Antecedentes. Las restricciones abióticas, el efecto histórico de la última glaciación y la dispersión diferencial son posibles explicaciones para la disminución latitudinal del tamaño de las bellotas en especies de encinos de amplia distribución en los EE.UU. y Canadá.

Hipótesis. Se probó específicamente la hipótesis de las restricciones abióticas sobre el tamaño de las bellotas de encinos en un área geográfica sin influencia de la historia de colonización postglacial.

Descripción de datos. Se colectaron bellotas procedentes de siete poblaciones del encino blanco *Quercus rugosa*, abarcando la distribución de la especie en México.

Sitio de estudio y fechas. México, 2009-2010.

Resultados. La longitud de las bellotas, el ancho, la masa y el volumen difirieron significativamente entre las poblaciones y mostraron una marcada reducción latitudinal clinal en el tamaño de la bellota. Un modelo de regresión múltiple reveló que esta reducción en el tamaño (medido como volumen de bellota) puede explicarse por dos variables bioclimáticas importantes (precipitación en la temporada de crecimiento y días-grado por encima de 5 °C de la temporada de crecimiento), mientras que las variables espaciales (latitud y longitud) no fueron significativas. Adicionalmente, el porcentaje de germinación se correlacionó significativamente con el volumen y la masa de las bellotas.

Conclusiones. Los principales determinantes de la disminución latitudinal del tamaño de las bellotas son los factores climáticos que limitan su desarrollo. Esta disminución afecta el establecimiento de las plántulas, lo cual tiene implicaciones importantes en el estudio de los factores que limitan la distribución de las especies.

Palabras clave: distribución latitudinal, factores climáticos, *Quercus*, tamaño de bellotas, variación geográfica.

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Seed size and seed mass are key ecological traits that play a fundamental role in the life history of plants, influencing many aspects of the patterns of natural regeneration of species, including the number of seeds that can be produced with a given amount of resources, seed predation and dispersal, seedling survival rate, and fitness (Venable & Brown 1998, Leishman *et al*. 2000, Dalling & Hubbell 2002). Seed size variation has been widely studied in a large number of species, in different habitats, and at global and local scales (Moles & Westoby 2004, Moles *et al*. 2007). A general pattern that has been documented at the global scale is the reduction in seed size by two or three orders of magnitude with latitude, from the equator to 60 °N (Moles & Westoby 2003, Moles *et al*. 2007).

In genus *Quercus* L., acorn size has been correlated positively with the rates of germination, and seedling emergence, survival and growth, both within and among species (Tripathi & Khan 1990, Bonfil 1998, Jakobsson & Eriksson 2000, Moles & Westoby 2004). Larger acorns also have higher frost resistance and, in general, are more stress tolerant (Aizen & Woodcock 1992, Gómez 2004). However, larger acorns may suffer higher predation rates (Gómez 2004, Muñoz & Bonal 2008, Yi & Wang 2015, Zhang *et al*. 2015) and bird dispersers usually prefer smaller acorns (Moore & Swihart 2006), suggesting the existence of conflicting selection pressures on acorn size (Gómez 2004).

Two main patterns of geographical variation related to acorn size have been described for oaks in North America. The first is a positive association between acorn size and geographical range among species, probably because species with larger acorns have greater success in seedling establishment, especially under limiting climatic conditions (Aizen & Patterson 1990). The second is a within-species latitudinal clinal decrease in acorn size that could potentially be explained by three different hypotheses (Aizen & Woodcock 1992, Koenig *et al*. 2009). The first is the abiotic constraints hypothesis, which postulates that acorn size is limited by precipitation, temperature, primary productivity, or some other factor that decreases with increasing latitude (Moles *et al*. 2007), predicting a strong correlation between environmental factors and acorn size independently of latitude, in the direction of smaller acorns being produced at sites with more constrained conditions. According to the second hypothesis, called the vicariance hypothesis, acorn size is related to abiotic factors such as soils or nutrients associated to the historical effect of the last glaciation, and thus the latitudinal pattern can be explained by whether areas were glaciated or not. The third hypothesis states that differential dispersal by blue jays, which prefer smaller acorns, is responsible for the latitudinal cline. An examination of the three hypotheses in *Quercus macrocarpa* gave strong support to the first hypothesis and to the second in a lesser extent, but the third hypothesis was unsupported (Koenig *et al*. 2009).

Quercus rugosa Née is the white oak species with the broadest latitudinal distribution in Mexico, from the Sierra Tarahumara in Chihuahua south of the border with Arizona up to the subtropical mountains in the highlands of Chiapas in southeastern Mexico (Rzedowski 1986, Uribe-Salas *et al*. 2008). Since Mexico was not glaciated, and the distribution of temperate forest tree species was probably affected only moderately by climatic changes during the glacial cycles (Jaramillo-Correa *et al*. 2009, Gugger *et al*. 2011, Ornelas *et al*. 2013), it is unlikely that historical post-glacial colonization could have left an imprint on acorn size of Mexican oak species, as has been proposed for U.S. and Canadian species. However, Mexico is characterized by substantial climatic gradients that could strongly influence phenotypic traits of wide ranging tree species, offering an excellent opportunity to test the abiotic constraints hypothesis in the absence of the confounding influence of glacial history and related dispersal history. So far, no data are available on the geographical variation of acorn size in any Mexican oak species. Therefore, in this study, we evaluated if there is geographical variation in the acorn size of *Q*. *rugosa* along the latitudinal and climatic gradient of its distribution to test the abiotic constraints hypothesis. Also, considering the ultimate importance of acorn size on the population dynamics of tree species, we also determined the geographical variation in germination percentage of *Q*. *rugosa* acorns and its correlation with acorn size.

Materials and methods

Study species. *Quercus rugosa* (section *Quercus*) is an ecologically important tree that can reach 25 m in height. It is an evergreen or sometimes brevideciduous species. The leaves are usually cupped, rarely flat, thick and leathery with a thick yellow-brown tomentum on the abaxial surface and up to 10 cm in length. The bark is brown and scaly. The acorn of *Q. rugosa* is ovoid, elongated and wider at the base than at the apex. It is produced individually or in groups of 2 - 3 with a cup of 10 - 15 mm in diameter with brown or blackish scales. The cotyledons are usually reddish or pinkish, which is a distinctive trait of the species. *Quercus rugosa* has a wide geographical distribution, with a latitudinal range in Mexico that extends from the temperate zones of the Sierra Tarahumara in the State of Chihuahua, to the subtropics in the highlands of Los Altos de Chiapas in southern Mexico, and Guatemala at altitudes ranging from 1,700 m to 3,550 m (Rzedowski 1986, Uribe-Salas *et al.* 2008). It is one of the dominant species over much of this range, and it can be found in monospecific stands or cohabiting with other species of oak or pine.

Acorn collection and measurement. During the last week of October and the first week of November of 2009 we collected a total of 2,810 acorns in seven populations representing the latitudinal gradient of the distribution of the species in Mexico, from Chiapas to Chihuahua (Figure 1, Table 1). Mature and undamaged acorns were collected directly off the tree or from the ground

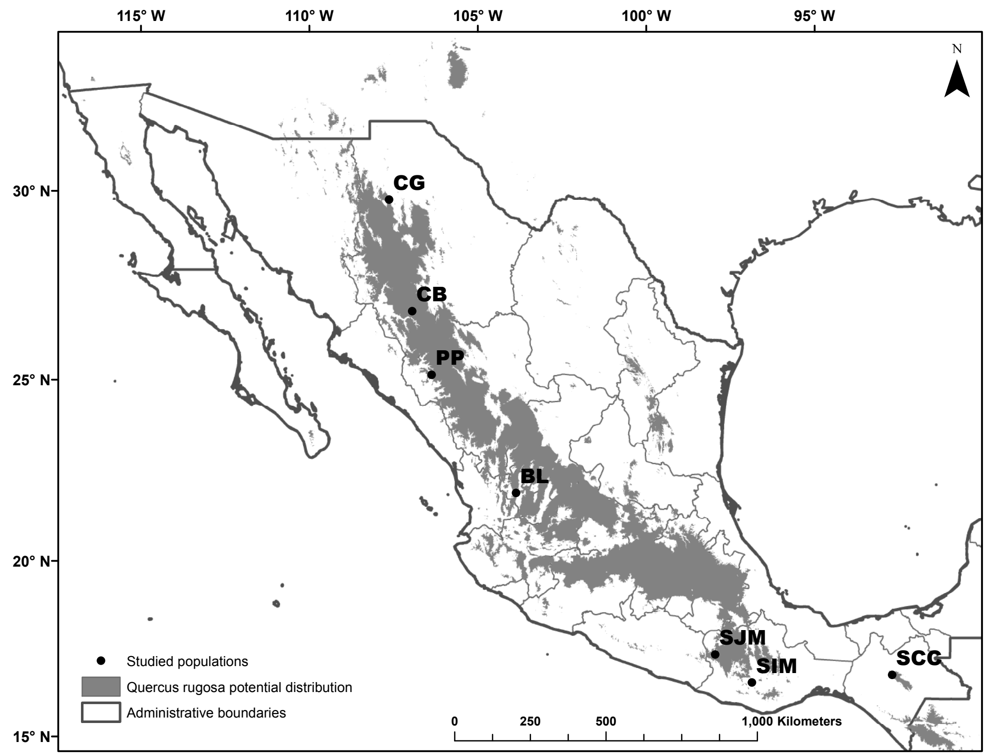

Figure 1. Map showing the seven *Quercus rugosa* populations collected in Mexico along the latitudinal/climate gradient. The numbering of populations is as in Table 1.

Table 1. Population name and population code, state, geographical, and climate data for the seven sampled sites listed south to north.

Population	Code	State	Latitude	Longitude	Altitude	GSP[a]	GSDD5[b]
1. San Cristóbal de las Casas	SCC	Chiapas	16.7639	-92.6935	2362	964	3338
2. Santa Inés del Monte	SIM	Oaxaca	16.9321	-96.8724	2527	760	3913
3. San Juan Mixtepec	SJM	Oaxaca	17.3454	-97.9510	2699	1059	2960
4. Bolaños	BL	Jalisco	21.8889	-103.8596	2300	771	3396
5. Papasquiaro	PP	Durango	25.1277	-106.3656	2573	849	1145
6. Caborachic	CB	Chihuahua	26.8343	-106.9455	2389	581	1359
7. Casas Grandes	CG	Chihuahua	29.7668	-107.6303	2409	409	1701

[a]GSP = growing season precipitation
[b]GSDD5 = growing season degree-days above 5 °C

below isolated trees from five different individuals per site. The number of seeds collected per mother tree varied between 16 and 180 and per site it varied between 240 (Casas Grandes) and 625 (San Cristóbal de las Casas) (Table 2). Groups of acorns from the same mother tree were packaged together in plastic burlaps, placed in a plastic cooler at environment temperature and transported to the laboratory where they were processed immediately. Transportation time was no longer than one week in all cases.

In a sample of 15 randomly chosen undamaged acorns from each of the five mother trees per population, we separated the cup from the nut and obtained the nut length (mm) and width (mm) with a digital caliper, and the fresh mass with an analytical balance. The volume (V) of each acorn was approximated assuming a prolate spheroid shape, using the formula $V = (4/3)\ \pi a^2 b$, where a is the width and b is the length (Aizen & Patterson 1990).

Table 2. Number of acorns collected per population, percentage of potentially viable acorns according to the water flotation test, and percentage of potentially viable acorns that germinated.

Population (code)	Number of acorns collected	Viable acorns (%)	Germination (%)
SCC	625	53.1	47.47
SIM	413	27.1	40.33
SJM	354	39.5	16.27
BL	298	81.9	39.58
PP	260	41.5	13.19
CB	620	54.0	21.04
CG	240	23.2	0.83

Viability and germination percentage. Acorns were sterilized by submerging them in water with 5 % chlorine bleach for ten minutes. At the same time, this served as a water flotation test of viability. In this way, for groups of acorns from each mother tree, we recorded the number and separated potentially viable seeds (the ones that sank) from inviable ones (the ones that floated). According with this test, the percentage of potential viability per population was between 27.1 and 53.1 % (Table 2). Then, all the potentially viable seeds were rinsed and humidified soaked in water for 24 h at 4 °C in a refrigerator. After that, acorns were individually sown in black plastic bags (25 cm long, 15 cm diameter, with drainage holes) filled with a substrate of 25 % agrolita, 25 % vermiculite and 50 % peat moss. Care was taken to introduce acorns into the substrate in approximately 2/3 of their length, with the apex pointing downwards. Bags were placed in a greenhouse with natural lighting in a randomized pattern and watered two times per week to keep a moisture level of approximately 30 % in the substrate. The position of the bags within the greenhouse was reshuffled every three or four weeks. The experiment was established in late November of 2009 and continued until early May 2010. Seeds were not moved or perturbed during this period and were considered germinated when the first leaves emerged. The germination percentage was recorded twice, in early March and in early May. After this date germination ceased and the results were analyzed, considering the total germination percentage.

Climatic variables. Climate data for each sampling site was downloded from the United States Department of Agriculture Forest Service web page (http://forest.moscowfsl.wsu.edu/climate/current/), a climate data set with derived variables designed for assessing plant-climate relationships (Rehfeldt 2006). We focused on two variables that capture the most important energy and water resource inputs for plants: growing season precipitation (gsp) and growing degree-days above 5 °C within the frost-free period (gsdd5) (a measure of heat accumulation) (Table 1).

Statistical Analyses. Differences among mother trees and among populations in acorn length, width, volume, and fresh mass were evaluated with nested analyses of variance. In these tests, both populations and mother trees within populations were considered to represent random samples from a larger pool. For each character, we calculated the proportion of the total variation (*i.e.* the variance components) due to differences at each of the two hierarchical levels. To compare germination percentage among populations, χ^2 tests were used. These tests were performed with the JMP 8 software (SAS Institute, Cary, North Carolina).

To test the abiotic constraints hypothesis, we performed multiple regressions of acorn volume on latitude, longitude, gsp, and gdd5 using R v3.0.0 languaje. All variables were centered prior to analysis and added variable (partial regression) plots were made to visualize the partial correlation of each climate variable after controlling for all other variables. Similar tests were done without including longitude or with only one climate variable at a time, and simple linear regressions were performed for each climate variable with each dependent variable to confirm their correlation. If the two derived climate variables were significant in the multiple regression models after accounting for the spatial variables (especially latitude), then we found support for the abiotic constraints hypothesis.

Results

The nested analyses of variance showed highly significant (P < 0.001) differences among mother trees within populations and among populations for the four morphological acorn traits evaluated (Table 3). However, the proportion of the total variation explained by differences among mother trees wihin populations was in general much smaller (7.47-11.9 %, depending on the trait) than the proportion explained by differences among populations (75.11-79.53 %). The residual variance (9.13-14.39 %) was interpreted as being explained by differences among acorns within mother trees. The population mean values for the four variables evaluated clearly indicated that southern populations had larger acorns than northern populations (Figure 2). Simple linear regressions indicated significant, positive relationships of acorn volume with gsp

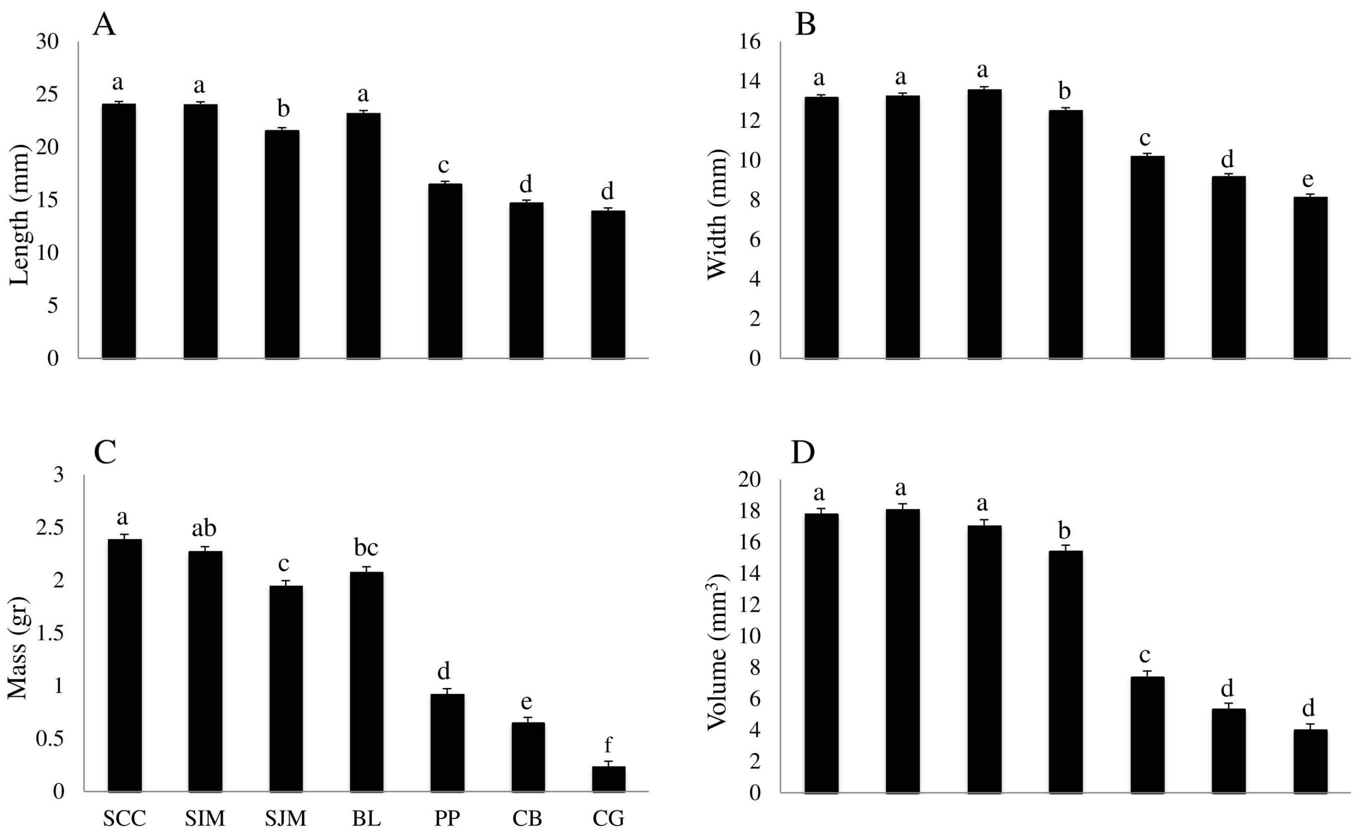

Figure 2. Mean and standard error for the four acorn morphological traits in the seven study populations: (a) length, (b) width, (c) mass, (d) volume. Different letters indicate significant differences according to an analysis of variance followed by Tukey-Kramer tests.

Table 3. Partitioning of variance by hierarchical level for four variables measured in the acorns of *Quercus rugosa*. Variance components and significance levels were determined with a nested ANOVA.

Variable	Level: Among populations	Level: Among mother trees	Level: Residual
Length	78.97***	11.90***	9.13
Width	79.53***	7.47***	12.99
Volume	75.57***	10.14***	14.29
Fresh mass	75.12***	10.49***	14.39

***$P < 0.0001$

($R^2 = 0.57$, $P = 0.049$) and with gdd5 ($R^2 = 0.86$, $P = 0.003$) and a strongly negative relationship with latitude ($R^2 = 0.94$, $P = 0.0003$).

According to the χ^2 tests, populations differed significantly in germination percentage (χ^2 = 239.6; d.f. = 6; $P < 0.0001$) (Table 2). In general, germination percentage decreased latitudinally from 47.5 % in population San Cristobal de las Casas, Chiapas to 0.83 % in Casas Grandes, Chihuahua, although the relationship was only marginally significant ($R^2 = 0.54$; $P = 0.06$). Importantly, we found that germination percentage was significantly correlated with acorn volume ($R^2 = 0.60$; $P = 0.04$) and acorn fresh mass ($R^2 = 0.74$; $P = 0.013$), highlighting the importance of seed size on germination success.

In the multiple regression model of acorn volume with the two climate variables controlling for spatial variables, both climate variables were significant ($P < 0.034$), whereas spatial variables were not ($P > 0.23$) (Table 4, Fig. 3). This model has $R^2 > 0.99$. Multiple regression tests without longitude and with only one climate variable at a time gave similar results (not shown). These tests were not repeated for acorn fresh mass because of the high correlation (R^2=0.97; $P < 0.0001$) between this variable and volume.

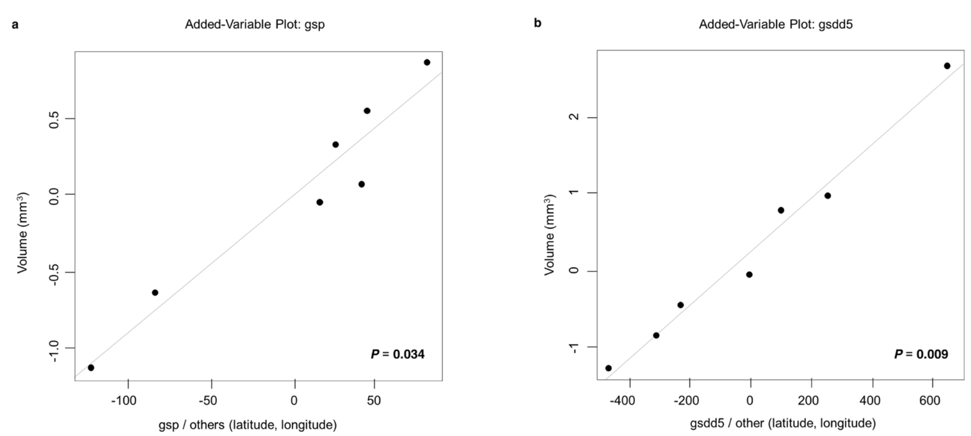

Figure 3. Added variable (partial regression) plots showing the partial correlation of (a) growing season precipitation (gsp) and (b) growing season degree-days above 5 °C (gsdd5) with acorn volume.

Discussion

Latitudinal variation in acorn size. *Quercus rugosa* showed a clinal pattern of south-north decrease in population mean acorn mass and volume across the distribution of the species in Mexico (Figure 2). According to the multiple regression analysis, growing degree-days > 5 °C and growing season precipitation are both significant when controlling for latitude and longitude, supporting the abiotic constraints hypothesis (Table 4, Figure 3). What is striking is that these relationships are highly significant even with a small sample size of seven sites. Although the relationship of latitude with acorn volume might become significant with increased sampling, this possibility would not change our interpretation. Most importantly, it is the significant correlations with climate that strongly support the abiotic hypothesis and specifically support the

Table 4. Results of the multiple regression analysis of acorn volume on spatial and climate variables of the seven acorn collection sites.

Acorn volume	Estimate	SE	*t*	*P**
Intercept	6.7E-10	0.12	0	1
Latitude	-0.26	0.15	-1.71	0.230
Longitude	-0.05	0.07	-0.73	0.541
GSDD5	3.5E-03	3.29E-04	10.76	**0.009**
GSP	8.8E-03	1.66E-03	5.31	**0.034**

*Bold values are significant

idea that primary water and energy inputs are important for acorn size and germination percentage in *Q. rugosa*.

Reduced seed size along latitudinal gradients in species exhibiting substantial northward postglacial migration have been interpreted as evidence of selection on small seed size because more dispersable seeds would be more likely to advance and establish northward (Cwynar & MacDonald 1987, Koenig *et al*. 2009). Our results from a Mexican oak whose history is not confounded by glacial migration history question that idea and instead support studies showing that the main determinants of within-species variation in acorn size are climate factors that constrain seed development.

Germination success. Several studies have shown a positive effect of acorn size on germination success, and seedling survival and growth at the intraspecific level (Bonfil 1998, Tripathi & Khan 1990, Tilki 2010, Urbieta *et al*. 2008, Sage *et al*. 2011). These effects are mostly due to the amount of resources stored in the seed, because larger seeds can survive for longer periods of time under unfavorable conditions, while smaller seeds will consume their food reserves in the process of respiration and physiological adjustment. After germination, seedlings that emerge from larger seeds will have more energy for initial growth and for recovery from herbivore attack (Bonfil 1998, Urbieta *et al*. 2008). However, most of these studies have involved a single or few populations, and in few cases the relationship between acorn size and germination success has been examined along large geographical or environmental gradients.

One important question that arises from the detection of a clinal pattern in acorn size is whether variation is a result of plastic responses to the limiting climatic factors or is genetically determined, as a result of selection for the production of viable offspring under the constraints of local climatic conditions (Aizen & Woodcock 1992). Our results showed that the latitudinal decrease in population mean acorn size was correlated with a concomitant reduction in germination percentage. In fact, the germination success in the northernmost population was extremely low, less than 1 %. However, it must be acknowledged that, in general, the germination percentages reported in this study are somewhat lower than the ones found in other studies with geographically restricted samples of the same species (40-92 %) (Bonfil & Soberón 1999, López-Barrera & Newton 2005, Huerta-Paniagua & Rodríguez-Trejo 2011). These differences could be due to methodological issues related to transportation and storage of the acorns but, most probably, to the criteria used to score germination. In other studies, seeds have been considered germinated when the radicle reaches a size equal to the length of the same seed (*e.g*. Huerta-Paniagua & Rodríguez-Trejo 2011), while in our case we waited until the emergence of the first leaves. However, even in this case, the extremely low germination percentage in the Casas Grandes populations seems odd and it could be explained if during the year of collection trees or acorns were subjected to an extreme stress factor (*i.e*. frost or drought). Therefore, further studies should also consider interannual variation in seed size and viability.

Nevertheless, we consider that our data in general reflect the fact that seed production and development faces more severe constraints at the northernmost part of the range of *Q. rugosa*. Overall, our results do not seem to support the size-optimization-through-selection hypothesis to explain acorn size variation in *Quercus rugosa*. Also, according to our personal observations, populations of this oak species become progressively smaller and its distribution more fragmented towards the north, suggesting limited recruitment success at higher latitudes. As was also stated by Aizen & Woodcock (1992), this evidence indicates that the latitudinal decline in acorn size is maladaptive for seedling establishment, with important implications for the delineation of northern limits of species ranges.

Acknowledgements

The authors thank S. Ramos-Ortiz for field assistance, H. Rodríguez-Correa for map preparation and two anonymous reviwers for their constructive comments to improve previous versions of the manuscript. This paper constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the National Autonomous University of Mexico (UNAM). J. Llanderal-Mendoza acknowledges the scholarship and financial support provided by the National Council of Science and Technology. This project was supported by CONAFOR-CONACyT 176316 and DGAPA-PAPIIT IV201015 to KO.

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Received:
August 24th, 2015

Accepted:
December 2nd, 2015

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