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Paleozoic Seed Bank and Their Ecological Significance

Petra Seka Yehnjong
East Tennessee State University

Paleozoic Seed Banks and Their Ecological Significance

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by

Petra Seka Yehnjong

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Dr. Christopher Liu, Chair

Dr. Michael Zavada

Dr. Thomas Jones

Dr. Istvan Karsai

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ABSTRACT

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Soil seed banks are a reservoir of viable seeds present in the soil in plant communities. They have been studied and characterized in various ways in different habitats. However, these studies are limited to modern seed banks. This study extends seed bank studies to the Paleozoic Era. It was hypothesized that size distribution and seed density in Paleozoic seed banks exhibit similar patterns as in modern seed banks. Seed sizes and seed density of fossil seed from Wise Virginia were estimated. Modern seed bank information was obtained from published data. Data were analyzed using one-way ANOVA and Kruskal-Wallis test. The Paleozoic size distribution was predominated by larger seeds and the estimated seed density of 19 200 seeds m^{-3} falls within the range of modern seed banks but at a higher end of modern seed bank densities. During the Paleozoic they were sufficient to insure regeneration of these economically important forests.

DEDICATION

I dedicate this work to God Almighty who supplies me with abundant strength, discernment, and wisdom for all my academic accomplishments. May He forever be glorified. Most importantly, I dedicate this thesis to my parents Mr. Yenwong-Fai Napoleon and Mrs. Yenwong-Fai Odilia for their interest and investment in my education, especially facilitating my venture to pursue this masters degree in Biology at East Tennessee State University. Finally, I dedicate this work to my brothers, their wives, and my grandmother whose support and encouragement made this work a success.

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I appreciate the Department of Biological Sciences at East Tennessee State University for giving me Graduate Assistantship to support my graduate study and this research. It was an honor and a big opportunity to be a laboratory instructor for undergraduate laboratory course which has given me lots of experience.

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CHAPTER 1

INTRODUCTION

Soil Seed Banks

Soil seed bank is considered one of the most interesting areas in agricultural science, forest regeneration, and restoration ecology today. A soil seed bank represents a reservoir of viable seeds with preservative potential in many plant communities (Dessaint et al. 1997). Darwin (1859) observed seeds emerging from a soil sample from the bottom of a lake. This observation prompted further study on seed banks, its processes, and the evolution of seed plants. Many processes serve to bury seeds in plant communities. For instance, seeds are dispersed across floodplains and are eventually buried under sediments and organic debris by flooding waters (Xiong et al. 2001). Soil drying, cracking, soil freezing and thawing, and animal activities contribute enormously to seed burial. Buried seeds can remain viable in the soil for a long period of time awaiting the development of ideal germination conditions (Baskin and Baskin 1998). Their emergence and recruitment may restore part of the original plant community. Some buried seeds, once part of the soil seed bank, may become fossilized with time and their study can provide pertinent ecological information about paleo-seed assemblages and the evolution of seeds in seed banks.

Seed plants are first recognized in the fossil record in the late Devonian (Rothwell and Schecker 1988) and originated from the progymnosperms. According to Hilton and Bateman (2006), these early seed plants gave rise to 2 branches. One branch led to the evolution of the Pteridospermophyta, Cycadeoidophyta, and Geophyte, and the other branch to the evolution of the Coniferophyta, Ginkgophyta, Cycadophyta, and Angiospermophyta. This latter branch consists of the main seed bearing plants living today. Among the extant seed bearing plants, gymnosperms have about 800 living species and angiosperms have approximately 250,000 living species (Cantino et al. 2007), and are observed in most modern seed banks. These taxa have seeds that vary in size, color, shape, seed coat thickness, and accessory structures, e.g., wings, parachutes, and internal air channels that aid in dispersal of the seeds. Angiosperms have evolved a variety of characteristics that fall well outside of the morphological diversity of seeds in the Paleozoic Era. Even though Paleozoic seeds have been studied (Arnold 1938; Harper et al. 1970), basic aspects of the seed banks (species composition, seed size, seed size distribution, seed bank density) associated with Carboniferous habitats that produced coal are not well known due to low sample size.

Basic Aspects of Soil Seed Banks

Seed Bank Composition

The species composition of a seed bank reflects the local plant community or vegetation that may span decades depending on the persistence of viability. Several studies have reported a lack of congruence between the species presents in the soil seed bank and the aboveground vegetation in different habitats such as grassland (Thompson et al. 1997), wetlands, and woodlands (Verheyen and Hermy 2001). The lack of similarity is due to the persistence of viability derived from the changes in local vegetation present at the site over decades. For instance, high densities of *Calluna vulgaris*, *Carex pilufera*, and *Funcus spp* found in the soils of conifer plantations (Hill and Stevens 1981), but absent in the aboveground flora, originated from the heathland vegetation preceding afforestation. In addition, the general lack of correspondence between seed bank species composition and current vegetation in temperate woodlands is a result of loss of light requiring early successional species (these species require light for establishment due to a little amount of reserved energy in their seeds) from the current flora but remain viable in soil (Thompson and Grime 1979). Soil seed bank composition varies from one ecosystem to another, and even ecosystems with similar vegetation community have considerable differences in their composition. Not every plant found in the community produces seeds that are preserved in the soil. This is evident in fossil record because only a fraction of seeds produced are preserved. Although a number of studies have revealed differences in the soil seed bank species composition and standing vegetation, in highly or frequently disturbed habitats such as arable fields are usually similar. Likewise, there is a high congruence of the old temperate deciduous forest (Leckie et al. 2000) and some European forests (Olano et al. 2002; Wodkiewicz and kwiatkowska-Falinska 2010; Abella and Springer 2012). This congruence may be found in seed banks in the present study of mature Carboniferous swamp forest.

Seed Size

Seed size is considered one of the least plastic components in plants although it varies greatly (Harper et al.1970). Seed size variation is observed among plants, within plants, and in different communities, as well as different localities. In the temperate zone, differences between communities account for approximately 4% of the variation in seed size between species (Leishman et al. 1995). There is a larger difference in seed size between tropics and temperate zone. Nonetheless, the seed size variation within a habitat remains a major component in the variation among species. Mole et al. (2005) demonstrated that the greatest divergence in the seed size (mass) is between angiosperms and gymnosperms and together with other divergences led to the wide range of seed sizes observed today. Erickson et al. (2000) on the other hand revealed that the wide radiation of angiosperms is due to changes in community composition and structure and not emergence of seed dispersers. However, new evidence point out that seed dispersal syndromes have a role to play in seed size changes over time (Eriksson 2008)

Seed size variation is well documented in literature (Harper et al. 1970; Leishman and Westoby 1994; Vaughton and Ramsey 1997). Variations within species are thought to be more or less constant but increasing numbers of studies have reported differences within species about 4 fold (Vaughton and Ramsey 1997, 1998). Among species variation span over 10 orders of magnitude with a remarkable range of seed weight from a tiny seed of Orchidaceae through a double coconut seed *Lodoicea seychellarum* approximately 10000g (Harper et al.1970; Westoby 1994). These variations within and among species have been linked to the environmental conditions under which species establish new growth and successional stages in various habitats (Gross 1984). Species from mature habitats and late successional stages have higher average seed mass/size than species from an open habitat and early succession stages (Mazer 1989). Because shaded conditions favor the establishment of larger seeds, their productivity is a function of increasing seed size (Venable and Brown 1988). In partially open or shaded habitats due to some disturbance (Reader and Buck 1986), small seeded plants have greater variability of success in space and time. Larger seed plants have high reproducibility and survivorship in shaded or closed habitat, especially the forest (Salisbury 1942). The wide range of seed sizes in the forest is also reflected in the soil seed bank but narrower than what is observed in the above ground vegetation in different habitats. Persistent seed bank have shown to be composed of small, round compact seeds (Thompson et al. 1993), but this trend is not observed in Australia where persistent seeds are neither smaller nor compact in comparison to transient seeds with seed mass ranging from 0.000217g to 0.6489g (Leishman and Westoby 1994). Several studies on modern seed banks of different habitats have similar seed size pattern (Thompson et al. 1993;

Mole et al. 2000; Peco et al. 2003; Cerabolini et al. 2003). Most of these plant communities reveal the mixture of transient and persistent seed banks demonstrating the heterogeneity of seed size in seed banks. Paleozoic seed size and size distribution studies from fossil deposits (mostly from Euramerican coal belt) show a gradual increase in seed sizes from the origin of seed plants in the Devonian to the Permian (Sims 2012).

Seed Density

Seed density, expressed as number of seeds per unit square meter or cubic meter, varies from one sampling area to another. According to Thompson (1987), the densities of buried seeds declined with increasing altitude, latitude, and successional age. The number of seeds in a seed bank depends on seed mass and the habitat. Small seeds with smooth seed coats are capable of forming persistent seed banks. Large seeds that are ornamented, i.e., equipped with hooks, awns, spines, and other projections on their seed coat have greater probability of forming transient seed banks. Nonetheless, relatively large seeded species (*Gallium palustre*, *G. saxatile*, *Potentilla recta*, and *Trifolium repens*) form persistent seed banks (Thompson and Grim 1979). Transient seed banks with large seed mass probably will have few numbers of seeds per m^2 than persistent seeds banks with small compact seeds. Buried seed densities vary widely, with rather low densities beneath subartic and artic forest soils, mature tropical forest (Hall and Swaine 1980), grasslands of Europe and North America, and mature temperate woodlands (Kramer and Johnson 1987). However, larger seed banks have been documented in grasslands where arable farming has occurred previously (Schenkeveld and Verkaar 1984). Likewise, high seed densities are found in soils of disturbed or agricultural lands in the tropics (Young et al. 1987). Much higher densities are encountered beneath disturbed habitats such as arable fields, heathlands, and some wetlands (Leck et al. 1989). The seed density of Paleozoic seed banks may fall within the range of modern wetland seed bank density because Carboniferous forests have been reconstructed as a swampy forest that led to the formation of most coal deposits mined today (Gastaldo et al. 2004). The physical setting of ancient wetlands resembles the modern swamp environment despite the variation in plant communities.

Ecological Significance of Soil Seed Banks

Seed banks, natural storage of seeds within soils, play a key role in the regeneration and restoration of plant communities (Thompson and Bakker 1997). For instance, a rapid revegetation of disturbed sites by wildfire, catastrophic weather, agricultural operations, and timber harvesting is largely due to the soil seed bank. The restorability of communities from a disturbance is determined by presence or availability of viable seeds in a seed bank with potentials to stabilize ecosystem processes under variable environmental conditions (Bekker et al. 1998). The forest and wetland ecosystems have specialized or functional species that produce seeds that persist in the soil until favorable conditions for germination and establishment occur. The recruitment of some new individuals of some trees, especially early successional species, depends on the seed bank. Because the restoring ability of vegetation during primary and secondary successions depends on the absence or the presence of viable seeds in soil seed banks, their absence greatly hampers the establishment of vegetation during primary succession (Van der valk 1981), while their availability enhances rapid development of species rich ecosystem during secondary succession. For example, an annual plant with no seed bank would become extirpated on the first occasion that either reproduction or establishment fails completely.

Some studies have discovered that the seed banks play an important role in colonizing small disturbances, while others found that this role is negligible (Thompson 2000). Although seed banks are very important in regeneration of vegetation communities, they are of little importance in restoring the entire plant community. In most studies the above ground vegetation and the soil seed bank strongly differ in their species composition and proportions of species abundance (Hopfensperger 2007; Wellstein et al. 2007). Studies done on temperate salt marshes reveal seed bank containing mainly annual species and the dominant perennial species in the vegetation absent in the seed bank (Egan and Ungar 2000) support this assertion. These differences reflect the importance of individual species' life histories in determining the extent to which they become incorporated in seed banks (Thompson 1987).

Seed banks are important in the recovery of endangered plant species and supposedly extinct species. For example the germination of *Viola persicifola* from the soil samples of Cambridgeshire, where it has supposedly been extinct for 60 years (Rowell et al. 1982), reveals the recovery ability of seed banks. Therefore, a soil seed bank has a potential of restoring endangered species, bringing back to life species thought to have been extinct and changing the vegetation of the ecosystem. The seed banks may also be vital in the reconstruction of the past vegetation if these seeds are correctly described, identified, and named. For example knowledge of type of seeds in the Paleozoic seed bank will give useful information about seed plants that inhabited that area.

The purpose of this study is, 1) to determine the characteristics of Paleozoic seed bank, 2) to make comparisons between extant and the Paleozoic seed banks, and 3) to understand the ecological significance of these patterns. To be able to accomplish this, the following questions must be answered.

1. Which Paleozoic seed bank characteristics can be evaluated?
2. How do these preserved characteristics compare to extant seed banks and what are their ecological implications?

Data on fossil seeds were recovered from exposures of the Wise Formation in the Blackwater Coal Mine; southwest Virginia. Data from extant soil seed banks (angiosperms and gymnosperms) were used to test the following hypotheses:

1) Size distribution of seeds in the Paleozoic seed bank exhibit the same average and range distribution as extant seed banks. This should be the case because seed incorporated into the soil is influenced by seed size. In modern seed banks smaller seeds make up the greater portion because they easily crack their way down into the soil.
2) Paleozoic seed banks resemble modern seed banks with regard to frequency distribution of seeds per unit volume. Paleozoic swamps and the modern wetlands have the same setting but are occupied by different seed producing taxa, the density of seeds in the seed banks should be the same.

CHAPTER 2

MATERIALS AND METHODS

Site Description

Geology

Virginia is well known for coal production. Coal deposits here occur in 3 areas: Richmond and Farmville basins (Triassic), Valley coal field (Mississippian), and southwest Virginia coal field (Pennsylvanian) (Henderson 1979). The southwest Virginia coal field is the source of all current production in Virginia and ranges from high- to low-volatile bituminous coal. The coal-bearing strata are generally horizontal to gently dipping. The formations in southwest coal field in ascending geological age order are: Pocahontas Fm., Lee Fm., Norton Fm., and Wise Fm. These formations are composed of sequences of nonmarine coal, sandstone, siltstone, shale, and are occasionally intercalated with thin clastic, calcareous sediments of marine origin. The plant rich Pennsylvanian sediments in Ohio belong to the Pottsville and Allegheny Groups. These sediments are comprised of sandstones, limestones, shales, and coals and are both of terrestrial and of marine origin. The coal peel samples and processing were done by Thomas N. Taylor from the University of Kansas, Lawrence, Kansas.

The seed bearing sediments from southwest Virginia (Wise Formation) are believed to represent autochthonous deposition because of the following phenomena:

1. The sediments are unsorted;
2. The seeds are randomly oriented;

3. The range of seed size is highly variable and comparable to the range of sizes observed in the autochthonous assemblage of seeds from the Pennsylvanian coal balls of southeastern Ohio(see Fig 1)

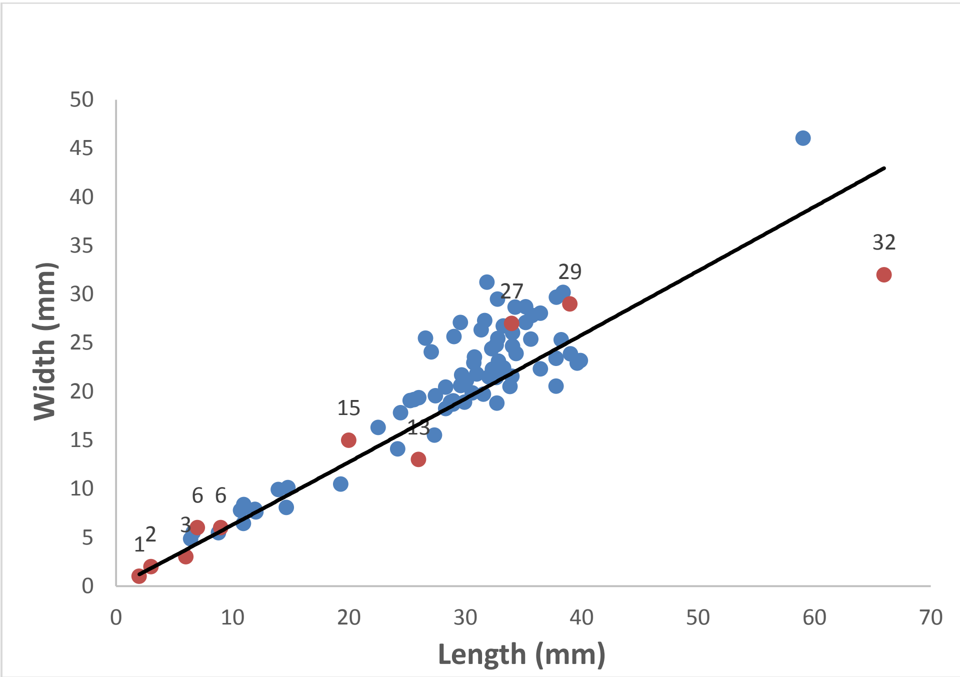

Fig 1. A graph showing the size of fossil seeds from southwest Virginia and structurally preserved and identified seeds from coal balls in Ohio. The blue dots represent fossil seeds, while the red represent known or structurally identified seed fossils from Ohio.

Fossil Seed Collection and Measurements

Paleozoic seeds used in this study are from the Wise Formation in the southwest Virginia coalfield. The seeds were gathered from the matrix of sediments along with seeds in situ during mountain top mining operations at the A&G Coal Corp., Black mountain, Virginia by Bo Tussing of Wise, Virginia. A total of 77 seeds were excavated from the matrix, cleaned, and labeled. Coal balls collected from Pennsylvanian sediments of southeastern Ohio were processed to obtain acetate peels of the structurally preserved seeds. All samples and processing were done in the lab at the Thomas N. Taylor, University of Kansas, Lawrence Kansas.

The fossil seed dimensions, viz: length (a), width (b), and breadth(c), were measured using a digital caliper with 0.1mm precision. The volume (V) was estimated as an ellipsoid base on the seed dimension measurement using the formula $V=4/3\pi abc$ (Tiffney 1984; Erickson et al. 2000; Sims 2012). Tiffney (1984) documented a log-linear relationship between the dry weight (grams) and the volume (mm^3) of modern angiosperm seeds (n = 52 species, R^2= 0.928). This relationship has not been evaluated in modern gymnosperms. This log-linear relationship provides a method for estimating the fossil seed weight. Direct weight measurement of fossil seeds is meaningless to paleobotanists because of the permineralization. The frequency distribution of the seeds per cubic meter of soil is determined using counting method and its volume by the water displacement method. In this method a volume of water (initial water level) is poured in a beaker and a chunk of rock containing fossil seeds is placed in it gradually to prevent splashes. The volume (final water level) comprising of water and the seed will be recorded and the volume of the sample is determined using the formula below;

Volume of the sample = final water level – initial water level.

Modern Seed Weight Measurements

Tiffney (1984) measured the seed size of angiosperm seed using the volume. He tested the assumption that volume and weight are related in seeds using 52 angiosperms and found a positive correlation. This relationship remains unknown in gymnosperm and pteridosperms. In order to test the assumption, seeds of 64 gymnosperm species from 8 families were obtained as donations from West Virginia University herbarium in Morgantown, Montgomery Botanical

Center of Cycad, Tim Thibault (curator of woody collections, the Henry E. Huntington Library & Art Galleries), USDA forest services and US National herbarium at Smithsonian institution. The weight of seeds was measured using scale balance mettle Toledo with 0.00001g precision. There is great confusion in the literature about the accurate definition of seed, as a result I used the term to refer to "any potential unfertilized dispersed ovule of basal spermatophyte or fertilized ovule of angiosperms" (Hillman and Bateman 2006; Sims 2012). All the weight data are dry weights. For each plant species, seed mass was the average of 10 seeds. More seeds were used when available especially for species with lower seed mass (e.g. for some species, in lots of 100 seeds). Seed length, width, and height were measured for 10 seeds per species and volume computed using the Ellipsoidal-ovoid volume estimation. Before the application of Ellipsoidal volume estimation, the sphericity index of seeds was determined according to Mohsenin (1986) who expressed the degree of sphericity as follows:

$\Phi = (ABC)^{0.333}) /A \times 100$

Φ represents sphericity index

A, length of seed

B, width of seeds

C, breath

The sphericity index of above 50% was regarded as more or less spherical and the ellipsoidal-ovoid volume method was then applicable. The collection was not limited to the species native to temperate zone.

Modern Seed Bank and Data Collection

Modern seed banks included in this research are those with published species composition and seed density. Seed weights of species occurring in modern seed banks were downloaded from the Royal Botanic Gardens Kew Seed Information Database (SID) (Royal Botanic Gardens Kew 2008) and the species whose weight could not be found were eliminated from this study.

Paleozoic Seed Density Determination

The seed bank density is one of the most interesting seed bank characteristics and can be determined by measuring the volume of chunks of rock containing seeds using water displacement method as described and then counting and recording number of seeds per volume of the chunk. The mean seed density/volume was determined using the formula below.

$$Ave. seed\ density = \frac{\#\ of\ seeds\ 1 \quad + \quad \#\ of\ seeds\ 2 \quad + \quad \#\ of\ seeds\ 3}{Volume\ (mm)\ 1 \quad + \quad Volume\ (mm)\ 2 \quad + \quad Volume\ (mm)\ 3}$$

A good estimate of the number of seeds in the chunk is determined by counting the number of well-preserved seeds in it. Estimated density on the ground surface is determined using simple proportion and conversion. For example, if there are 2 seeds/ 1000cm^3(2seeds/0.001m^3) present in the total chunks of rock, density in the field will be 2000seeds/1m^3. The seed density is reported as number of seeds per unit volume, as is traditional/customary for seed bank density to be given in seeds/unit area in most seed bank studies

Statistical Analysis

To test the assumption of a linear relationship between seed weight (g) and volume (cubic mm), we used the log-linear regression model using excel 2013.

To determine the similarity in seed size distribution and seed density between the Paleozoic seed bank and modern seed banks, the seed weight data for the different seed banks were subject to Kolmogorov-Smirnov test for normality and those that failed to show normal distribution were normalized by log-transformation. The nonparametric test (Kruskal Wallis test) was applied to data that were not normally distributed after data transformation. One-way ANOVA was used for normally distributed data and then post-hoc comparisons using the Tukey test. All analyses were performed using Statistical Package for the Social Sciences software (SPSS ver. 21)

CHAPTER 3

RESULTS

Relationship between Weight and Volume of Modern Gymnosperm Seeds

A regression of weight against volume of seeds of 64 modern gymnosperm species gives R^2 = 0.8204 revealing a positive correlation between these two (see Fig 2). The assumption that there exists a linear relationship weight and volume of seeds is accepted based on R value in this study value (R^2=0.928) from regression of weight versus volume of 52 propagules of extant angiosperm species in Tiffney (1984). The positive correlation provides the bases for estimating the fossil weight from the regression line equation ($Y=9030.3x^{0.8926}$)

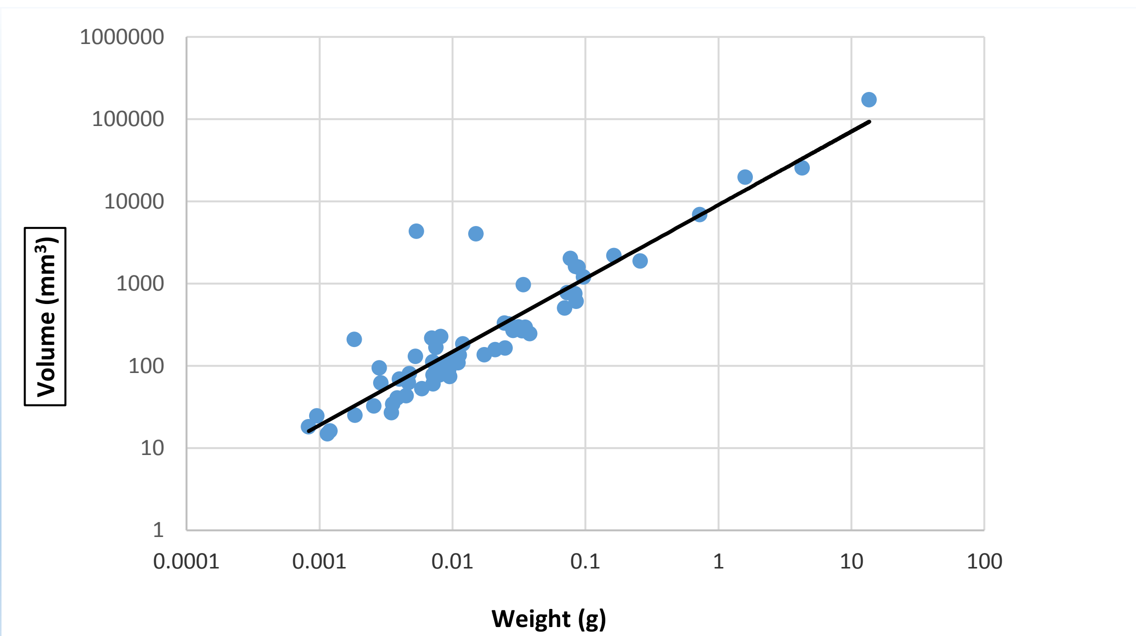

Fig 2. Log-log plot of weight against volume of seeds of 64 gymnosperm species. *Zamia loddigessi* and *Zamia paucijuga* appear as outliers

Normality Test for Weight Data Distribution

Test for normality was performed on both the Paleozoic and modern seed banks using Kolmogorov-Smirnov test (Normality check is important to determine the statistical method that will be used or whether data need transformation before analysis.). This test indicates that the dataset from Paleozoic seed bank and modern seed bank are not normally distributed (all *p*-values > 0.05) except data from Black mountain mine in Virginia (p = 0.168, n = 76). All nonnormally distributed data were log transformed prior to analysis to restore the data to normality (see Table 1). Three of the modern seed banks were not restored to normality after log transformation, tall grass prairie Illinois (p= 0.017, n=26), Werrington park estate (p = 0.026, n = 32.), Mount Hilaire (p = 0.008, n = 28). Although the Levene test was not significant, Tukey test was used for comparing size distribution in different seed banks according to Leech et al. 2011.

Table 1 Normality test for seed weight data distribution in modern and Paleozoic seed banks. The number of species is represented by n except Paleozoic seed bank Virginia whose species content was not determined (n for Paleozoic seed bank (Virginia) represent number of seeds). Kolmogorov-Smirnov was determined after log transformation of seed weight data.

Seed bank	n	Kolmogorov Smirnov	*p*
Paleozoic seed bank Virginia(PV)	76	0.086	0.200
Patuxent river, (PR)	13	0.195	0.191
Eagle lake (EL)	22	0.132	0.200
Hamilton marsh(HM)	19	0.164	0.190

Table 1 continued

Delaware river(DR	24	0.165	0.090
Riverine swamp(RS)	38	0.107	0.200
Mount St. Helens (MH)	15	0.163	0.200
Spring-Fed Marsh(SFM)	17	0.143	0.200
Delta Marsh(DM)	11	0.149	0.200
San Francisco bay (SFB)	13	0.122	0.200
Cache river (CR)	17	0.199	0.072
Pampean Prairie (PP)	15	0.168	0.200
North Iowa Marshes (NIM)	28	0.084	0.200
Tallgrass prairie Illinois (TPI)	26	0.187	0.017
Tallgrass prairie, Missouri (TPM)	14	0.138	0.200
Mt hilaire (MH)	28	0.194	0.008
Koeni, Centra Estonia (KCE)	28	0.138	0.186
Le Nouvion Forest (LNF)	25	0.096	0.200
Meerdaal Forest (MF)	33	0.094	0.200
Yarner wood (YW)	10	0.254	0.066
longleat woods (LW)	17	0.110	0.200
Tavistock wood (TW)	18	0.115	0.200
Werrington Park estate (WPE)	32	0.165	0.026
Buckley woods (BW)	47	0.103	0.200
Sonian forest (SF)	29	0..101	0.200
KWS forest (KWS)	35	0.089	0.200

Table 1 continued

Kauri forest (KF)	32	0.130	0.186
Pinus ponderosa forest (PPF)	15	0.170	0.200
Coastal plain forest (CPF)	19	0.123	0.200
Afromotane forest (AF)	21	0.150	0.200

Soil Seed Bank Characteristics

Seed Size and Size Distribution

Fossil seeds from the black mountain mine form the Paleozoic seed bank in Virginia. This seed bank has seed sizes ranging from 0.0171g to 80.34836g with larger and heavier seeds predominating. This predominance of larger and heavier seeds pushes the average seed size to higher ends in this bank (see Fig 3 and 4). Of the 77 fossil seeds recovered, only 13 seeds have weight < 1g resulting in the under representation of smaller seeds. This produces size distribution that becomes increasingly right skewed. The seed size distribution in the modern seed banks is different from the distribution in the Paleozoic seed bank; therefore, the hypothesis that the seed size distribution in Paleozoic seed banks is similar to the average seed size distribution in extant seed banks was rejected based on the central tendencies (ANOVA), $F = 14.895$, $p < 0.001$). Similar results were obtained for modern seed banks with nonnormally distributed weight data (Kruskal Wallis test, $p < 0.001$). Multiple comparisons of seed banks using Tukey HSD post hoc test revealed that all modern seed banks are not significantly different from each other but different from Paleozoic seed bank (see Table 2)

Table 2 Multiple Comparison of seed banks using Tukey HSD. The numbers represent value for each comparison. The seed banks are written using their initials to ensure that all enter the table. This test excludes tall grass prairie Illinois, Werrington park estate, and Mount Hilaire due the lack of normality it the data

SB	PV	PR	EL	HM	DR	RS	MH	SFM	DM	SFB	CR	PP	NIM	TPM
PV		.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PR	.000		1.000	1.000	1.000	1.00	1.000	1.00	1.00	1.000	.979	1.000	1.000	1.000
EL	.000	1.000		1.000	1.000	1.00	1.000	1.00	1.00	1.000	.949	1.000	1.000	1.000
HM	.000	1.000	1.000		1.000	1.00	1.000	1.00	1.00	1.000	.997	1.000	1.000	1.000
DR	.000	1.000	1.00 0	1.000		1.00	1.000	1.00	1.00	1.000	.936	1.000	1.000	1.000
RS	.000	1.000	1.000	1.000	1.000		1.000	1.00	1.00	1.000	.603	1.000	1.000	.999
MH	.000	.996	0.993	1.000	.990	.814		.998	1.00	1.000	1.00	1.000	1.000	1.000
SFM	.000	1.000	1.000	1.000	1.000	1.000	1.000		1.00	1.000	.982	1.000	1.000	1.000
DM	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00		1.000	.999	1.000	1.000	1.000
SFB	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00		.999	1.000	1.000	1.000
CR	.000	.783	0.648	.931	.597	.151	1.000	.803	.972	.978		.936	.975	1.000

Table 2 continued

PP	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.997		1.000	1.000
NIM	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.998	1.000		1.000
TPM	.000	1.000	1.000	1.000	1.000	.999	1.000	1.00	1.00	1.000	1.00	1.000	1.000	
KCE	.000	1.000	1.000	1.000	1.000	1.00	1.000	1.00	1.00	1.000	.902	1.000	1.000	1.000
LNF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.992	1.000	1.000	1.000
YW	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.999	1.000	1.000	1.000
LW	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	1.00	1.000	1.000	1.000
TW	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	1.00	1.000	1.000	1.000
BF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	1.00	1.000	1.000	1.000
SF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.848	1.000	1.000	1.000
KWS	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.761	1.000	1.000	1.000
KF	.000	1.000	1.000	1.000	1.000	1.000	.670	1.00	1.00	1.000	.083	1.000	.990	.984
PPF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.464	1.000	1.000	1.000
CPF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.938	1.000	1.000	1.000
AF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.950	1.000	1.000	1.000
MF	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.000	.918	1.000	1.000	1.000

Table 2 continued

Seed Bank	KCE	LNF	YW	LW	TW	BF	SF	KWS	KF	PPF	CPF	AF	MF
PV	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PR	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EL	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
HM	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DR	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
RS	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MH	1.000	1.000	1.000	1.000	1.000	.976	0.914	.999	.650	.982	.991	.937	1.000
SFM	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DM	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SFB	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
CR	.878	.962	.998	.995	996	.402	.283	.743	.083	.607	.646	.374	.918
PP	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
NIM	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 2 continued

TPM	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.994	1.000	1.000	1.000
KCE		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LNF	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
YW	1.000	1.000		1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LW	1.000	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TW	1.000	1.000	1.000	1.000		1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000
BF	1.000	1.000	1.000	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000
SF	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000
KWS	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.00	1.000	1.000	1.000	1.000
KF	1.000	.998	1.000	.999	.997	1.000	1.000	1.000		1.000	1.000	1.000	.996
PPF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000	1.000
CPF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000
AF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
MF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	

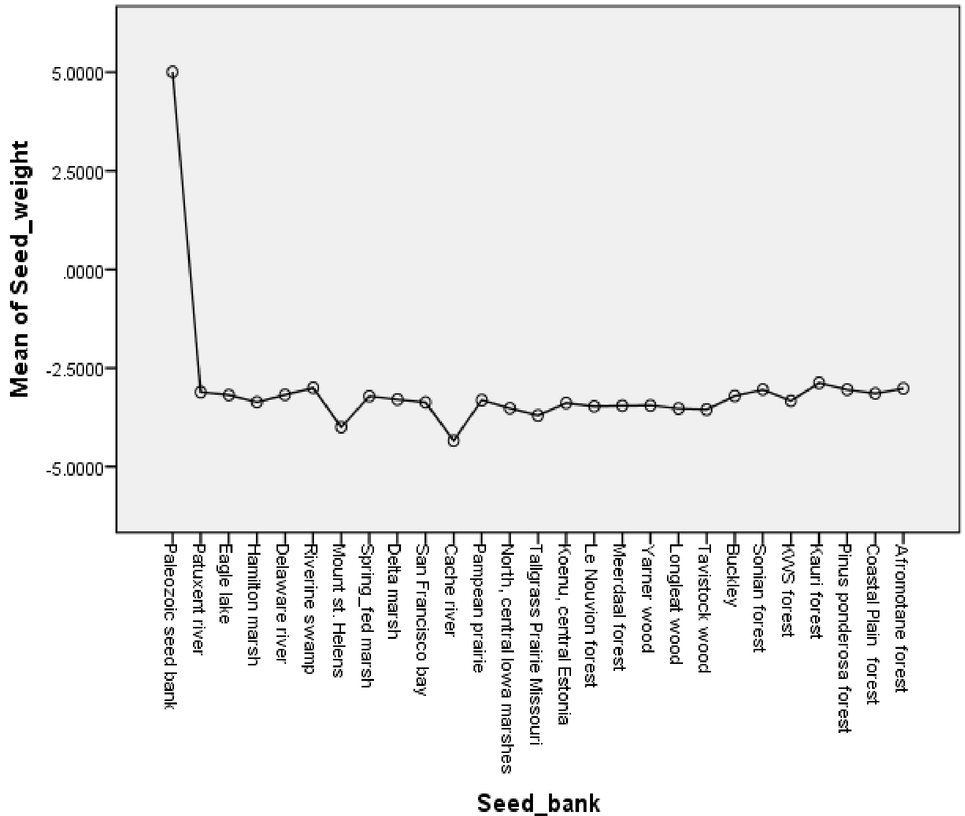

Fig 3. Mean plot of average seed size distribution in Paleozoic seed bank and Modern seed bank using log transformed data except Paleozoic seed bank

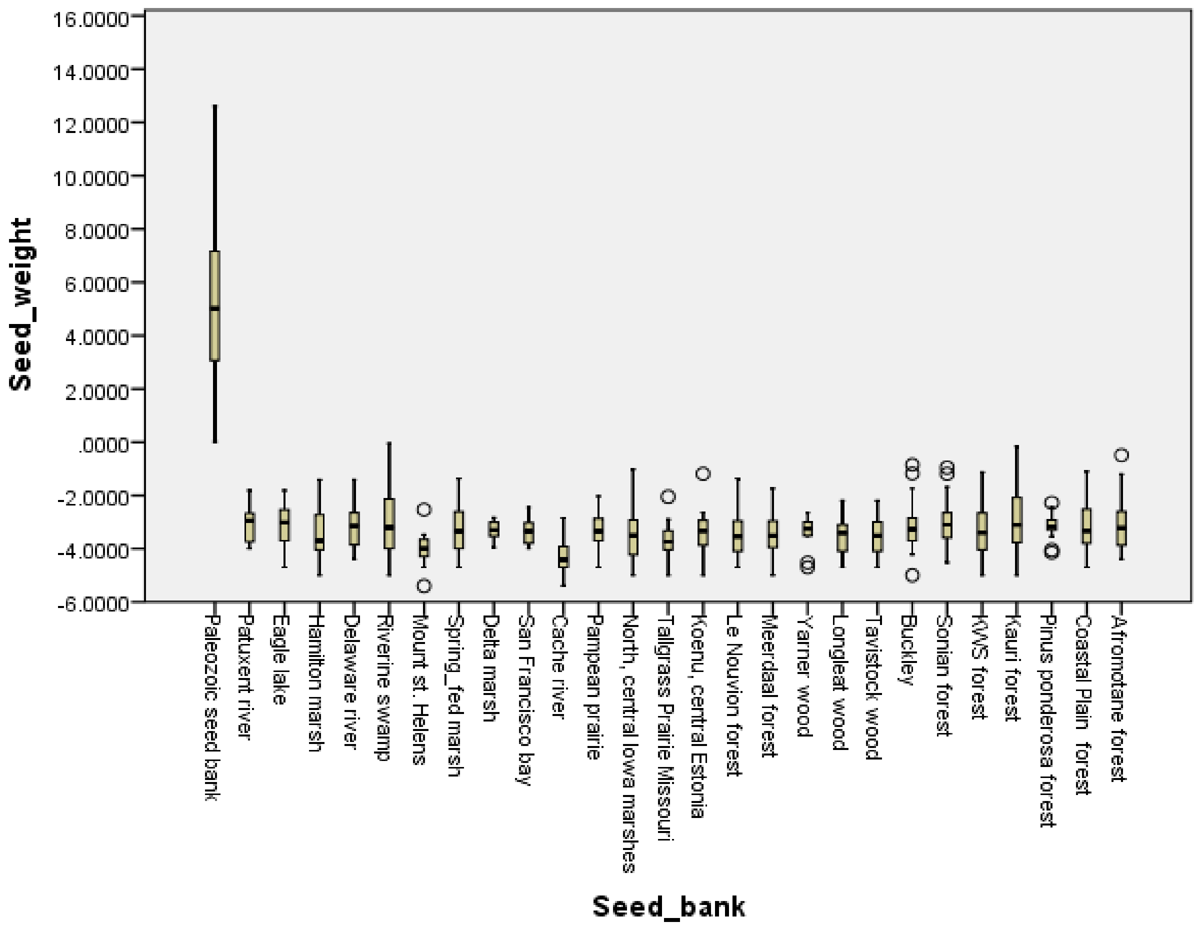

Fig 4. Boxplot of seed size distribution (log transformed data) in seed bank showing outliers. Some very bad outlines were removed.

Seed Density

The average seed density of modern seed banks range from 262 seeds m^{-2} to 50 060 seeds m^{-2} with the highest seed density occurring in woodland (see Fig 5). The seed density among seed banks from different habitats is not significantly different (Kruskal Wallis, p = 0.086). This is evident by the boxplot because the range of seed densities in each habitat overlaps that of the other habitats (Paleozoic seed density had just a single data point represented as an average).

The estimated Paleozoic seed bank of 19 200 seeds m^{-3} (it's assumed that cubic meter represent the area (length and width) X depth which makes it comparable to seed banks given in unit meter) from seed count method falls within the range of modern seed banks but at a higher end of extant seed bank densities. Forest habitats have the lowest average seed density, while the woodlands have the highest. Woodland and forest have been shown in modern seed studies to have low seed densities (see Table 3). The extreme high seed density in one of the woodlands is probably due to a disturbance phase which could be farming or logging producing high seed density made up pioneer species with little or no woody or forest species.

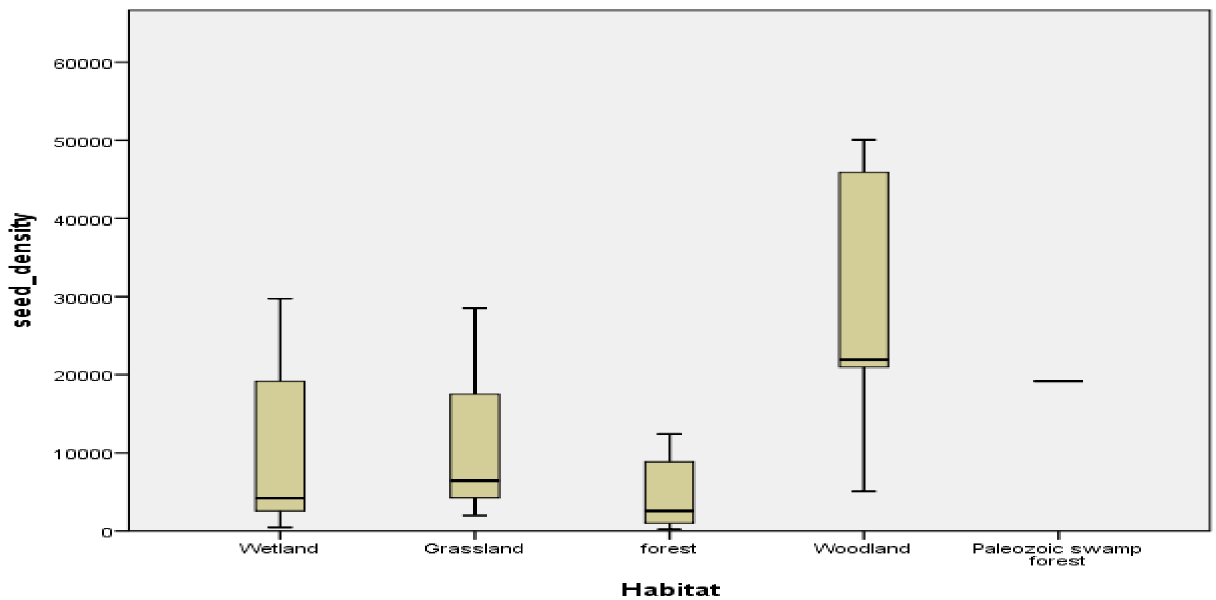

Fig 5: Box plot of seed density and habitat. Seed banks in river, marshes, and swamps were placed in wetland habitat. The Paleozoic seed density is shown as a line because it has just a single value

CHAPTER 4

DISCUSSIONS

Seed Bank Characteristics

Seed Size and Size Distribution

The results of this study reveals that Paleozoic seed banks have larger seeds (much larger than transient seeds in modern seed banks) compared to the modern seed banks composed of angiosperms and gymnosperms (colonizers or pioneer species). Most modern seed banks are composed of lineages with small-seeded species driving the average seed size to lower end of the seed size spectrum despite wide range of seed sizes in plant communities that produced these seed banks (Harper et al. 1970; Harper 1977) in modern plant communities. The size distribution of seeds in modern seed banks in this study is not significantly different between each other ($p > 0.05^*$) (see Table 2). This trend is attributed to the fact that small seeds are capable of incorporating into the soil profile more easily than large seeds (Thompson et al.1994; Bekker et al. 1998). Moreover, small-seeded species have persistent seeds than transient seeds (1.08g - 0.000 04g), although this trend is absent in Australia with persistent seeds not smaller and compact than transient seeds (Leishman and Westoby 1998; Mole et al. 2000). They have also developed strategies to avoid processes that impede penetration into the soil and as such persist until a disturbance event brings them back to the surface because they have little resources that are quickly exhausted and require the young plant to start photosynthesis (high light) to ensure the survival of the seedling (Foster and Janson 1985).

The variation among Paleozoic seed bank and myriad modern seed banks fail to support the hypothesis that seed sizes across different seed banks are same. The range of fossil seed size in the Paleozoic seed bank of Virginia is wider but predominated by larger and heavier seeds with the central tendency shifted to higher end of seed size spectrum. Although modern seed banks have the coexistence of both persistent and transient (transient seeds are believed to be larger), their average seed sizes are still at the lower end of the size spectrum compared to the Paleozoic seed bank (Virginia). This large seed size range does not necessarily suggest that it represents all of the seed sizes produced by Paleozoic seed bearing taxa. The full seed size spectrum in the Paleozoic flora may not be preserved in the death assemblage and seed size may vary between Paleozoic habitats as it does in the modern seed banks. Studies have shown taphonomic biases in preservation in fossil record because only a fraction of organisms that have lived at that time may be preserved (Lawrence 1971). Sims (2012) revealed that Pennsylvanian period (late Paleozoic) had greater preservation completeness and low preservation probability for small seed lineages than larger seeded lineages, but structurally identified seed fossils from Ohio coal ball have roughly similar proportion of small to large seeds. It is been shown that earlier seed lineages had relatively smaller seeds and subsequently evolved larger seed lineages. The declination in taxonomic diversity in the small seeded species became evident with radiation of larger seed lineages (Medullosales) by mid and late Pennsylvanian. Seed size distribution became increasingly left-skewed with evolution of larger seed lineages throughout Pennsylvanian (Sims 2012). This partly explains seed size distribution in the Paleozoic seed bank (Virginia).

There are many other possible explanations for the predominance of large seeds in this ancient seed bank. First of all, the prevalence of larger seeds suggests formation of the seed bank from a closed canopy habitat (k-selected strategies) that is more stable (Baker 1972). It's been observed that Pteridosperms broadened in the role of local canopy dominance during

Pennsylvanian period. For instance, Medullosans were characterized by large seeds, large prepollen grains, and generally low reproductive output; this suggests K-selected reproductive strategies (DiMichele et al. 2006). Secondly, the preponderance of large seeds in the Paleozoic seed bank may have selected to reduce the effects of insect predation. Insect predation is the major type of predation during this time (Pennsylvanian) revealed by their mouthparts (related to their feeding habit) and insect plant associations. The evidence of these insect plant associations includes sucking and piercing pteridosperm prepollen organs (Labandeira and Phillips 1996; Labandeira 1998), borings in pteridosperm stems and petioles, external feeding pteridosperm foliage. (Labandeira and Phillips 1996). The earliest indication of seed predation are circular holes in Trigonocarpus from the Early and Mid-Pennsylvanian of Illinois and England (Scott & Taylor 1983). There is some evidence that seed predation rate is related to seed size. Hughes et al. (1994) found that seeds larger than 0.1g tend to be adapted for dispersal by vertebrates and seeds smaller than 0.0001 g tend to be unassisted, but between 0.0001g and 0.1g many dispersal modes are feasible (wind, insects). Reader (1993) in an experiment to observe the effect of predation in seedling emergence, noticed that adding a cage to reduce seed predation had a significant increase in the emergence of larger seeds (0.000 15g – 0.0122 g). The seed sizes in Paleozoic seed bank are far larger than the larger seeds described in most modern seed banks, and this large size could have been an excellent weapon against insect predation. Large seeds tolerate rather than succumbing to seed predators by satiating them before they damage the embryo. Moreover, maternal investment of resources in the endosperms or cotyledonary tissues above the minimum requirement is an insurance against destructive seed predators (Mack (1998). Insect predation is diminished in larger seeds because damages do not preclude the germination of the seed (Ulft 2003). Studies of seed predation have found that rodents, birds, and other mammals have preference on larger seeds (Westoby et al. 1992), but large animal predation that could have had such preference is almost nonexistence during this era. Finally, the prevalence of large seeds in Paleozoic seed banks might be a strategy to effectively capture space in little gaps over short term due to large stored resources (Rees 1996; Turnbull et al, 1999; Nathan and Landau 2000;Yu 2007;). Studies have revealed that large nutrient reserves in large seeds have an advantage during seedling establishment especially in habitats with limited light conditions (Foster 1986). This suggests that Paleozoic swamp forest that led to the formation of this seed bank had tiny gaps to maintain the viability of these large seeds and subsequent germination since large gaps and long term exposure may result in desiccation (Foster1986)

There seem to be a decline in seed size in seed bank over time (see Fig. 4) but seed size and seed size distribution in Mesozoic seed banks are unknown. Mesozoic seed bank studies should be carried out to provide this useful information.

Seed Density

Seed density has been shown to vary between habitats and even within same habitat but the results of this study reveals that there is no significant difference in seed densities among habitats ($p = 0.074$). The modern seed bank habitats used in this study include wetlands, grasslands, forest, and woodlands. These habitats have been reported to have low seed densities (Hall and Swaine 1980; Kramer and Johnson 1987). Although the seed densities within these habitats vary, their distribution is not significantly different (See Table 6 and Fig. 5). The Modern seed bank with the highest seed density is longleaf woods, South-West England (50 060seedsm^{-2}). Woodland has been reported to have lower seed densities but logging or disturbance in these habitats may result in high seed densities. Paleozoic seed banks are at the high end of seed densities within a given seed bank (19 200seedsm^{-3}) especially wetland and grasslands. Paleozoic community that led to the formation of this seed bank has been reconstructed as wetlands and some wetlands and grasslands have been reported to have high seed densities (Leck et al.1989). The high seed banks in these wetlands is due to disturbance events such as flood pulsing (Middleton 1999). This high seed density suggests that the Paleozoic swamp forest could be regenerated. Many Paleozoic coal swamps were coastal and may have been exposed to disturbance e.g., storms or storm surges. In addition, fires appear to be common.

CHAPTER 5

CONCLUSIONS

The seed size distribution in the Paleozoic seed bank reveals a predominance of large seeds. The predominance of large seeds may be attributed to closed canopy forest with K-selected species that form a stable community. The large seeds and their associated food reserves may have increased longevity of the seed in the seed bank that was necessary in these highly stable environments. The larger seeds provided nutrients to capture space in a highly competitive environment when small forest gaps were formed. The larger seeds reduced the damaging effects of insect predation satiating the insects and reducing the chances of damage to the embryo. This strategy would be most successful in the absence of large predators. The high seed density could have be sufficient to restored, if not all, part of the Carboniferous forests (reconstructed as dense, wet forests) that led to the formation of most commercial coal deposits mined today The Paleozoic seed bank has a combination of characteristics that make sense in the context of the Paleozoic. Although these seed bank characteristics would continue to be modified with the diversification of plants and animals through time, during the Paleozoic they were sufficient to insure regeneration of these economically import

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APPENDICES

APPENDIX A

Measured and Estimated Fossil Seed Data from Southwest Virginia and Ohio

Table 3: Fossil seed measurements and fossil seed weight estimates using in regression line equation(Y=11990X)

Fossil seeds Virginia	Average length (mm)	Average Width (mm)	Average Breadth (mm)	Sphericity Index	Estimated Volume (mm^3)	Estimated seed Weight
1	-	-	-	-	-	-
2	59.045	46.03	39.81	80.39164	452 985.8792	80.3483
3	11.795	7.74	6.79	72.1341	2595.2372	0.2474
4	19.325	10.49	7.455	59.2382	6327.1921	0.6713
5	14.765	10.11	3.77	55.7988	2356.1034	0.2220
6	6.425	4.865	3.075	71.186	402.4107	0.0307
7	10.95	6.43	3.84	58.9423	1131.9434	0.0976
8	10.995	8.36	4.385	67.0492	1687.4833	0.1527
9	6.635	5.515	1.56	57.9532	238.9898	0.0171
10	10.7	7.77	3.64	62.6265	1266.9940	0.1108
11	13.96	9.915	4.43	60.7267	2567.1441	0.2444
12	12.04	7.63	6.74	70.6393	2592.2645	0.2470
13	14.635	8.085	7.53	65.6014	3730.2343	0.3714

Table 3 continued

14	11.935	7.875	6.68	71.5915	2628.5596	0.2509
15	8.815	5.48	4.74	69.2763	958.6269	0.0810
16	32.895	21.89	10.995	60.4080	33 146.62162	4.2923
17	38.25	25.32	21.385	71.5591	86 710.7176	12.6059
18	32.67	24.795	17.37	73.6613	58 908.9728	8.1748
19	34.315	28.675	11.805	65.7929	48 631.96367	6.5948
20	39.63	22.915	9.555	51.6957	36 328.1272	4.7564
21	31.575	19.705	10.8	59.5884	28 132.7339	3.5718
22	32.225	21.46	13.365	64.9256	38 695.4580	5.1050
23	35.21	27.1	20.91	76.7769	83 532.9336	12.0894
24	35.645	25.375	18.47	71.4854	69 942.3065	9.9085
25	31.015	21.79	14.615	68.9667	41 351.9715	5.4992
26	28.98	18.69	15.81	70.3835	35 851.5500	4.6866
27	24.215	14.105	6.405	53.4722	9158.9372	1.0160
28	28.335	18.23	14.585	68.9800	31 541.6715	4.0601
29	29.005	19.03	11.22	63.1294	25 928.2317	3.2598
30	37.835	20.535	12.055	55.5436	39 212.4560	5.1815
31	36.465	28.025	15.58	68.7680	66 658.8286	9.3889
32	29.05	25.645	17.735	81.1223	55 315.7006	7.6183
33	32.04	21.49	13.345	65.1732	38 469.4419	5.0716
34	33.86	20.495	15.45	64.9218	44 888.1539	6.0287
35	30.745	22.955	11.675	65.4973	34 496.6616	4.4886
36	37.81	23.41	10.18	54.8690	37 724.5661	4.9617

Table 3 continued

37	31.39	26.34	12.73	69.6006	44 066.0248	5.9052
38	34.015	21.57	13.96	63.6495	42 881.9399	5.7277
39	36.475	22.33	15.225	63.2588	51 917.0144	7.0959
40	35.75	27.81	12.44	64.4850	51 780.4476	7.0750
41	31.695	27.285	11.135	66.9190	40 315.6179	5.3451
42	27.09	24.065	19.87	86.4207	54 232.6871	7.4514
43	31.89	31.215	18.935	83.1792	78 913.5449	11.3430
44	37.855	29.685	15.51	68.2685	72 969.3515	10.3902
45	34.09	24.645	15.095	68.1922	53 095.4524	7.2766
46	32.8	29.485	13.21	71.0477	53 486.7461	7.3367
47	26.59	25.485	9.995	70.9469	28 356.6000	3.6037
48	39.065	23.875	18.99	66.5092	74 152.2884	10.5791
49	33.285	26.715	12.91	67.5629	48 061.6157	6.5082
50	29.965	20.79	15.065	70.1791	39 292.1951	5.1933
51	34.385	23.885	13.09	63.9880	45 009.3049	6.0470
52	29.72	21.68	14.55	70.7323	39 249.9819	5.1870
53	39.92	23.185	12.2	56.0245	47 274.3807	6.3889
54	38.42	30.175	13.05	64.1684	63 340.7988	8.8669
55	32.86	23.09	11.36	62.2077	36 085.9554	4.7209
56	32.36	22.295	14.495	67.3695	43 782.70542	5.8626
57	34.09	26.04	18.67	74.5482	69 387.4111	9.8205
58	32.83	25.435	15.095	70.6655	52 772.0696	7.2269

Table 3 continued

59	32.735	18.785	18.18	68.0943	46 804.3058	6.3178
60	29.605	27.085	*16.515*	79.6621	55 442.2527	7.6378
61	32.29	24.4	20.585	78.1385	67 901.1496	9.5851
62	33.3	22.425	10.245	58.9962	32 030.0069	4.1306
63	35.215	28.705	13.58	67.7779	57 471.6146	7.9517
64	30.805	23.525	14.685	71.1833	44 554.6648	5.9786
65	24.45	17.825	12.71	72.1591	23 191.1528	2.8768
66	30.61	19.845	13.31	65.3730	33 850.1715	4.3945
67	22.535	16.315	14.29	76.9239	21 996.0782	2.7112
68	30.125	21.13	12.125	65.4053	32 312.9557	4.1715
69	32.67	21.44	19.27	72.6484	56 509.8318	7.8029
70	29.64	20.61	9.23	59.8766	23 606.2106	2.9345
71	27.365	15.5	13.765	65.6120	24 443.9705	3.0514
72	29.97	18.885	13.255	65.1252	31 408.8365	4.0410
73	25.285	19.07	12.885	72.4945	26 011.5636	3.2715
74	28.33	20.445	12.03	67.2211	29 172.1005	3.7110
75	26.025	19.35	10.76	67.2965	22 685.7094	2.8066
76	27.45	19.56	11.18	66.0160	25 131.6723	3.1478
77	28.735	18.895	16.015	71.3462	36 404.3621	4.7676
78	25.605	19.175	11.985	70.3048	24 635.7947	3.0783

Table 4: Fossils seed dimension data from coal peels in Ohio. The length and width measured using a ruler.

Fossil Seeds	Length(mm)	Width(mm)
Pachytesta vera	39	29
Pachytesta stewartii	26	13
Pachytesta saharasperma	7	6
Pachytesta hoskinsii	9	6
Pachytesta illinoensis	6	3
Pachytesta gigantea	66	32
Pachytesta muncii	34	27
Conostoma oblongum	3	2
Stephanosperm elongtum	2	1
Hexapterospermum delevoryii	20	15

APPENDIX B

Modern Gymnosperm Seed Data

Table 5 Modern gymnosperm seed data from several herbaria. A few species had sphericity indices less than 50% but their volume was estimated using ellipsoid formula.

Gymnosperm Species	Average Weight(g)	Average Length(mm)	Average Width(mm)	Average Breadth(mm)	Sphericity Index	Volume (mm^3)
Junperus osteosperma	0.0698	6.153	4.711	4.141	80.0427	502.544
Thuja occidentalis	0.0012	4.463	1.778	0.449	34.2077	14.9167
Juniperus communis	0.0080	4.353	2.389	1.944	62.5187	84.6388
Juniperus ashei	0.0382	5.404	3.898	2.793	71.8738	246.318
Juniperus pinchotii	0.0314	5.427	3.976	3.291	76.1964	297.305
juniperis virginiana	0.0072	3.574	2.221	1.807	67.9225	60.0523
Picea mariana	0.0012	2.581	1.697	0.875	60.6052	16.0452
Pinus elliottii	0.0286	6.06	3.729	2.839	65.9683	268.596
Juniperus scopulorum	0.0173	4.053	3.173	2.515	78.5203	135.411
Pinus banksiana	0.0036	3.831	1.945	1.093	52.4809	34.0973

Table 5 continued

Pinus palustris	0.0842	15.828	6.591	3.694	45.8849	1613.42
Pinus flexilis	0.0854	7.891	5.374	3.405	66.3739	604.526
Pseudotsuga menziesii	0.0113	5.887	3.198	1.713	54.0066	135.020
Picea pungens	0.0045	3.902	1.917	1.375	55.6903	43.0606
Chamaecyparis thyoides	0.0008	2.367	1.936	0.945	68.8284	18.1303
Taxodium distichum	0.0773	14.627	7.71	4.268	53.4682	2015.13
Abies homolepis	0.0210	6.436	3.047	1.91	51.9238	156.816
Abies nordmanniana	0.0834	11.552	5.124	3.04	48.7870	753.370
Abies bornmuelleriana	0.0729	11.583	5.109	3.114	49.0436	771.514
Cedrus deodara	0.0970	14.896	6.061	3.163	44.1248	1195.59
larix laricina	0.0018	3.318	1.624	1.104	54.5770	24.9058
Taxodium ascendens	0.0880	13.576	6.429	4.332	53.1582	1582.97
Sequois sp	0.0047	4.585	3.214	1.011	53.6186	62.3742
Picea glauca	0.0026	3.088	1.796	1.394	63.9895	32.3679

Table 5 continued

Kousa x balsam fir *	0.0093	5.116	2.797	1.487	54.1092	89.0845
Pinus rigida	0.0073	4.671	2.438	1.504	55.1327	71.7068
Abies fraseri	0.0071	5.116	2.818	1.856	58.3996	112.026
Pinus clausa	0.0110	4.854	2.771	1.934	60.9761	108.908
Picea engelmannii	0.0035	3.159	1.71	1.182	58.6908	26.7320
Pinus resinosa	0.0080	4.213	2.558	1.712	62.6592	77.2439
Picea meyeri	0.0059	4.104	2.134	1.434	56.5905	52.5798
Cupressus arizonica	0.0093	4.697	3.52	1.621	63.6432	112.206
Pinus ponderosa	0.0334	5.798	3.916	2.803	68.7652	266.448
Juniperus occidentalis	0.0354	5.919	4.013	2.941	69.4823	292.470
Abies grandis	0.0266	9.004	3.829	2.234	47.1850	322.457
Picea abies	0.0096	4.625	2.238	1.702	56.2061	73.7564
Pinus echinata	0.0084	4.491	2.704	1.897	63.2910	96.4463
Abies balsamea	0.0084	5.048	2.691	1.712	56.4856	97.3655
Pinus taeda	0.0246	5.401	4.49	3.264	79.3810	331.390
Abies balsamea	0.0084	5.048	2.691	1.712	56.4856	97.3655
Pinus taeda	0.0246	5.401	4.49	3.264	79.3810	331.390
Zamia loddgiessii	0.0151	14.262	8.546	7.885	69.0357	4023.59
Zamia paucijuga	0.0054	14.487	8.827	8.063	69.5739	4316.75

Table 5 continued

Dioon spinulosum	13.63	49.555	30.003	27.549	69.3151	171485
Encephalartos ferox	4.262	28.253	15.794	13.628	64.4175	25459.9
Ginkgo biloba	1.594	20.461	17.027	13.434	81.5217	19594.7
Pordocarpus falcastus	0.725	12.999	11.646	10.862	90.5768	6884.38
Pordocarpus macrophyllus	0.259	9.322	7.005	6.844	81.8496	1871.09
Taxodium macrosatum	0.007	6.332	2.974	2.757	58.8383	217.364
Sequoia sempervirens	0.004	4.602	3.651	0.981	55.2489	69.0074
Tsuga canadensis	0.0010	3.456	1.611	1.055	52.1768	24.5918
Pinus sylvestris	0.0085	4.704	2.782	1.504	57.3401	82.4026
Pinus virginiana	0.0089	4.557	2.704	1.789	61.4665	92.2921
Pinus strobus	0.0249	6.419	3.837	1.587	52.8057	163.645
Abies eraseri	0.0072	5.045	2.553	1.427	52.2592	76.9492
Picea ruben	0.0039	3.474	1.867	1.495	61.3357	40.5960
Larix kaempferi	0.0048	4.584	2.53	1.65	58.2923	80.1157
Chamaecyparls	0.0028	4.939	2.337	1.947	57.0775	94.0875
Araucaria araucana	0.0029	3.026	2.628	1.85	80.9029	61.5934

Table 5 continued

Pinus albicaulis	0.0342	8.918	5.376	4.812	68.6482	965.875
Pinus cembroides	0.1639	11.269	7.31	6.311	71.2049	2176.55
Ephedra antisyphilitica	0.0075	6.308	3.566	1.78	54.1675	167.634
Ephedra nevadensis	0.0082	6.814	3.17	2.496	55.3676	225.722
Ephedra trifurca	0.0018	9.025	2.495	2.215	40.7334	208.814
Epedra viridis	0.0053	6.621	2.98	1.571	47.3898	129.773

APPENDIX C

Average Seed Weight and Seed Density in Modern Seed Bank

Table 6: Average seed weight and seed density of modern seed banks from published data. The seed weight for species occurring in modern soil seed banks was downloaded from Kew Seed Information Database (SID) and seed density from the literature. The mean were calculated (back transformation) from log transformed seed mass data except mean of the Paleozoic seed bank of Virginia, Warrington Park estate, Tall grass prairie, Illinois. The modern seed density is given in number of seeds/m^2 but seed density estimate for Paleozoic seed bank (Virginia) is in seeds/m^3.

Seed bank	Average seed weight(g)	Seed density/m^2	Habitat	Reference
Patuxent river, USA	0.7771	12 860	Wetland	Balwin et al. 2001
Eagle lake, USA	0.6608	29 753	Wetland	Van der valk and Davis 1978
Hamilton Marsh	0.4316	2430	Wetland	parker and leck 1985
Delaware River	0.6645	26 956	Wetland	leck and simpson 1987
southeastern riverine swamp, USA	0.9983	4159	wetland	Schneider and shantz 1986
Mount St. Helens, Washington, USA	0.1011	25 511	Wetland	Mandy et al. 1998
Spring-Fed Marsh in Southeastern Arizona	0.6156	467	Wetland	Titus and titus 2008

Table 6 continued

Delta Marsh, Manitoba, Canada.	0.5074	2726	Wetland	Pederson 1979
San Francisco bay ,USA	0.4286	700	Wetland	Hopkins and Parker 1984
Cache river Illinois , USA	0.0458	4197	Wetland	Middleton 2003
North Central Iowa Marshes	0.3808	7368.7	Wetland	Galatowitch et al. 1996
Pampean prairie seed bank	0.488 271	28 523	Grassland	Silvia et al. 1994
Tallgrass prairie, illinois	0.002 354	2019	Grassland	Johnson and Anderson 1996
Tallgrass prairie, Missouri	0.189 177	6470	Grassland	Rabinowitz 1981
Yarner wood, Sourth west England	0.29 939	21 950	Woodland	Warr et al. 1994
longleat woods, South-West England	0.280 461	50 060	Woodland	Warr et al. 1994
Tavistock wood land Estate, South West England	0.62 339	20 993	Woodland	Warr et al. 1994
Werrington Park estate	0.001 173	45 896	Woodland	Warr et al. 1994
Buckley woods, south-West England	0.903 778	5105	Woodland	Warr et al. 1994

Table 6 continued

Sonian forest Brussel	0.4662	9192	Forest	Godefroid et al. 2006
Mt hilaire Southwestern Quebec, Canada	0.6837	1670.59	Forest	leckie et al. 2000
Koeni, Central Estonia	0.4119	900	Forest	Robel et al. 2007
Le Nouvion forest, France	0.3402	8296	Forest	Decocq et al. 2003
Meerdaal forest complex, Belgium	0.3584	12426	Forest	Bossuyt et al. 2002
KWS(forest under pine plantation) New Zealand	1.3311	8841	Forest	Moles and Drake 1999
Kauri forest, New Zealand	0.8988	1131	Forest	Enright and Cameron 1988
Pinos ponderosa forest, Northern Arizona	0.7203	1031	Forest	Korb et al. 2005
Coastal plain forest, Southern New Jersey	0.9656	262	Forest	Matlack and Good 1990
Afromotane forest(church forest)	0.3532	3492	Forest	Wassie and Tekelay 2006
Paleozoic seed bank Virginia	5.0057	19 200	Paleozoic swamp forest	Present study

VITA

PETRA SEKA

Education:	M. S. Biology, East Tennessee State University, USA 2014
	B. S. Geology, University of Buea, Cameroon, 2010
Experience:	Teaching Assistant, Department of Biological Science, East Tennessee State University 2012-2013
Technical Skills:	SPSS, dissection of mammals, microscopy, collection and measuring of seed volume and weight