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A META-ANALYSIS ON THE RELATIONSHIP BETWEEN SEED SIZE, SEED SHAPE AND PERSISTENCE IN SOIL SEED BANK

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Abstract

The recent literature on seed size, shape and persistence in soil seed bank and the data from the seed plant traits database in Western Europe was collected. A total of 1656 information on seed size, shape and seed bank properties, 1518 species were obtained. Effect size of each grade seeds forming a persistent seed bank was calculated by Non-Comparative Binary Data and random effect models. Furthermore, the relationship between the grade of seed size and seed shape, a continuity data, and effect size was responsed by the regression analysis. The results show that seed size can predict the persistence of soil seed bank, but it reflects the obvious stage on the grades. At Grades 1 to 7, seed size is positively correlated with the probability of forming a persistence soil seed bank, and negatively correlated at Grades 7 to 15. Seed shape can also be a good predictor of seed bank persistence. With the increase of seed shape variance, the probability of persistent in soil seed bank will reduce as the seed becomes flattened or elongated from near spherical shape.

Key words: Meta-analysis; Seed shape; Seed size; Soil seed bank persistence.

Introduction

There is in an increasing demand for precise and reliable information on seed banks, with a crucial characteristic of plant species (Thompson & Hodgson, 1993; Bakker *et al*., 1996). Soil seed bank is the material basis of natural vegetation regeneration, which is of great significance for biodiversity research and ecological restoration (Ma *et al*., 2010; Chen *et al*., 2016). The size of soil seed bank determines the possibility and speed of ecosystem restoration after disaster and disturbance. Potential seed bank can restore some disappeared or damaged surface vegetation (Schwienbacher *et al*., 2010). On the contrary, lack of a persistent soil seed bank would have imposes a serious drawback on the conservation of the species, since extinction of all the above-ground subpopulations would means the extinction of the metapopulation (Washitani *et al*., 1997). Therefore, probing the characteristics of the soil seed bank is helpful to understand the species diversity of the community and the potential of vegetation restoration, and to provide a basis for the formulation of reasonable vegetation restoration decisions (Ma *et al*., 2018).

Seed persistence and seed longevity are estimated by three different approaches: (1) Method for measuring seed germination in a laboratory by sampling soil in a suitable season (Moles *et al*., 2000). (2) Bury the seeds in the laboratory and determine the germination of the seeds for at least five years (Hölzel & Otte, 2004; Jurand *et al*., 2013). (3) Prediction of soil seed bank persistence using Thomson's method based on seed size and seed shape (Thompson & Hodgson, 1993; Schwienbacher *et al*., 2010). It is not only time-consuming to determine whether the original seeds have ability to form a persistent soil seed bank by germination tests or extracting the seeds contained in the soil samples, but the collection of the original seed bank data is often inconclusive and the results from rare species digging the soil below is obviously not advisable (Bai & Jiao, 2006).

If seed size and seed shape are used as a feasible predictor of a soil seed bank persistence, it can provide a rich and intuitive data source for vegetation management. Therefore, the relationship between seed size, shape and soil seed bank has received much attention from scholars since 1993. Thomson conducted experiments on a series of British herbage, and found for the first time that seed size and shape are related to the persistent soil seed bank, that is, the species with large and loose seeds do not (Thompson & Hodgson, 1993). In the New Zealand (Moles *et al*., 2000), on Italian from Alps to Mediterranean coasts (Cerabolini *et al*., 2003), temperate mountain grasslands of Argentina (Funes *et al*., 1999) and other areas, it also found the phenomenon. The mechanism may be that small, round (or flat) seeds are more likely to be buried in the soil because buried seeds are much less likely to be preyed than seeds left on the soil surface (Garner & Witkowski, 1997). Predation is one of the main determinants of seed persistence (Yu *et al*., 2007). In addition, if the seeds are buried deeply, the seeds lack the conditions for germination, which will also lead to the persistence of the seeds in the soil (Chen *et al*., 2012). In Australia, however, neither seed size nor seed shape is a good predictor of persistence, because in this flora, rodents are not important, whereas small animals like ants prey on small seeds (Leishman & Westoby, 1998). Up to now, whether and how seed mass and shape are related to seed persistence in soil is a controversial topic in plant ecology. As for the size, shape and persistence of seeds in soil, there have been four patterns: (1) Smaller, rounder seeds are more likely to form persistent soil seed banks (Thompson & Hodgson, 1993; Funes *et al*., 1999); (2) Smaller seeds are more persistent in the soil seed bank, but the shape of the seed has nothing to do with durability (Thompson *et al*., 2001; Peco *et al*., 2003); (3) Seed morphology is a good predictor of seed persistence, and seed size seems to be less important (Schwienbacher *et al*., 2010); (4) The size and shape of seeds are not related to persistence (Leishman & Westoby, 1998).

There is still, however, little information about the relationship between seed size, shape and persistence in most of the world's ecosystems. The seeds of a study usually come from the same flora, obtaining information of the persistence of seeds by measurement or different query methods. But due to the large workload and lack of information and uncertainty, the sample size is small. So far, there is no meta-analysis on the prediction of seed size and shape, so it is necessary to make a new quantitative review on whether seed size and shape can be used to predict the persistence of seed bank. This study to explore the questions: Can seed size and seed shape predict the type of seed bank durability without distinguishing the life forms of plants?

Material and Method

Data search: We have extensively reviewed literature obtained across Web of science and Baidu scholars. The literature obtained was supplemented with studies cited in the reference lists of the articles surveyed (secondary search). The keywords used were seed size, seed shape, soil seed bank, persistent. We did not include the words in Portuguese, because the majority of the studies published in Portuguese include a title, abstract and keywords in English. We selected studies that contained detailed data about species name, family, seed persistence, seed size and seed shape variance. When the study did not report seed size and seed variance data, they were not included in our study. We obtained a total of 10 studies that fulfilled our study selection criteria (Appendix S1), as well as a web-based database. The 10 studies we selected summarised 10 experiments, conducted in 8 countries, involving 1656 plant seeds.

The seed information of the seed plant traits database in Western Europe is different from the research information. It is necessary to calculate the mean and standard deviation of the seed size and seed shape, and further unify the seed persistence information. The information for the same seed comes from much literature, and the persistent information is greater than two. When the number of the persistent soil seed bank is greater than the transient soil seed bank, the seed will be considered as a persistent seed bank, otherwise as a transient seed bank. When two numbers are equal, seeds are not included in the study.

Meta-analysis: Before appraising the data, the data of seed mass were normalized by data normalization, which is the indexation of statistical data. In each of the literature we collected, the seeds were weighed differently by seed number. In order to improve the variance level, the data of seed mass were normalized by min-max before analysis. The normalization of seed mass can be divided into two steps: (1) Convert seed mass to 100-seeds weight; (2) The100-seeds mass is mapped to the value x in the interval [0, 1] by min-max normalization, and the formula is as follows:

$$NM_{100} = (OD-MIN) / (MAX-MIN) \qquad (1)$$

where MAX and MIN are the maximum and minimum values for seed mass of the collected data respectively; OD is the original data of seed mass and NM_{100} is normalization of 100-seed mass. In the process of normalization, some data on the number of seeds that are not clearly expressed by seed weight are discarded. The normalized data of seed size is divided into 15 grades, without specific classification standard for these grades, but it needs to reflect the sequential increase of seed weight, and ensure that there is a certain amount of data in each grade. Seed variance of all was calculated following the methods of Thompson *et al*., (1993), as the variance of seed length, width and depth after transforming all values so that length was unity, to give a measure of seed shape (Thompson & Hodgso, 1993). The variance of diaspore dimensions is a subset between [0, 1], so the original data were not quantified.

According to the collected data, seed quality was divided into 15 grades and seed shape into 13 grades. In addition, seed bank is divided into two types: transient soil seed bank and persistent soil seed bank. The “immediate germination seasonal dormancy only” is regarded as the transient soil seed bank, “dormant fire-promoted germination” as the persistent soil seed bank. We calculated the incidence (P) and standard error (SE) of seed bank persistence at various grades of seed size and shape, and evaluated effect size and heterogeneity, which is an important characteristic in meta-analyses, because it allows us to evaluate whether the variation in the effect sizes collected is explained with the population variation or by chance. So, we used the I^2 as a standard of heterogeneity of each analysis by review manager 5.1.

Results

We obtained a total of 10 studies that fulfilled our study selection criteria (Appendix S1). A total of 1,656 plant seeds, 1518 species were collected from the published papers and the seed plant traits database in Western Europe (https://uol.de/fileadmin/user_upload/biologie/ag/landeco/download/LEDA/Data_files/seed_mass.txt). Among them, 636 seeds were temporary seeds, 944 seeds were persistent seeds, and 75 seeds were not classified. The seed content is between 0.002mg and 10082.800mg, a difference of more than 5 million times. The minimum value of seed main scale variance is 0.000, which is close to spherical, and the maximum value is 0.504. A total of 1181 seeds are from 10 floras, and 475 species are from websites without flora information.

The effect size of seed size and seed shape: The meta analysis is a mature research method that evaluates the heterogeneity between different research data according to the test results to judge the accuracy of the research results. Seed mass(SM) is divided into 15 grades according to the maximum and minimum values of seed mass and the data of seeds in different mass ranges: Grade 01 ($0.00000 \leq SM < 0.00005$), Grade 02 ($0.00005 \leq SM < 0.00010$), Grade 03 ($0.00010 \leq SM < 0.00015$), Grade 04 ($0.00015 \leq SM < 0.00020$), Grade 05 ($0.00020 \leq SM < 0.00025$), Grade 06 ($0.00025 \leq SM < 0.00100$), Grade 07 ($0.00100 \leq SM < 0.00200$), Grade 08 ($0.00200 \leq SM < 0.00300$), Grade 09

(0.00300≤SM < 0.00400), Grade 10 (0.00400 ≤ SM < 0.00500), Grade 11 (0.00500≤SM < 0.01000), Grade 12 (0.01000≤SM < 0.01500), Grade13 (0.01500 ≤ SM < 0.02000), Grade 14 (0.02000 ≤ SM < 0.04000), Grade 15 (SM ≥ 0.04000). The inverse variance (IV) method was used for statistical analysis, and the Risk Difference (RD) value was taken as the effect size, with the combined statistical test results, Z=13.25 ($p < 0.00001$), indicating that the results were statistically significant. Meta analysis show that seed shape was highly heterogeneous among studies of different grades ($I^2 = 79\%$), 95% confidence interval CI = 0.41 [0.35, 0.47] (Table 1 and Fig. 1). In review manager 5.1., I^2 was used to determine the heterogeneity between the study seeds, and heterogeneity was acceptable when $I^2 \leq 50\%$. Before that, we tried to reduce the heterogeneity among different grades by removing the literature in each grade, and the result still showed high heterogeneity. Therefore, we chose the Random effects (RE), with the total effect size of 41%.

In the same way, the seed shape variance (SV) is divided into 13 grades: Grade 01 (0.0000 ≤ SV < 0.0200), Grade 02 (0.0200 ≤ SV < 0.0400), Grade 03 (0.0400≤ SV < 0.0600), Grade 04 (0.0600 ≤ SV < 0.0800), Grade 05 (0.0800 ≤ SV < 0.1000), Grade 06 (0.1000≤ SV < 0.1200), Grade 07 (0.1200 ≤ SV < 0.1400), Grade 08 (0.1400 ≤ SV < 0.1600), Grade 09 (0.1600≤ SV < 0.1800), Grade10 (0.1800 ≤ SV < 0.2000), Grade 11 (0.2000 ≤ SV < 0.2500), Grade 12 (0.2500≤ SV < 0.3000), Grade 13 (SV ≥ 0.300). The IV method was used for statistical analysis, and the RD value was taken as the effect size, with the combined statistical test results, Z = 20.25 ($p <0.00001$), indicating that the results were statistically significant (Table 2 and Fig. 2). The total effect value RD of seed shape was 0.38, with confidence interval CI = [0.34, 0.41]. There is moderately heterogeneous ($I^2=50\%$) that the fixed-effect model is selected. Nevertheless, it was high heterogeneity ($I^2>50\%$) before this, and the high heterogeneity was reduced medium heterogeneity by deleting data of the study from Leishman and Westoby (1998) and from Cerabolini *et al*., (2003) respectively in Grade 10 and Grade 11 respectively.

Table 1. Meta-analysis of seed mass.

Study or subgroup	Risk difference	SE	Weight (%)	Risk difference	Iv, Random 95% CI
Grade 01	0.3122	0.0220	9.0	0.31	[0.27, 0.36]
Grade 02	0.5306	0.0504	7.5	0.53	[0.43, 0.63]
Grade 03	0.3889	0.0663	6.6	0.93	[0.26, 0.52]
Grade 04	0.4483	0.0923	5.1	0.45	[0.27, 0.63]
Grade 05	0.4357	0.0887	5.3	0.44	[0.27, 0.61]
Grade 06	0.4733	0.0320	8.6	0.47	[0.41, 0.54]
Grade 07	0.5714	0.0500	7.6	0.57	[0.47, 0.67]
Grade 08	0.3333	0.0680	6.5	0.33	[0.20, 0.47]
Grade 09	0.6000	0.0828	5.6	0.60	[0.44, 0.76]
Grade 10	0.3750	0.0856	5.5	0.38	[0.21, 0.54]
Grade 11	0.4227	0.0502	7.5	0.42	[0.32, 0.52]
Grade 12	0.4182	0.0665	6.5	0.42	[0.29, 0.55]
Grade 13	0.2917	0.0928	5.1	0.29	[0.11, 0.47]
Grade 14	0.3518	0.0750	6.0	0.32	[0.17, 0.46]
Grade 15	0.2029	0.0484	7.6	0.20	[0.11, 0.30]
	Total(95% CI)		100.0	0.41	[0.35, 0.47]

Heterogeneity: $Tau^2 = 0.01$; $Chi^2 = 0.65.71$, df = 14 ($p<0.00001$); $I^2 = 79\%$
Test for overall effect: Z=13.25 ($p<0.00001$)

Table 2. Meta-analysis of seed shape variance.

Study or subgroup	Risk difference	SE	Weight (%)	Risk difference	Iv, Random 95% CI
Grade 01	0.4035	0.0216	14.0	0.40	[0.36, 0.45]
Grade 02	0.3813	0.0384	9.9	0.38	[0.31, 0.46]
Grade 03	0.4395	0.0396	9.7	0.44	[0.36, 0.52]
Grade 04	0.4248	0.040	9.6	0.42	[0.35, 0.50]
Grade 05	0.4880	0.0447	8.6	0.49	[0.40, 0.58]
Grade 06	0.4000	0.0438	8.8	0.40	[0.31, 0.49]
Grade 07	0.4123	0.0461	8.4	0.41	[0.32, 0.50]
Grade 08	0.2987	0.0522	7.3	0.30	[0.20, 0.40]
Grade 09	0.3220	0.0608	6.1	0.32	[0.20, 0.44]
Grade 10	0.2766	0.0652	5.5	0.28	[0.15, 0.40]
Grade 11	0.2653	0.0631	5.8	0.27	[0.14, 0.39]
Grade 12	0.2353	0.0727	4.8	0.24	[0.09, 0.38]
Grade 13	0.3000	0.1449	1.5	0.30	[0.02, 0.58]
	Total(95% CI)		100.0	0.38	[0.34, 0.41]

Heterogeneity: $Tau^2 = 0.00$; $Chi^2 = 24.01$, df = 12 ($p<0.02$); $I^2 = 50\%$
Test for overall effect: Z = 20.24($p<0.00001$)

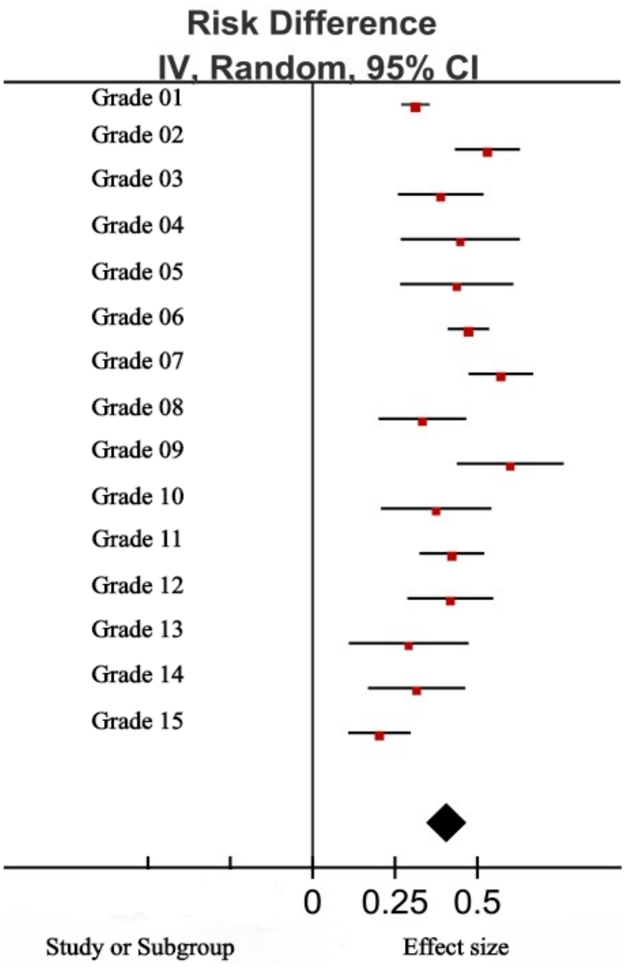

Fig. 1. Dots represent the OR of each study, and dot sizes represent the study weight in the analysis. The horizontal line represents the 95% CI of each study, and if the horizontal line intersects the invalid line, the study at that level is not statistically significant. Diamonds represent the overall effect size, and diamond widths represent the overall 95% CI.

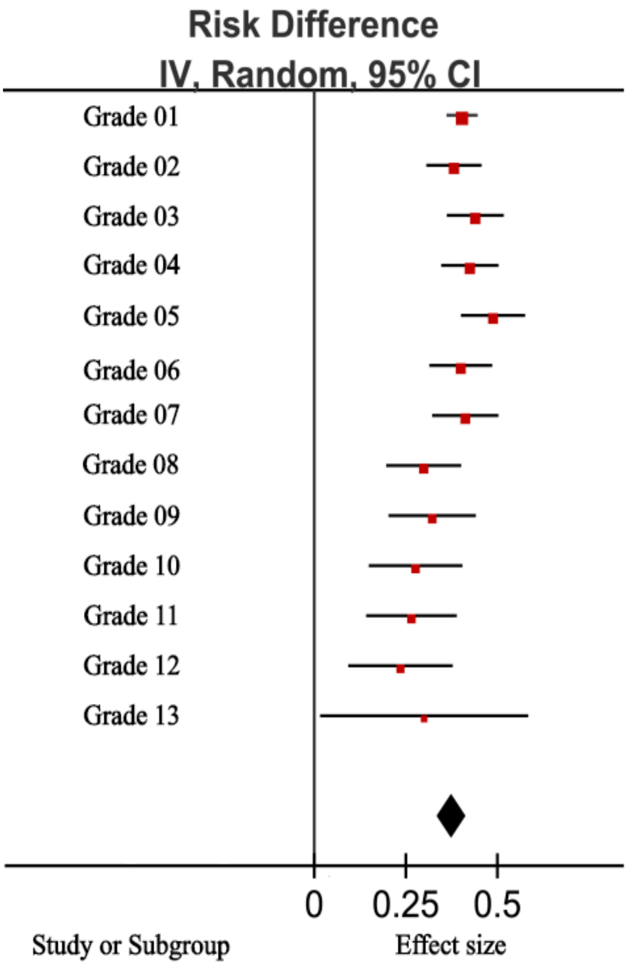

Fig. 2. Dots represent the OR of each study, and dot sizes represent the study weight in the analysis. The horizontal line represents the 95% CI of each study, and if the horizontal line intersects the invalid line, the study at that level is not statistically significant. Diamonds represent the overall effect size, and diamond widths represent the overall 95% CI.

Relationship between the seed size, shape and persistence: In the past, the seed information of the same research usually came from the same flora, having four patterns for the relationship between seed size, seed shape, and seed bank persistence in different floras. The study data come from different flora with wider range of seed mass and seed shape variance, exploring the relationship between the seed size, seed shape and the seed bank persistence. The seed size can predict the persistence of the soil seed bank, which does not show that smaller seeds are more persistent, but there is an obvious class nature. As shown in Fig. 3A, the relationship between seed size and effect value is shown as a curvilinear regression equation of $Y_1= -0.0037X_1^2+0.0496X_1+0.3203(R^2 = 0.5212)$. In accordance with the equation, among the Grade 15, when the Grade is 6.7 (approximately 7), the maximum effect size of seed size is 0.49, and the possibility of seed bank persistence is the greatest. Obviously, the probability of forming a persistent soil seed bank increases with the improvement of seed mass in the range of Grade 1 to 7, but decreases gradually in the range of Grade 7 to 15. Thompson found that not only seed size is a good predictor, but seeds within 3 mg can form a persistent seed bank (Thompson & Hodgson, 1993). Our study differs from Thomson in that it can form a persistent seed bank regardless of the 100-seed weight. Although there is no threshold value, there is a clear trend. According to formula (1) and the maximum value (23745.2000 mg) and minimum value (0.0020 mg) of the seeds, it can be known that the 100-grain weight ranges of grades 1~7 and 7~15 are (0.0002 mg ≤ SM < 47.7900 mg), (47.7900 mg ≤ SM < 23745.20000 mg). The 100-seed weight ≤ 47.790 mg, seed quality and persistence were positively correlated, while the 100-seed weight > 47.790 mg, it was negatively correlated.

The shape of the seed is also a good predictor, and round seeds are more likely to form a persistent seed bank. As shown in Fig. 3B, there is a linear relationship between the seed shape level and the effect value: $Y_2 = -0.0156X_2 + 0.469$ ($R_2^2 = 0.6274$). The curve shows an obvious tendency that seed shape is positively correlated with effect size. In other words, spherical seeds have a higher probability of forming a persistent seed bank, but with the increase of seed shape variance, seeds gradually become slender or flat, and the probability of forming a persistent seed bank gradually decreases.

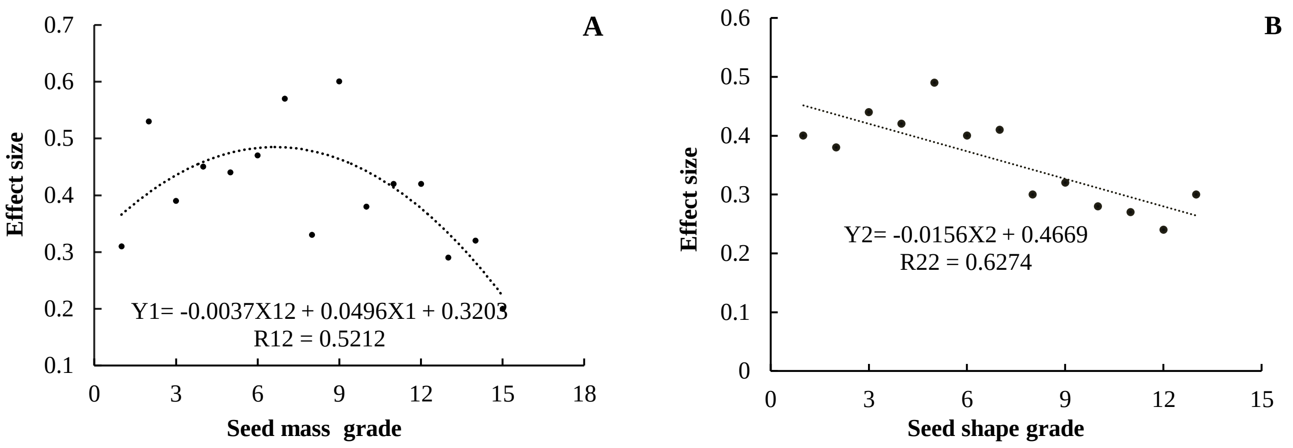

Fig. 3. The relationship between effect size and seed mass grade (A) or seed shape grade (B).

Discussion

The soil seed bank essential part of the potential regeneration capacity of vegetation, and it can provide stable propagules for community succession, regeneration, and restoration of degraded ecosystems (Kebrom & Tesfaye, 2000). So far, the relationship between seed size, seed shape and soil seed bank persistence is still a hot issue that has attracted much attention from scholars. This relationship appears to show different results in different plant floras. Previous studies on the persistence in soil seed banks have mainly attached importance to the seeds from a flora to explore the relationship. In this study, we collected the seed species information from different plant floras for the first time, which has a wider range of seed size, seed shape, the space-time scale, and the life type. The study discovers that seed size and shape were good predictors of the persistence of soil seed bank, even across different life forms and flora. It is worth noting that there are two kinds of relationships between seed size and soil seed bank. Before grade 7, with the increase of seed size, the probability of forming persistent seed bank was increased; after grade 7, with the increase of seed size, the probability was decreased.

The prerequisite for a persistent seed bank is that the seeds enter the soil, do not germinate immediately, and can remain active in the soil for more than one year (Troumbis, 1996; Andrade & Miranda, 2014). Small seeds have a better chance of getting into the soil than large ones, the most likely burial mechanisms will operate small, compact seed more efficiently, such as active events (earthworms ,seed self-burial) and passive events (cracks, rainfall and frost heave) (Thompson *et al*., 2001). In general, there is an expectation that small seeds will have a better chance of surviving after seed dispersal than larger seeds, spend less time on the soil surface, are less likely to be spotted by animals, and can successfully escape rodent predation. The relationship in Britainillustrates this mechanism well (Thompson & Hodgso, 1993). However, in Australia, neither seed size nor seed shape can be used as a predictor of soil seed bank persistence, because the conditions of burial and interference operations in the Australian environment are different from those in the Britain, Australian ants will prey on small seeds (Leishman & Westoby, 1998).

Our study found that before 47.7900 mg, the probability of seeds forming a persistent seed bank increased with seed size, which may be based on a wide range of sources of data and other influencing factors other than burial mechanisms. The size of a species seed bank is determined by the combined action of seed production, dispersal and secondary seed movements, predation, viability, dormancy and germination (Troumbis, 1996). Seeds that remain dormant in the soil must maintain their vitality and resist attacks from soil invertebrates and microorganisms to further form a persistentseed bank (Davis *et al*., 2008; Casas *et al*., 2017). If larger seeds are lucky enough to get into the soil, their chances of survival may increase dramatically (Majeed *et al*., 2019), which may be why even large seeds in our collection can form lasting seed bank. In data we collected, the seed mass of Seed Banks in Western Europe is generally relatively large, and the largest is Echinocystis lobata, Cucurbitaceae, whose 100-seed weight is 23745.200mg. Among the 477 seeds in the Seed Bank in Western Europe, 196 seeds can form a persistent seed bank. The largest seed of persistence is *Lupinus angustifolius* of Fabaceae, with the 4594.6286 mg 100- seed weight. The underlying cause is likely to be the seed coat thickness, which is positively related to seed quality (Davis *et al*., 2008). Fabaceae also accounts for a large proportion of Seed Banks in Western Europe, with 22 of the 60 species forming persistent seed Banks. The fact find that most Fabaceae in central Spain having persistent seed bankprovides evidence for the assumptions (Zhao *et al*., 2011). A study suggests that seed coat structure may play a key role in the dormancy mechanism, with mechanical hindrance and impermeability of seed coat making it difficult for certain seeds to germinate, such as *Oxytropis coerulea*, *Vicia unjuga*, and other hard, poorly permeable seed coats that need to be treated to allow seeds to grow (Zhang & Yuan, 2017). In short, larger seeds can also form persistent soil seed bank, which may reflect different energy and nutrient reserves and thicker seed coats (Garner & Witkowski, 1997). However, some studies have attached great importance to the dependence of larger seeds on dormancy, providing a large number of nutrients for seedlings, increasing their chances of growing under adverse conditions, and large seeds producing better supplies and larger seedlings. Thus larger seeds produce a better supply and larger seedlings that perform better under adverse conditions and have a higher germination rate (Casas *et al*., 2017). The interaction between seed dormancy and burial mechanisms and the ubiquity of seed sources may have led to two trends for the relationship of seed mass and persistence, although similar conclusions have not been found in other studies.

For seeds of a certain size, rounder, more compact seeds are more capable to persistence than flat, slender seeds, which is the equivalent as the conclusions about the shape and dominance of different flora (Moles *et al*., 2000; Cerabolin *et al*., 2003; Wang *et al*., 2011), with main reason that round seeds need to enter the soil more easily (Schwienbacher *et al*., 2010). Nevertheless, unlike previous studies, our study did not find a threshold for distinguishing the shape differences between persistent and transient seed Banks, but rather a trend. The threshold of shape variance persistent seed bank varies by flora, the upper limit in Argentina is about 0.18 (Funes *et al*., 1999), and 0.14 in North China (Zhao *et al*., 2011), it is not an inevitable divider, with exceptions on both sides of the boundary.

The shape and size of seeds can be used as good predictors. Although the theoretical and empirical results are consistent, our data and analysis tools are limited, and some studies that cannot obtain shape variance and seed mass information are discarded, which will be an important area for future research. Admittedly, measurements of seed shape and size affect only the first important step in seed persistence, so it may be surprisingly instructive for future seed retention.

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